Studies on three congeneric species of fleas (Siphonaptera) from the nests of *Delichon urbica urbica* in England.

by

Frank Clark

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ProQuest LLC
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106-1346

DEDICATIONS

To Linda, Sarah, Loopy and Kassy for the many flea bites endured.

'While ruder heads stand amazed at those prodigous pieces of nature, as Elephant, Dromidaries, and Camels; These I confesse, are the colossus and Majestick pieces of her hand; but in these narrow Engines there is more curious mathematicks, and the civility of these little citizens, more nearly sets forth the wisdome of their makers'.

Sir Thomas Browne, *Religio Medici* 1642.

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Contents

Chapter one

Introduction

Fleas (order Siphonaptera : class Hexapoda) are holometabolous ectoparasites of homiothermic vertebrates. Based on the similarity in the thorax and jumping mechanisms they are thought to have evolved from a mecopteroid ancester (Tillyard 1935, Hinton 1958, Schlein 1979). The adult fleas feed on the host's blood; they do not usually stay on the host for any great length of time (corporeal population) but, with the eggs,larvae and pupae, form a suprapopulation in the host's home (see Cole & Koepke 1947, Esch, Gibbons & Bourque 1975). Exceptions to this are found in the family Vermipsyllidae where eggs and larvae are free living, and in *Uropsylla tasmanica* Rothschild (Pygiopsyllidae) whose adults and ova occur solely on the fur of the host (*Dasyurus* spp. and *Sarcophilus* sp.) while the larvae live subdermaly (Dunnet 1970).

The earliest known fossil fleas are of two specimens from the Lower Cretaceous (Riek 1970). One specimen, in many respects, resembled modern sticktight fleas (*Echidnophaga* spp.), the other was an impression of an askewed squashed insect. Smit (1972) throws doubt on this being siphonapteran. A specimen found in Baltic amber, (since lost, see Holland 1964), which dated from the lower Eocene (Dampf 1910), was classified as *Paleopsylla klebsiana* Dampf a member of the family

Hystricopsyllidae. This family is associated with rodents and insectivorous mammals. *P.klebsiana* is very similar to modern forms of the genus *Paleopsylla* which today mainly parasitize shrews. Since the genus is very specialized Peus (1968) concluded that the order as we know it today was fully developed by the Eocene.

The family Ceratophyllidae are more recent and are thought to have arisen from the family Leptopsyllidae, which today are found only on the rodent genus *Mus* (Traub, Rothschild & Haddow 1986). The earliest known fossil murids are from the Miocene (24 million years BP) with their precursors in the Eocene (*circa* 40-70 million years BP, Macdonald 1984). The Leptopsyllidae presumably evolved after this time. Both the Leptopsyllidae and the Ceratophyllidae are considered monophyletic, the link between them being based on morphology and zoogeography (Traub *et al. op.cit.*).

In general ceratophyllids are not found on primitive or more ancient groups of mammals eg. marsupials and tend to parasitize more recently evolved sciurids and certain cricetids or have secondarily adapted to birds.

This family of fleas is overwhelmingly boreal in distribution; the evidence strongly suggests North America as the aboriginal homeland as it is for their major rodent host families Sciuridae and Cricetidae. These two rodent families appear in the fossil record in the Oligocene (25-40 million years BP). It is inferred

therefore that ceretophyllids evolved after this time.

The history of this family's secondary adaptation to birds is unclear but today 47 of the 155 families of birds (30%) are major hosts to the family. The evidence for a recent evolution is the remarkable similarity between different genera in the modification of the 8th sternite of the male into claspers. Such morphological homogeneity, which is unparalleled in the order, suggests recent evolution without the need or time frame for the development of the gross anatomical differences which are typical between genera in other families of Siphonaptera.

Of the 47 families of birds parasitized by ceratophyllids, the Hirundinidae is the most heavily infested group with 30 species of ceratophyllids being recorded in association with different species (Traub *et al. op. cit*). The evolution of the Hirundinidae is unclear as few fossils have been found. In this study only one reference was found to fossil hirundines, this was for the North American species *Petrochelidon pyrrhonota* (now *Hirundo pyrrhonota*), found in deposits of the late Pleistocene (Wetmore 1956). It was during the Pleistocene that much of the Northern hemisphere was periodically covered with ice with warmer inter-glacials intervening. Today *H.pyrrhonota* is still a widely distributed breeding species in North America, nesting in caves and on cliffs and is parasitized by 5 species of ceratophyllids. Excavations at an archaeological site at Lovelock Cave, Nevada (Nelson 1972) produced

specimens of the fleas *Ceratophyllus petrochelidoni* Wagner and *Ceratophyllus celsus* Jordan, two of the species associated with *H.pyrrhonota* today. The level at which these specimens were found was radio-carbon dated at 4570±110 years BP. No remains of *H.pyrrhonota* were found at this site but today *C.petrochelidoni* is specific to *H.pyrrhonota* while *C.celsus* has also been recorded from the sand martin, *Riparia riparia*. Since both *C.petrochelidoni* and *C.celsus* are now associated with *H.pyrrhonota* and its' remains have been found in deposits pre-dating this time, it seems probable that the two sub-fossil *Ceratophyllus* were from the nests of *H.pyrrhonota*.

It seems likely therefore that hirundines have colonised the northern hemisphere since at least the late Pleistocene (*circa* 11000 years BP) and that the species of ceratophyllids associated with them today have evolved sometime after that. Further, at least in the case of *H.pyrrhonota*, it may be presumed that the association has existed for at least 4500 years.

The family Hirundinidae comprises 17 genera and some 77 species which are found throughout the world, although most are tropical. Members of this family are insectivorous, feeding almost entirely on the wing. Their nesting habits fall into two categories:

(1) building nests of mud under overhangs on either cliffs or buildings:

(2) nesting in holes either excavated in soft river banks, quarries, etc., or in existing holes in trees.

The 11 species breeding in the northern hemisphere are migratory with those breeding in North America overwintering in South America whilst those in western Europe overwinter in Africa. Species breeding in eastern Europe and N.Asia overwinter in India and S.E. Asia. Between them they are parasitized by 30 species of ceratophyllid and 9 of these are associated with the house martin *Delichon urbica* and its sub-species.

Three sub-species of *Delichon urbica* L are recognised. These have different breeding ranges throughout Europe and Asia and are *Delichon urbica urbica* , *D.u.meridionalis,* and *D.u.lagopoda* (Howard & Moore 1980). All of these sub-species build enclosed dome shaped nests of mud under overhangs on cliffs or buildings. The sub-species found in Britain is *D.urbica urbica* which breeds throughout Europe and West and Central Asia. It is a common summer visitor breeding throughout the British Isles and often nesting in colonies under the eaves or overhangs of buildings (Bouldin 1968) or under overhangs on cliffs (Clark & McNeil 1981). Reproduction, energetics, growth rate and feeding of this sub-species has been studied extensively in Britain by Bryant (1973, 1975a, 1975b, 1978a, 1978b, 1979) and Hails & Bryant (1979). The process of nest building in *D.u.urbica* was first described by White (1788) whilst the characteristics of nest sites and nest architecture have been examined more recently by McNeil & Clark (1977,1983).

Ectoparasitic arthropods often form complex

suprapopulations on the bodies or in the homes of their hosts. The sub-species of *D.urbica* have 12 species of flea associated with them (*Ceratophyllus hirundinis* (Curtis), *C.farreni farreni* Rothschild, *C.rusticus* Wagner, *C.delichoni* Nordberg, *C.maculatus* Wagner, *C.caliotes* Jordan, *C.orites* Jordan, *Orneacus watersoni* (Jordan) and *O.oreinus* (Jordan) (Ceratophyllidae) and *Frontopsylla laeta* (Jordan & Rothschild, *F.cornuta* Ioff and *F.setegera* Smit (Leptopsyllidae). Also commonly associated with the body or nest of *D.u.urbica* are at least one species of hippoboscid (*Crataerina hirundinis* L), one hemipteran (*Oeciacus hirundinis* Jen.), one mite (*Dermanyssus hirundinis* Hermann), and two mallophagans (*Philopterus excisus* Nitzsch and *Degeeriella gracilis* (Nitzsch)).

All of the flea species, of course do not share precisely the same geographical ranges and this would exclude the possibility of inter-specific competition between them. This is true of a number of flea species for example the small mammal fleas *Anomiopsyllus walkeri* Barnes and *A.nudatus* Baker which occur on the same species of host (*Neotoma fuscipes* Baird) but are separated by altitude (Barnes 1965, Barnes, Tipton & Wilde 1977). However, a number of species of martin fleas have been recorded together. For example Dunnet & Allan (1955) found *C.farreni, C.rusticus, F.laeta* and *O.watersoni* in the same nest on sea cliffs in Scotland. Dunnet (1962) in Norway records *C.hirundinis* and *C.caliotes* and Mehl (1967) also in Norway found

C.farreni, *C.rusticus* and *C.delichoni*; Jordan (1937) records *C.hirundinis*, *C.orietes*, *C.caliotes* and *O.oreinus* in Kashmir; Darskaya (1964) in the USSR records *C.hirundinis*, *C.farreni* and *C.delichoni*.

In Britain 7 species of flea have been recorded from the nests and bodies of *D.u.urbica*. Three of these, *C.hirundinis*, *C.farreni farreni* and *C.rusticus* are recorded from nests located on buildings and cliffs. Two other species, *O.watersoni and F.laeta*, are recorded from nests on sea cliffs only (George 1974). The two remaining species *Ceratophyllus gallinae* (Schrank) and *C.fringillae* (Walker) have a wide range of passerine hosts and are usually introduced into house martin nests by intruding house sparrows (*Passer domesticus* L.) (George *op. cit.*).

Previous studies on these species have tended to examine temporal effects, distribution and abundance (Dunnet *et al. op. cit.*, Rothschild 1947, 1963, Claassons 1965) and a few have examined the abiotic and biotic factors which may affect distribution and abundance. Jurik (1974) in Czechoslovakia examined the effects of some physical parameters such as nest lining material and elevation (*sic*) of the nest, but could not demonstrate any differences in abundance of *C.hirundinis* and *C.rusticus* with these variables. Darskaya (*op. cit.*) in the USSR also commented on nest lining material but made no critical appraisal.

A relationship that allows the three congeneric and monoxenous species of flea *C.hirundinis*,

C.farreni and *C.rusticus* to share the same host and inhabit the same nest suggests that either intra-specific control is sufficiently strong to minimize inter-specific competition, or coexistence is permitted either by sufficient niche segregation or through extrinsic controls such as predation. Day & Benton (1980) consider that fleas have three major mechanisms to avoid competition; 1) spatial separation while feeding; 2) selection of different micro-habitats; 3) temporal separation.

In this study I have attempted a detailed examination of some of the abiotic and biotic factors which may influence distribution and abundance of each flea species, as well as those factors which may control inter- and intra-specific competition. To achieve this the following aspects were examined.

1) The effect of different geographical localities within England, and the characteristics of each nest site and nest which may influence the flea community. This was studied by the collection of nests and examination of each abiotic factor in relation to the numbers of each species in each nest.

2) All stages of the life cycle of these fleas species are found in the nest, therefore, nest environment both in the presence and absence of the martins was studied.

3) Flea emigration was investigated because the numbers of each flea species in a nest will depend on the numbers arriving at a newly built nest.

4) Survival of the fleas in the absence of the host was investigated in both field and laboratory studies.

Therefore, in nests used by the martins for a second season a flea community will be established; the size and composition of this community will to some extent be controlled by the ability of the fleas to survive the winter and then to breed in the next season.

5) The metabolic activity of the fleas will vary throughout the year with different environmental conditions. This will control survival of the fleas throughout the year, therefore metabolic activity was investigated using a respirometric method.

6) Feeding of adult fleas was investigated using a number of unusual hosts since survival of each species will depend on reproduction for which an adequate food supply is required.

7) To investigate inter- and intra-specific competition, the increase of each species populations throughout the martins' breeding season was investigated in the field and by experimentation in the laboratory.

Chapter Two

Nest construction, study areas, nesting sites, nest environment, collection of nests, collection and identification of fleas.

2.1 Nest constuction by *Delichon u. urbica*.

Nests are built under eaves or other suitable overhangs on buildings or, more traditionally, on cliffs that erode to form angular niches. The outer wall of a nest is constructed of mud by both sexes. The source of the mud is usually close by the nest site although martins have been known to travel as far as 1.25km (*pers. obs.*), when other potential sources were much closer. The mud is collected and transported in the martin's mouth, (Plate 1): the volume of each mouthful is approximately $0.21cm^3$.

Initially the mud is stuck to the wall of the building or rock face just below the eaves or a rock overhang and forms a platform on which the wall of the nest is built upwards and outwards until it reaches the overhang, the whole structure thus forming a cup with the entrance hole at the top (Plates 2,3 & 4). The mud varies in thickness from 3cm at the base to 1cm at the entrance hole. The volume of mud used and time taken to construct the nest varies depending on the angle that

the wall of the nest has to fill and the distance travelled to collect the mud. Recorded volumes varied from $180cm^3$ to $600cm^3$. The constuction of a nest containing $500cm^3$ of mud would take 12 to 14 days and require around 2,500 mouthfuls of mud (McNeil & Clark 1977).

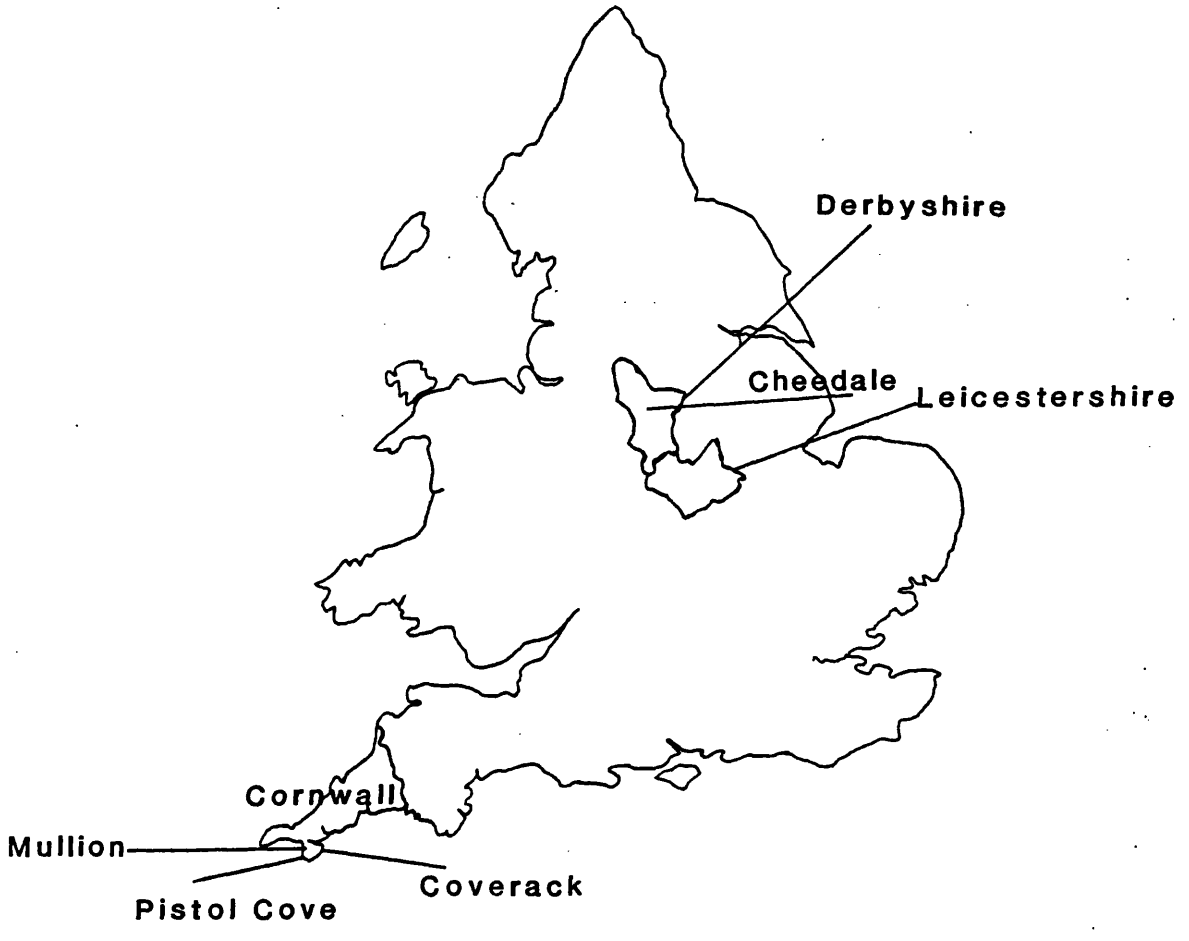
On completion the bottom of the nest is lined with suitable materials found in the vicinity of the nest site; materials favoured most are grass and feathers. By the end of the breeding season the nest lining is compressed into the bottom of the nest to form a pad not usually deeper than 2cm.

2.2 General description of study areas.

2.2.1 Leicestershire (including Rutland).

Leicestershire is situated in the east midlands of England (Fig.1). Leicester City itself covers an area of 73.37 Km^2 and although numerous streams, parks and gardens offer a source of nesting material few buildings within the city boundary provide suitable overhangs to allow nest building. Elsewhere in the county many towns and villages have since the nineteen sixties been greatly expanded by housing developments. The nature of the designs for buildings within these developments has led to an enormous increase in potential nesting sites for martins. Many

Fig. 1 Study areas



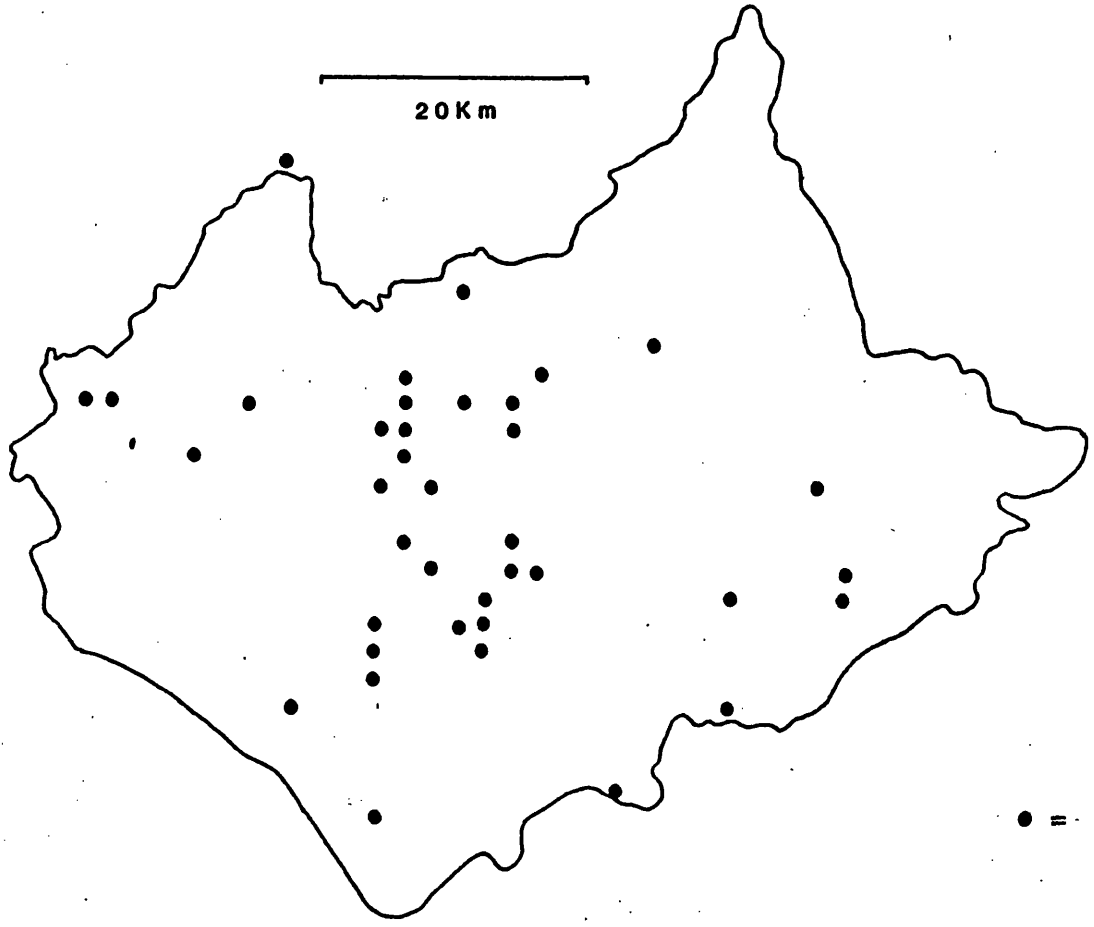


Fig.2

Leicestershire showing localities where nests were collected.

Plate 1.

Martin's collecting mud from the bank of a stream.

Plate 2.

Martin's nest after building for four days.

Plate 3.

Martin's nest after building for eight days

Plate 4.

Complete martin's nest.

of these towns and villages have streams or rivers flowing through or close by them and the margins of these water courses provide a source of mud for nest constuction. Gardens provide a ready source of nest lining material particularly grass from lawn cuttings. In the more rural areas grass cuttings are replaced or added to with cut stems of cereals. Feathers from a variety of bird species are also commonly used with these other materials. Nests were collected from a large number of different localities in this county (Fig. 2).

2.2.2 Cornwall.

Cornwall is the most south western county of England occupying the tip of the south west peninsula. All the nest sites were on the Lizard close by the sea. Of the three sites where nests were collected Mullion (grid ref SW6819) was approximately 1km from the sea; the three nests collected at this site were on a building. The mud used in the construction of these nests and the nest lining material was collected from the margins of a stream approximately 200m from the house (*pers.com* house ownner). The nests at Coverack (grid ref SW785182) were on two buildings within 30m of the sea. The mud used in the constuction of these nests probably came from the intertidal zone of the beach as many sea urchin spines were found in the mud walls. Nests at Pistol Cove (grid ref SW 7011) were located on

a sea cliff which is formed from Serpentine. This cliff has supported a colony (1-9 nests) of martins since at least 1975 (Clark & McNeil 1980). No source of mud for building the nests was obvious and mud examined from the nests gave no clue as to the source. Possibly, as at Coverack the beach exposed at low tide was the nearest source. The nest lining materials at all three sites consisted of grass, feathers, and at Coverack and Pistol Cove a few pieces of twig and seaweed. The lining materials occured either singly or in combination. All these materials were common in the accumulated debris at the high tide mark.

2.2.3 Derbyshire.

The county of Derbyshire lies in the north west midlands of England. Nests were collected from only one site in this county, limestone cliffs in Cheedale, (grid ref. SK 1272). Limestone cliffs erode to form angular niches and overhangs which provide excellent nesting sites for martins (Plate 5).The cliffs rise to approximately 30m above the River Derwent. A colony of martins has nested at Cheedale since at least 1939 (Jourdain & Witherby 1939); between 1979 and 1980 approximately 62 nests were recorded but only 15 of these were accessible for collection. Large numbers of shells of the gastropod *Hydrobia jenkinsi* were found in the mud walls of these nests indicating that the banks of the Derwent were the source of the

mud as this mollusc was abundant along its margins. The linings found in these nests comprised feathers,grass and occasionally sheeps' wool, all of which could be gathered close to the nest site. The area around Cheedale is mostly grassland used for grazing sheep.

2.3 Environment in the nests.

Fleas develop in the nest therefore the micro-climate within the nest is relevant. The temperatures within three nests attached to a house eaves in Thurnby, Leicestershire (grid ref. SK 646039) were measured continuously from May 1976 to April 1977 using a Grant multichannel recorder. Thermistor probes (50mm long by 3.2mm in diameter) were inserted into each of the nests through a small hole (3.3mm in diameter) drilled in the base of the nest. The probes were allowed to rest between the mud wall and nest lining, while a fourth probe was attached to the house wall alongside the nests to measure ambient temperature (Plate 6). Wires connecting the probes to the recorder were passed through the top of a window into a room where they were connected to the recorder. Temperatures were recorded automatically every hour and collected for analysis at the end of each month when the recorder battery was renewed.

Relative humidity was measured in two ways.

Plate 5.

Martin's nest on a natural site.

Plate 6.

Grant recorder probes in nest (1), and measuring ambient temperature (2).

First, air samples were withdrawn from the nests with a 20cc hypodermic syringe the end of which was inserted through a small hole (3.3mm diameter) that had been drilled into the wall of the nest near its base and on the opposite side to the one bearing the thermistor. The syringe contained a strip of cobalt thiocynate paper 1.5cm wide by 3cm long. The assemblies were kept in sealed polythene bags containing silica gel until used, to ensure that they were completely dry. Immediately the air sample had been withdrawn from the nest a plastic cap was placed onto the open end of the syringe and the whole syringe was then resealed in a polythene bag. The hole in the side of the nest was plugged with a piece of plasticene. Two assemblies were kept unused on each occassion as controls.

Seventy two hours after the air sample was taken the cobalt thiocynate paper was removed from the syringe, placed between two slides with a small amount of liquid paraffin and examined in a comparator (*C.f* Solomon 1957). The method was tested in the laboratory before using in the field by withdrawing samples of air from just above saturated solutions of $MgCl_2 6H_2O$ (40%-45% RH) and NaCl (90%-95% RH) (*Cf* Winston & Bates 1960). The laboratory tests gave satisfactory results (within 5%). Samples were taken once a week from the three nests that contained the temperature probes as well as the ambient humidity but only during the time that the martins were in residence. During the winter months humidity was taken only once a month when the

temperature recorder battery was changed.

The second method used a Vaisala relative humidity meter and probe. The probe, which contained the humicap sensor, measured 3.5cm long by 1cm in diameter and, because of its size, was inserted into the nest via its entrance hole. Temperature was taken using a direct read Grant recorder with a thermistor probe which was inserted into the entrance hole of the nest at the same time as the humidity probe. Measurements were made once a week between May and October 1980 in one nest on the same eaves as the 1976/1977 data. This method was used to extend the previous data.

In two of the three nests studied in 1976/77 the lining material comprised grass and feathers; in the third nest which was taken over by sparrows in the autumn of 1976 a large amount of extra lining material had been introduced in the form of straw, feathers and newspaper. Nests taken over in this way usually have their entrance holes enlarged and the extra lining material can be seen protruding from the hole. The bottom of the nest, however, was lined with grass which was assumed to be the original lining used by the martins. The lining material in the 1980 nests comprised grass, feathers and some hair.

In figures 3-6 the temperature data for the three 1976 nests has been extracted for five day periods for each of the following nest conditions: martins incubating eggs (Fig 3.), martins with young

(Fig 4.), unoccupied nest in winter (Fig 5.) and a sparrow occupied martin nest in December (Fig 6). The temperature data were recorded to provide background imformation on how temperature varies under different conditions. Although the fleas in the nest will be affected by temperature fluctuations it was not possible to monitor the flea populations simultaneously, therefore the data collected here do not relate to the flea populations in the nest. As this was the case the temperature data was condensed by taking a mean for each hour for all three nests and then condensing further by taking the mean for each hour over a five day period for each of the above nest conditions to give the average fluctuations over a twenty four hour period. The graphs therefore show a mean and range of temperatures recorded.

Comparing the graphs Figures 3 and 4 there appears to be greater fluctuations in temperature when young are present ($22^{o}C$-$32^{o}C$). In the nests with young there is a peak around 2100 hr which is probably due to the adult birds coming in to roost, initially giving off heat as a result of flight and then, their output dropping as they settle and become inactive. Similar results have been reported previously for the house martin (Summers 1975), and for other passerine species eg. eastern house wren *Troglodytes aedon aedon* (Baldwin & Kendeigh 1932).The rise at 0600 hr is probably due to the adults becoming active prior to leaving for foraging.

Fig 3.
Mean and range of nest temperatures condensed from three nests for a five day period to give a mean reading and range for each hour over a twentyfour hour period. The means and ranges for the ambient temperature have been similarly treated.
Martins incubating eggs.

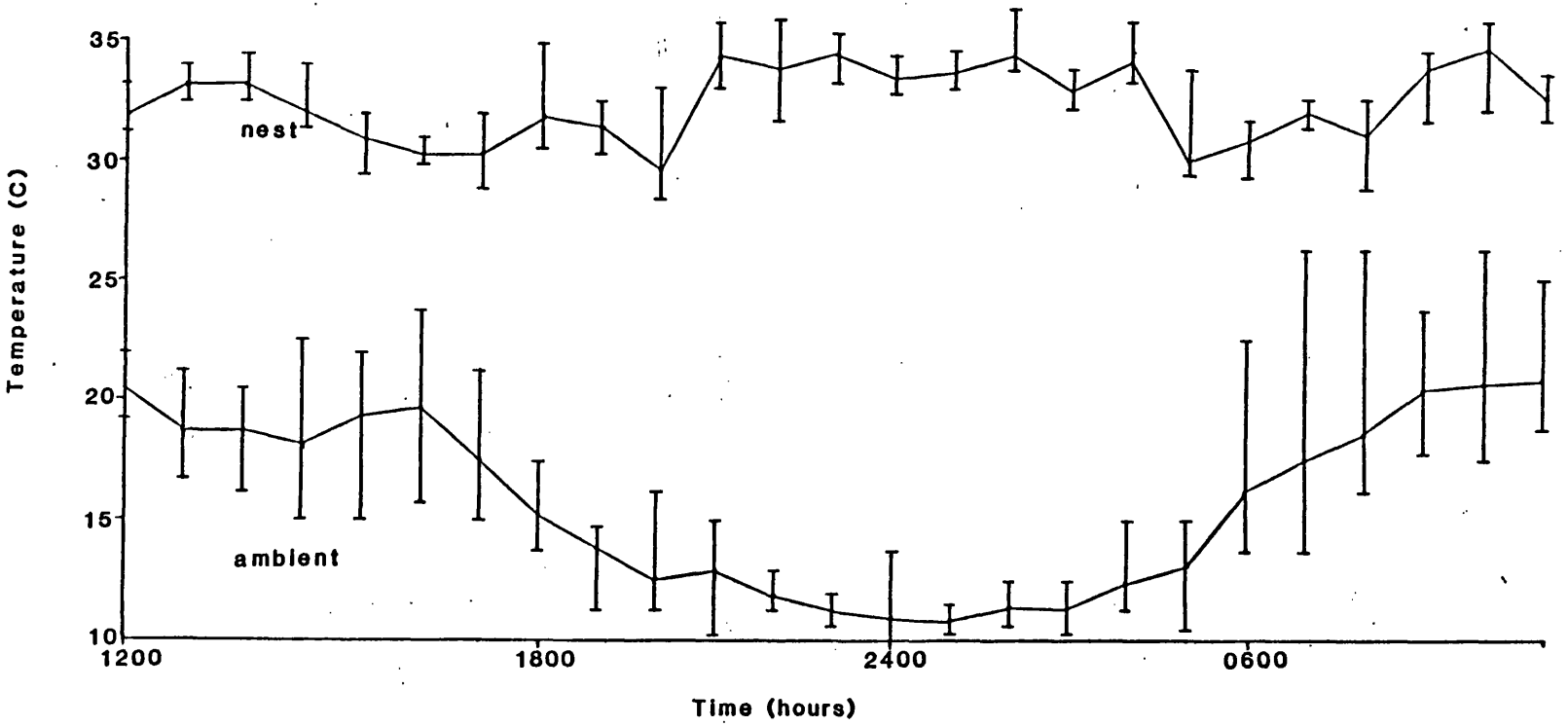


Fig 4.
Mean and range of nest temperatures condensed from three nests for a five day period to give a mean reading and range for each hour over twentyfour hour period. The means and ranges for the ambient temperature have been similarly treated.
Martins brooding young.

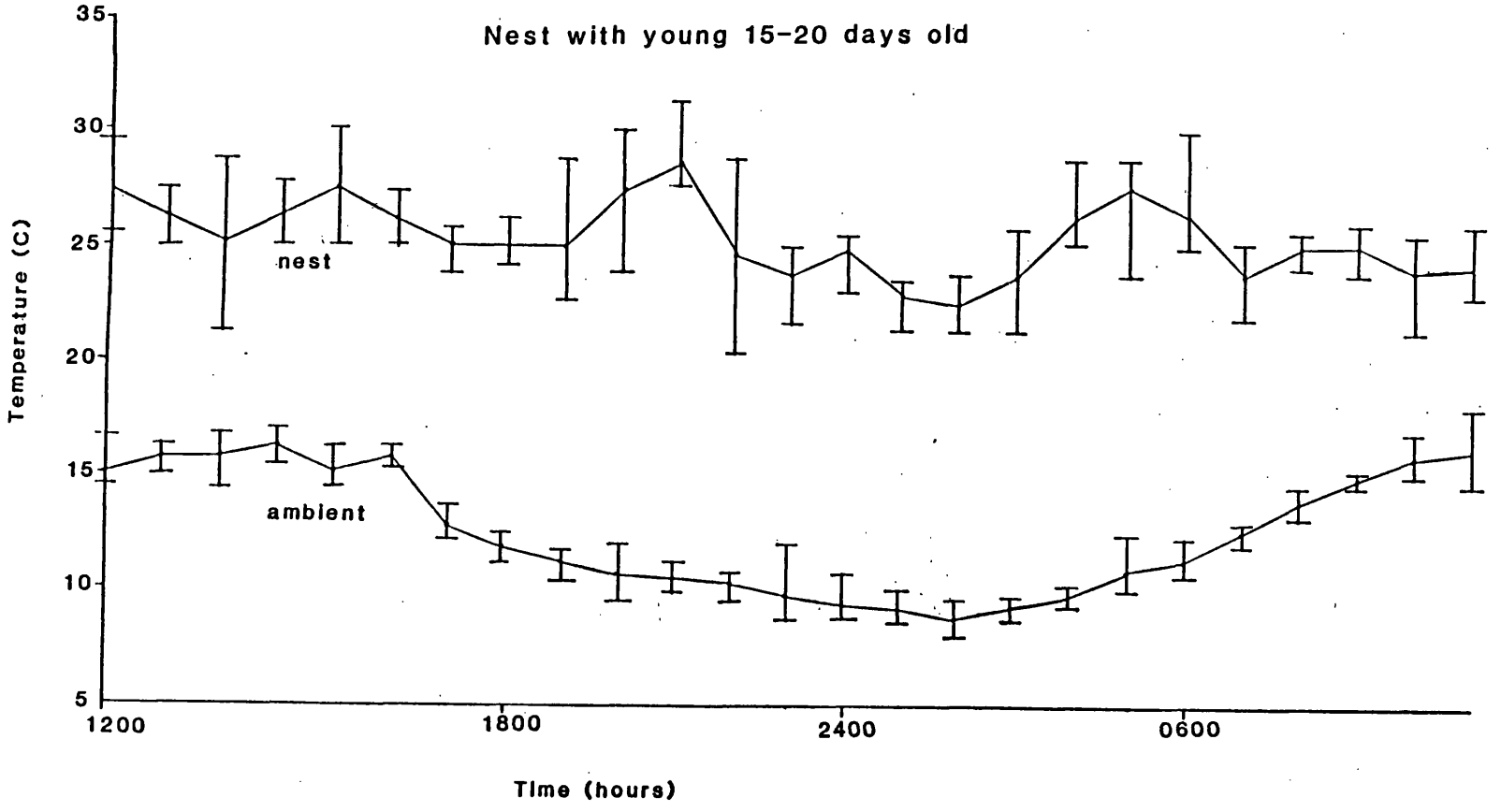


Fig 5.
Means and ranges of nest temperatures condensed from a five day period to give a mean reading and range for each hour over twentyfour hours for two unoccupied martin nests in winter. The means and ranges for the ambient temperature have been similarly treated. Only the ranges for ambient temperature are shown.

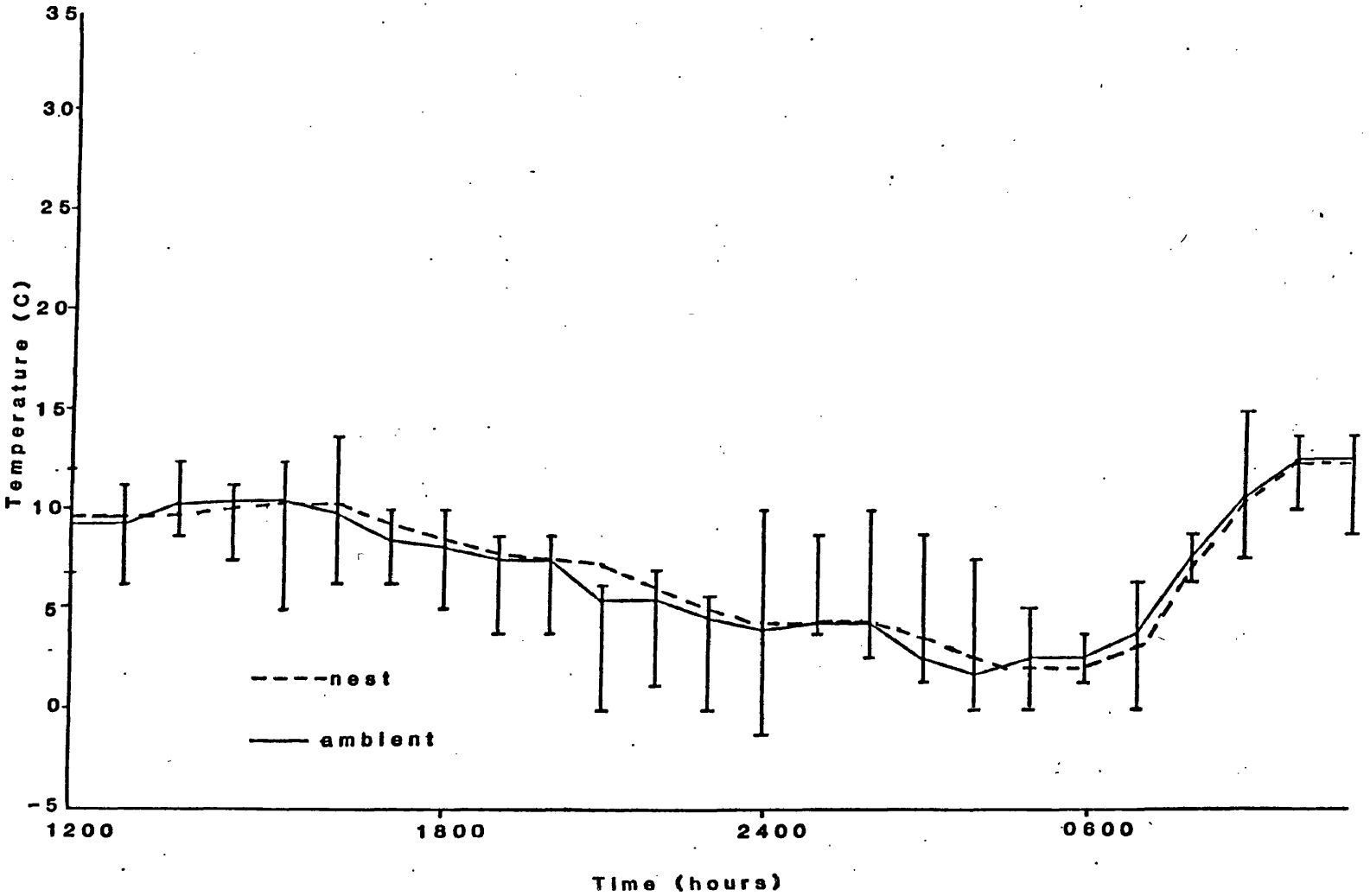
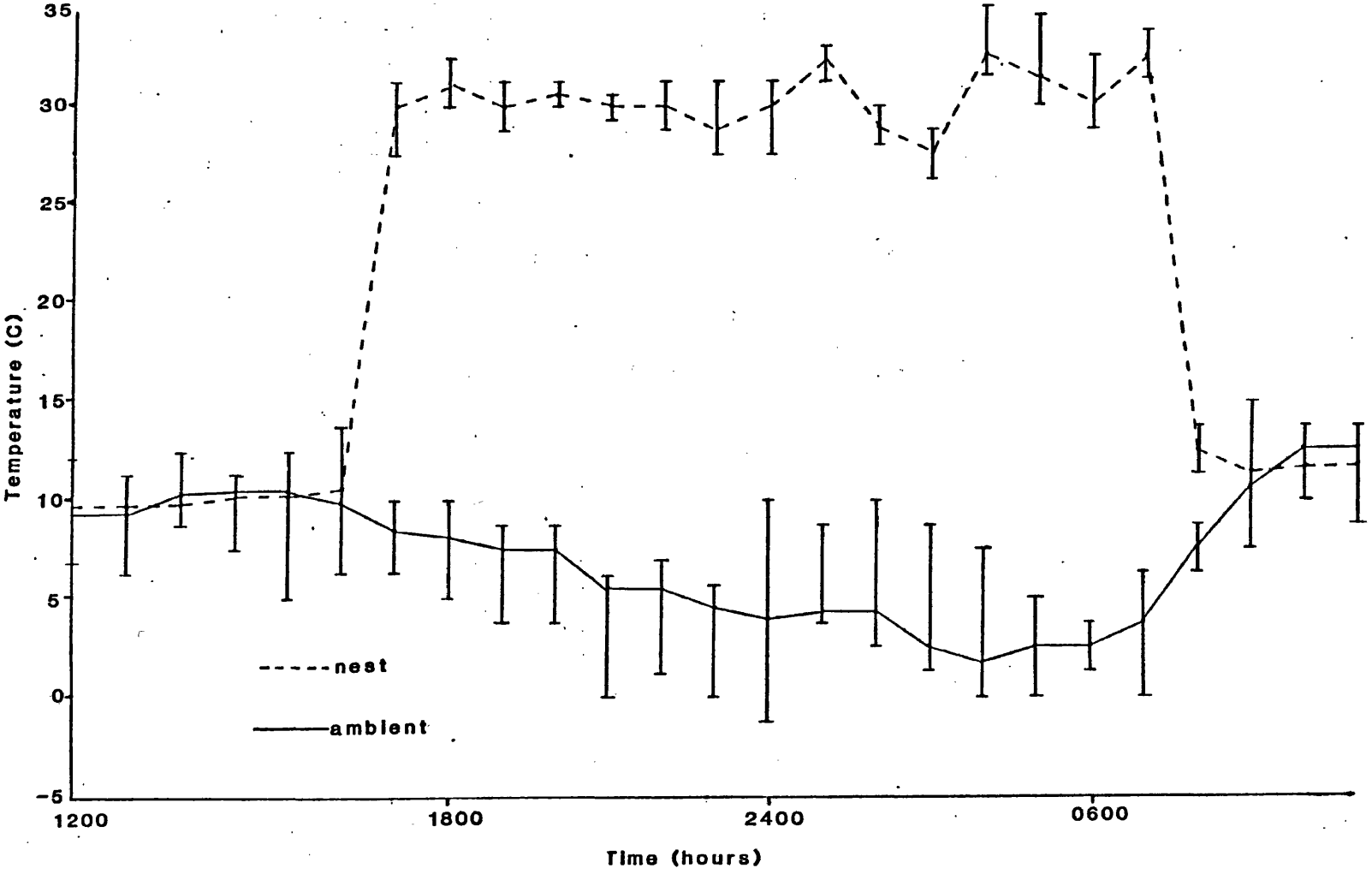


Fig 6.
Mean and ranges of nest temperatures condensed from a five day period to give a mean and range for each hour over a twentyfour hour period for a sparrow occupied martin nest in December. The means and ranges for the ambient temperature have been similarly treated. Where the lines are contiguous only the ranges for the ambient temperature are shown.



Fluctuations in temperature are less marked in incubating martins, ($29^{o}C$-$34^{o}C$) the variations in the data due to the adult martins changing incubation duties. During both incubation of the eggs and rearing of young the temperature inside the nest was usually between $5^{o}C$ and $10^{o}C$ above ambient. Throughout the time that the nests were empty during the autumn and winter months the temperature within the nests stayed within two degrees of ambient. In the nest that was occupied by sparrows in the winter the nest temperature during the day dropped almost to ambient and only rose a little before dusk; presumably the sparrows were only using the nest at night (1600-0800 hr) for roosting (max. temp. $34^{o}C$)(Fig 6.).

Humidity within these nests appears to be independent of the ambient humidity; Tables 2:1 & 2:2 show the mean and range for each month and for each nest condition. When the martins are present the relative humidity would be influenced by their presence eg. respiration, as well as the moisture contained in the nest lining materials and mud walls. The humidity in unoccupied nests would perhaps, be expected to be influenced more by the ambient humidity which does not always seem to be the case. Presumably with the ambient relative humidity undergoing continuous rapid changes the humidity within the nest is influenced more by the moisture in its mud walls. In both the unoccupied nests and sparrow occupied nest in winter the relative humidity was on average higher than martin occupied

Table 2:1.

Relative humidity readings taken from house martin nests at Thurnby Leicestershire. The values for the nest humidities are the mean of four readings taken from each of three nests in each month in the 1976 data. The values for the ambient relative humidity are the mean of four readings, one each week of the month.

Year	Month	Nest condition	Mean RH	Range	Ambient RH	Range
1976	May	Incubating eggs	62.5	55-75	57.50	50-70
--	June	Brooding young	53.75	50-60	48.50	45-55
--	July	-- --	61.25	55-75	66.25	60-75
--	August	Fully fledged young & adults	65.00	60-70	56.25	45-65
--	September	-- --	56.25	50-65	48.75	35-55
--	October	Unoccupied	66.25	60-75	63.75	55-70

Table 2:1 cont.

Relative humidity readings for the above nests in autumn 1976 and winter 1977, one of which was sparrow occupied and the other two unoccupied. The values given are a single reading taken once a month for the sparrow occupied nest and for the unoccupied nests a mean of two readings.

Year	Month	Nest condition	Mean RH	Range	Ambient RH
1976	November	Sparrow occupied	65.00		75.00
--	December	-- --	75.00		60.00
1977	January	-- --	70.00		85.00
--	February	-- --	80.00		55.00
--	March	-- --	60.00		60.00
--	April	-- --	80.00		85.00
1976	November	Unoccupied nest	65.00	55-70	75.00
--	December	-- --	70.00	65-75	65.00
1977	January	-- --	80.00	75-85	85.00
--	February	-- --	82.50	80-85	55.00
--	March	-- --	62.50	60-65	60.00
--	April	-- --	72.50	70-75	85.00

Table 2:2.

Relative humidity and temperature readings for a single nest at Thurnby Leicestershire in 1980. The humidity was measured with a Vaisala humidity probe and meter and the temperature with a Grant direct read temperature recorder. The values given are the mean of four readings in each month.

Year	Month	Nest condition	Mean Nest RH	Range	Ambient RH	Range	Mean Temperature	Range	Ambient Temperature	Range
1980	May	Incubating eggs	56.1	50-60	67.5	60-70	26.00	25-28	13.25	12-15
--	June	Brooding young	63.5	60-72	59.75	52-66	29.25	27-33	14.50	12-17
--	July	-- --	68.5	64-77	79.50	76-88	26.00	22-30	16.25	15-18
--	August	Fully fledged young & adults	62.50	57-68	77.5	65-90	30.75	27-31	15.00	12-18
--	September	-- --	57.75	54-67	55.75	45-62	26.25	24-28	16.50	14-18
--	October	Adults	62.25	59-66	74.25	68-85	26.75	26-28	10.25	9-11

nests in the summer (summer mean 60.8%, winter mean 72.0%). The mean ambient RH for these periods were (summer mean 55.5%, winter 70.0%). The range of humidities recorded between the nests and the ambient would indicate that overall the relative humidities in the nest are close to ambient.

The humidities obtained for nests occupied by young martins are similar to those recorded by Summers (*op. cit.*). He also used cobalt thiocynate paper in one artificial nest to measure relative humidity but because artificial nests were used they could be removed from the eaves without too much disturbance to the birds; he was therefore able to insert strips of cobalt thiocyanate paper into different parts of the nest lining. He left these strips in place for three days. On examination at the end of this period he recorded a low relative humidity at the bottom of the nest (45%), 50% in the middle and 65% at the surface of the lining material. The humidities in natural martins nests with young recorded in this study are close to the surface readings found by Summers (*op.cit.*).

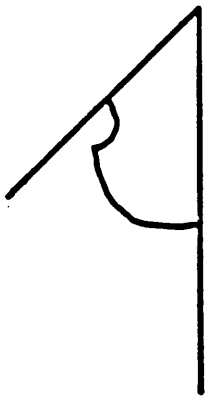
The methods used in this study (withdrawing an air sample and inserting a probe) would only record overall conditions and not pick up any differences as found by Summers in different parts of the nest. No evidence in the results obtained suggests any difference between the two methods used for measuring humidity.

2.4 Collection and recording nests.

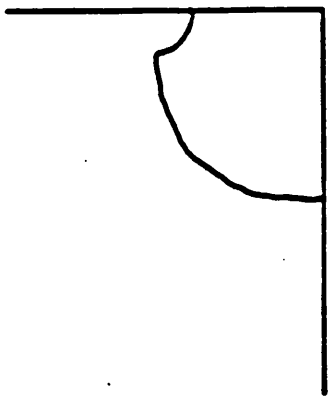
One hundred and fourty six nests were collected from the eaves of buildings at thirty six locations in Leicestershire and one location (Sutton Bonnington SK 504255) just over the county boundary in Nottinghamshire during the autumn of 1974. This last collection was incorporated in the Leicestershire collection. Each nest was removed by hand, and immediately sealed in a polythene bag and labled. This collection formed the basis for the analysis of populations. Other collections were made subsequent to this both from house eaves and two cliff sites. In Leicestershire (1977 25 nests, 1978 5 nests, 1984 18 nests & 1985 24 nests all from house eaves), Cornwall 1978(12 nests from house eaves),1979 (12 nests from house eaves and 4 from a sea cliff) & 1980 (11 nests from house eaves and 1 nest from a sea cliff), Derbyshire (1979 11 nests and 1980 4 nests from a cliff site) For each nest the following information was recorded:

1. Eave shape. This may influence the surface area of mud used in the nest constuction. Four shapes were recognized, grading from 1,which would present the smallest area, to 4, which presents the greatest (see Fig.7),

Fig.7



1



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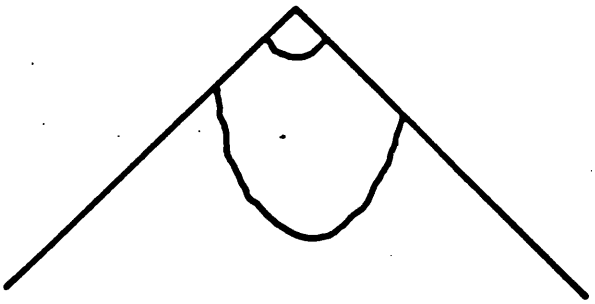
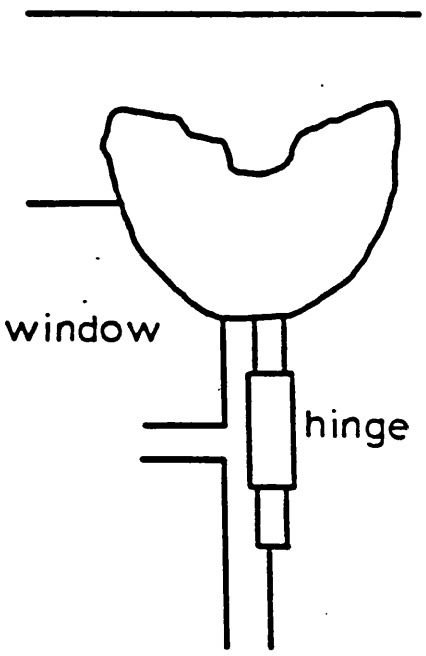


2



4

Types 1 and 3 in cross section.

Types 2 and 4 in front elevation

2. The texture of the wall material to which the nest was attached. Different wall materials have different insulation abilities which may influence nest micro-climate. The materials involved were plain brick, painted-dash, stone and plaster.

3. Orientation of the nest site, some directions may be more exposed than others and may in turn influence micro-climate. Direction was taken with a magnetic compass which was subsequently reduced to eight points of the compass in order to facilitate analysis.

4. Age of the nest. This was recorded because the population density of fleas may vary with age. It was however, difficult to obtain accurate ages for individual nests, unless they were built in that year. As a result, nests were classified where possible as 'new' (built in the year of collection) and 'old' (older than one year).

5. The weight of nest lining material. This was measured because the quantity of lining material may affect micro-climate and area of living space. The lining consisted mostly of grass, feathers and straw. These individual components were noted but were not weighed separately. As other materials, such as hair, occurred in so few nests it was decided that their presence would be unlikely to influence the flea populations.

6. Colonial and non-colonial nests. Nests at some localities occurred together on the same eaves or building. As some interchange of fleas may result under

these conditions this was recorded for consideration in the analysis.

The nests were classified into four groups:

1. Nests used by martins for breeding in the current season. These were invariably associated with a quantity of droppings immediately below the site, except when the householder had removed the mess.

2. Nests used by sparrows for breeding in the current season. In most cases the sparrows had introduced large quantities of extra lining material and built a normal sparrow nest inside the martin nest. Often the mud entrance hole had been enlarged and considerable structural damage was evident.

3. Nests built in the current season but not used (deserted). Often these showed structural damage and usually lacked any lining material. Where lining material was present it was always in an advanced state of decomposition. No droppings were evident either inside or outside such nests.

4. Nests built as temporary quarters. Such nests are built very quickly late in the breeding season, have very thin walls and no lining material (McNeil and Clark, 1977).

2.5 Sorting for fleas.

The nests were kept in a constant temperature room at 15^{o}c and sorted as soon after collection as

possible. Nesting material was sorted for fleas by removing a little at a time from the bag and gently rolling it between the fingers and thumb over a white tray. Fleas dropping from this material into the tray were collected by pooter. A small vacuum pump was employed with the pooter and a face mask worn to avoid inhalation of dust, feather scales and other irritant nest debris.

The fleas, both adults and larvae and other arthopods from the Leicestershire 1974 collection were preserved in 70% ethanol. Prior to identication the fleas were desclerotized in 10% KOH and cleared in clove oil (*cf.* Smit 1957). The nomenclature follows that of Kloet & Hincks (1975). Other arthropods collected were preserved in 70% ethanol and identified to the lowest taxinomic level that could be achieved in a reasonable time; these are listed in the appendix 1.

Fleas from nests collected in 1977/78/79/80/84/85 were anaesthetised with CO_2, placed alive onto a microscope slide under a cover slip and identified with the aid of a compound microscope. These fleas were used for a variety of experiments discussed in later chapters. In a few nests collected in winter and spring a pad of cotton wool soaked with ethyl acetate was introduced into the nest before collection in order to kill the fleas *in situ* to see if they overwintered in the cocoon or emerged before the martins returned.

Normally when nests are examined after collection the fleas are actively moving around and so it is difficult to know whether they had already emerged from the cocoon before collection. In addition to the nests collected for the field survey a number of nests were obtained for which the mud wall of the nest was missing and no imformation on the nests history was available and could not therefore be included in the rest of the field data. They were however a useful source of material for the various experiments discussed in later chapters. These nests came from Carlisle (6), Lincolnshire (10) and Rutland (6).

2.6. Identification of the fleas.

Five species of flea belonging to the family *Ceratophyllidae* were found ;*Ceratophyllus hirundinis* Curtis, *Ceratophyllus farreni farreni* Rothschild, *Ceratophyllus rusticus* Wagner, *Ceratophyllus gallinae* Schrank and *Ceratophyllus fringillae* Walker. The following characters were used in their identification using Smit's (1957) key and drawings.

Males.

Tergum nine in male fleas is modified into claspers which form a sexual clasping organ. This together with the shape of the apical membranous lobe of sternite eight are characteristic for each species (Figs.8-10).

Females.

The shape and angles produced by tergum eight and sternite seven are charcteristic for each species as is the shape and proportions of the bulga and hilla of the spermatheca (Figs 11-13).

2.7 Geographical distribution.

The first three species are monoxenous parasites of the house martin and are commonly found in both nests on buildings and on natural sites throughout the British Isles (George 1974),although *C.rusticus* tends to be more abundant in nests on sea cliffs (Dunnet *et al op.cit.*). The remaining two species have a wide range of passerine hosts and are usually introduced into martins nests by intruding house sparrows. Both these species are common over much of the British Isles although both species have yet to be recorded from Cornwall, indicating a possible scarcity in the west of the country.

Outside of Britain the following distributions have been recorded for these species by Traub *et al (op. cit.)*.

C.hirundinis.

Palearctic: Eurasia: Europe and European USSR, north almost to Artic Circle in Sweden, south to central Italy and Greece. Alps, but not Spain nor

France, nor steppe regions of European USSR, although occurring south in north Caucasus area, Caucasus and Crimean mountains, also Turkey, Lebanon and Algeria. Mountains of central Asia: Afganistan, Kashmir, Dzungarain Alatau, western Mongolia. Found from sea level to 1900 m in the west, and from around 1000-3200m in the east. Found in the nest of the house martin both in natural sites and (more commonly) on buildings.

C.farreni farreni.

Palearctic: British Isles eastwards to European USSR, northwards to include southern Sweden and Finland, southwards to Netherlands and northern plains of Germany and Poland; also found in Czechoslovakia, southern Greece, northern Algeria; European USSR excluding steppes, including Crimean mountains, Caucasus mountains and north Caucasus plateau. In east: mountains of central Asia: the Altay of Tuva ASSR and Mongolia, Barguzin Range east of Lake Baykal. Sub-species *C.farreni choi* in Japan in nests of the Japanese house martin *Delichon dasypus.*
Found from sea level to 1800m (northern Europe: sea level to 300m). In nests of the house martin in both natural and man made sites.

C.rusticus.

Palearctic: British Isles, east to Poland,

eastern Czechoslovakia and Baltic coast of USSR, north to southern Norway, central Sweden and southern Finland (Aland); to south. Alps of France, Switzerland, Austria, and northwestern Jugoslavia; Greek and Caucasus mountains. Found from sea level to 1700m in nests of the house martin on natural sites and on buildings.

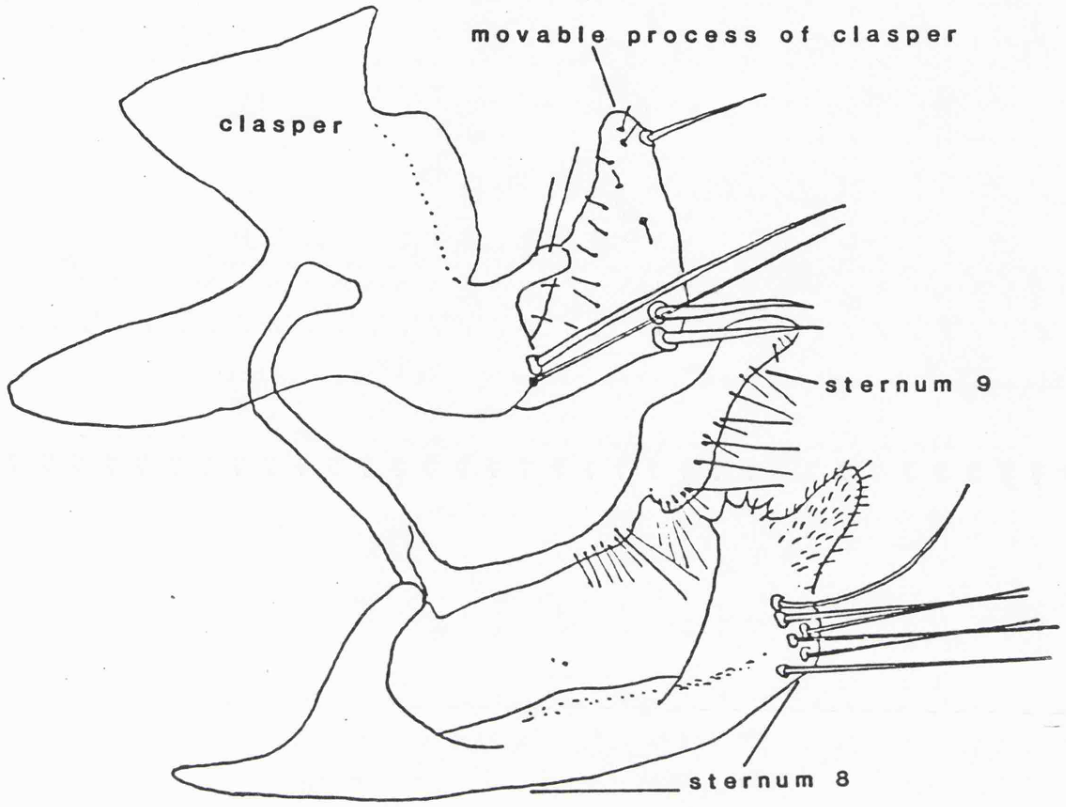
C.fringillae.

Palearctic: Europe, east to Ciscaucasia around the Aral Sea, Ust-Yurt, Tadzhikistan and Afganistan.

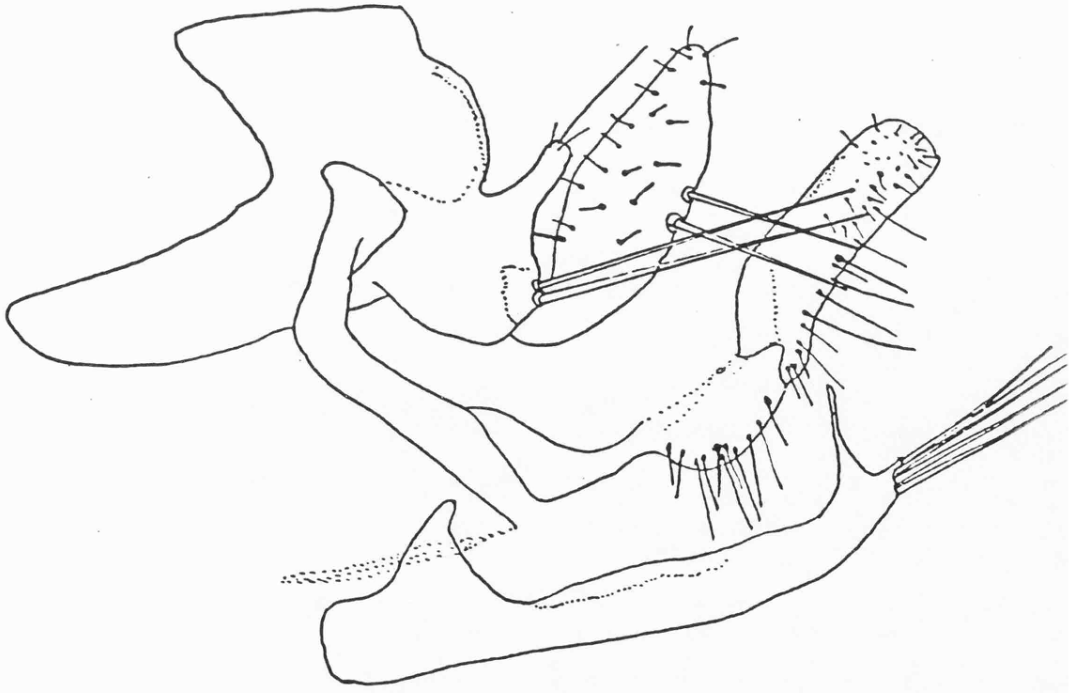
C.gallinae.

Holarctic & Australasian: Europe, east to the Caucasus and western Siberia; also introduced into eastern USA.,Alaska,Australia and New Zealand.

Fig.8



C.hirundinis male
Clasper, sternum 9 and sternum 8



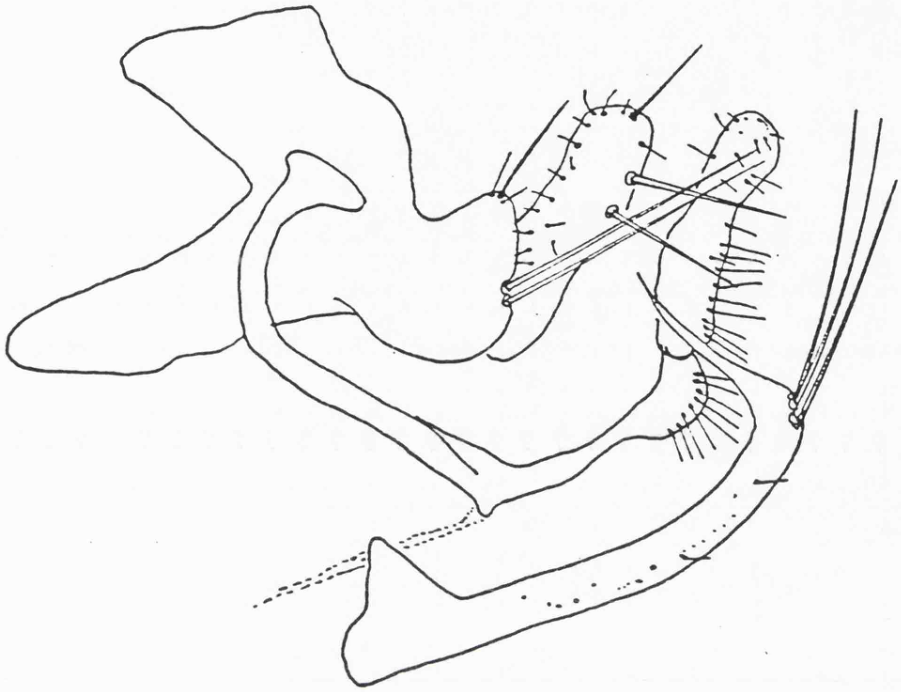
C.farreni male
Clasper, sternum 9 and sternum 8

Fig.9

C.rusticus male

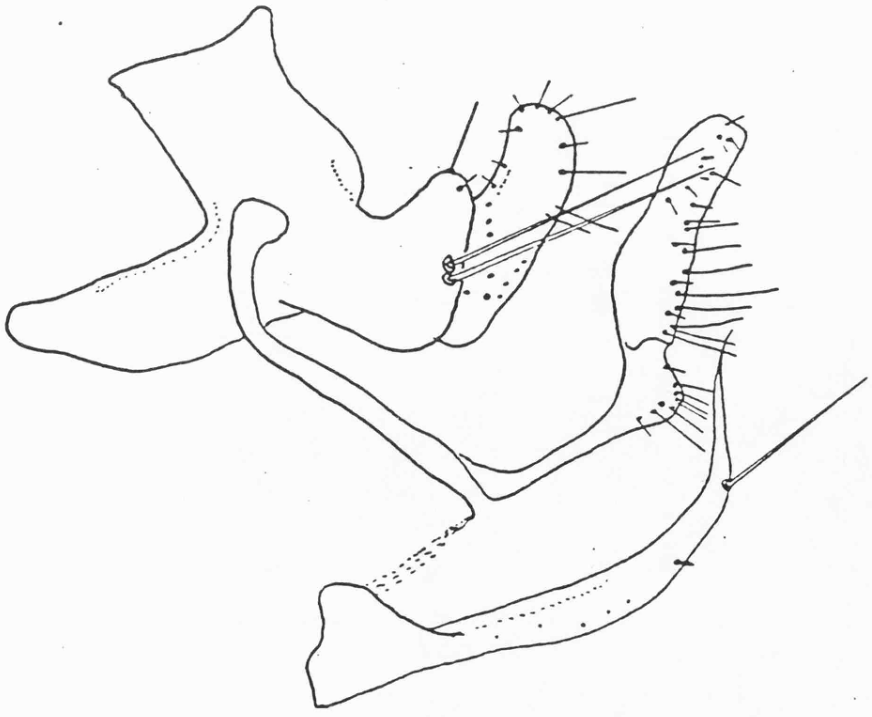
Clasper, sternum 9 and sternum 8

Fig.10



C.gallinae male

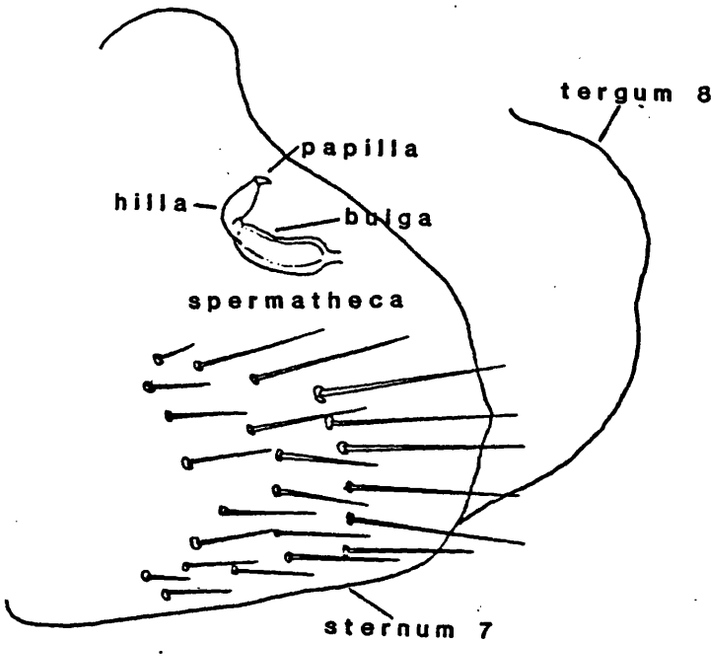
Clasper, sternum 9 and sternum 8



C.fringillae male

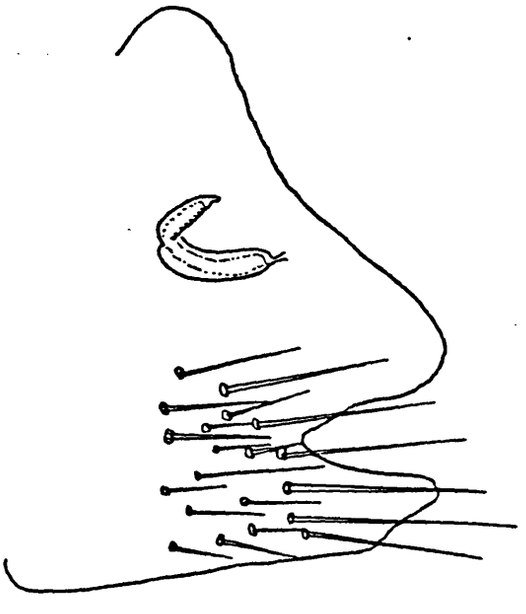
Clasper, sternum 9 and sternum 8

Fig.11



C.hirundinis female

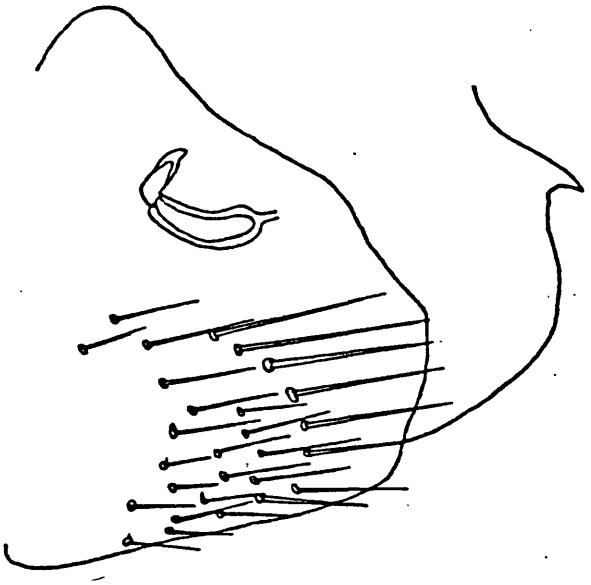
Sternum 7 and spermatheca,
and part of tergum 8



C.farreni female

Sternum 7 and spermatheca

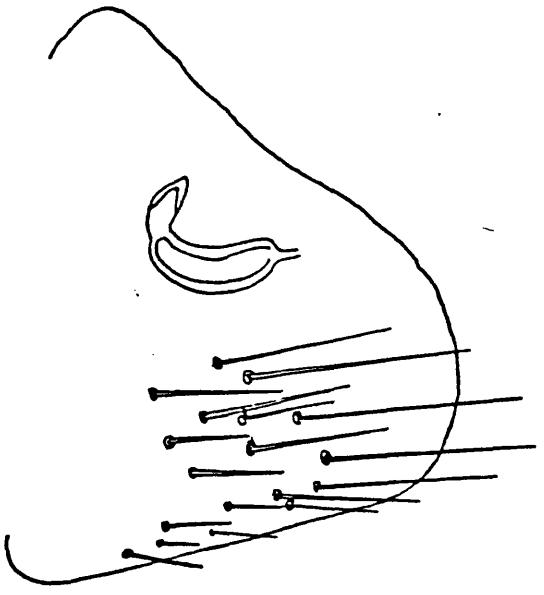
Fig.12



C.rusticus female

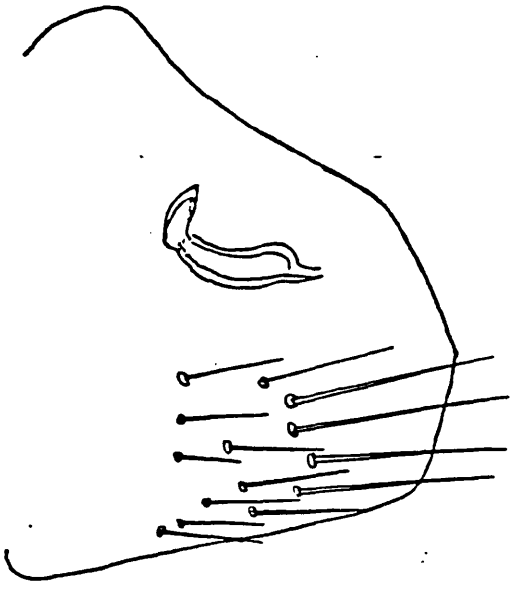
Sternum 7 and speratheca,
and part of tergum 8

Fig. 13



C.gallinae female

Sternum 7 and spermatheca



C.fringillae female

Sternum 7 and spermatheca

Chapter 3

Analysis of the initial survey.

3.1 Introduction

As already discussed in chapter 1, previously published works have examined the differences in abundances and indicate possible preferences of *C.hirundinis*, *C.farreni* and *C.rusticus* but have not attempted to examine in detail the factors which may determine their distribution and population densities. This initial survey was intended to examine some abiotic factors which may influence the fleas' distributions and population densities.

123 of the 146 nests collected in the autumn of 1974 had been used by martins in the 1974 season, and consequently these only could be used to examine the abiotic factors which might affect the densities of fleas in recently vacated nests. Using the variables listed in chapter 2 (pages 21-24) the relationship between the numbers of each species and the measured variables was examined using a number of statistical methods which are indicated where appropriate.

3.1 Results

The numbers of each species of flea for each nest with all the abiotic variables recorded are presented in Table 3:1. The total fleas recovered from the 146 nests examined was 22,723 comprising five species. Table 3:2 shows the total numbers for each sex

Table 3:1.

Numbers of each species of martin flea with all variables recorded for Leicestershire 1974.

>1=older than one year.

*=age not known.

N=north, S=south, W=west, E=east, NE=northeast, NW=northwest, SE=southeast, SW=southwest.

B=brick, S=stone, PD=painted dash, PB=painted brick, P=plaster.

M=martin occupied, S=sparrow occupied, T=temporary, D= derelict, C.h= *C.hirundinis*, C.f= *C.farreni*, C.r= *C.rusticus*.

Location	Grid ref	Dir	Eaves shape	Wall material	Weight nest lining material	Nest age	Nest use	Colonial/ non colonial	C.h ♂	C.h ♀	C.f ♂	C.f ♀	C.r ♂	C.r ♀
Anstey	SK552086	W	1	B	18.0	*	M	NC	57	100	1	0	36	64
Belton	SK815014	SW	1	B	6.4	>1	M	NC	7	9	0	0	1	4
Belton	SK815014	SE	4	PB	16.0	1	M	NC	9	13	13	25	0	1
Belton	SK816014	N	1	S	7.2	*	M	C	1	2	0	0	0	0
Belton	SK816014	N	1	S	16.0	*	M	C	15	31	0	0	0	0
Belton	SK816014	N	1	S	00.0	*	M	C	0	1	0	0	0	0
Birstall	SK595085	E	1	PB	32.7	>1	S	NC	1	1	5	8	0	1
Coalville	SK451147	NW	2	B	20.1	1	M	NC	592	864	28	67	4	1
Cosby	SP547947	NE	4	PD	00.0	1	M	NC	23	42	0	1	2	3
Cosby	SP547947	NW	1	B	00.0	*	M	NC	30	24	12	27	0	0
Cropstone	SK551110	SE	3	PD	00.0	1	T	NC	0	0	0	0	0	0
Foxton	SP701898	N	1	B	30.0	*	M	NC	20	26	0	1	9	8
Glaston	SK894029	E	3	B	14.0	1	M	NC	142	201	3	5	0	0
Glenfield	SK555063	S	1	PD	23.0	*	S	NC	0	0	0	3	0	0
Houghton	SK678037	NE	4	PD	2.0	1	M	NC	2	1	4	4	0	0

Table 3:1 continued.

Houghton	SK678037	SE	1	S	12.0	1	M	C	0	1	0	0	0	0
Houghton	SK678037	NE	1	B	6.0	*	M	C	20	25	0	1	2	4
Ibstock	SK408102	NE	2	B	6.0	*	M	NC	8	15	2	5	0	0
Ibstock	SK408102	NE	1	B	13.0	>1	M	C	19	37	13	26	0	0
Ibstock	SK408102	NE	1	B	14.7	>1	M	C	0	0	0	0	0	0
Leicester	SK609030	N	2	B	28.8	*	S	NC	0	0	0	0	0	0
Leicester	SK609030	SW	1	B	70.0	>1	S	NC	0	1	0	0	0	0
Lutterwth	SP545844	SW	3	PD	14.2	1	M	NC	245	381	2	4	10	5
M.Harboro	SP737877	E	3	B	4.2	1	M	NC	517	588	25	29	5	2
Medbourne	SP800930	SE	1	S	11.0	>1	M	C	53	69	2	1	0	0
Medbourne	SP800930	SE	1	S	12.0	1	M	C	0	3	0	0	0	0
Medbourne	SP800930	SE	1	S	9.0	>1	M	C	10	12	0	0	0	0
Medbourne	SP800930	SE	1	S	00.0	>1	M	C	30	31	0	0	0	0
Medbourne	SP800930	SE	1	S	18.5	>1	M	C	51	31	12	47	1	5
Medbourne	SP800930	SE	1	S	10.3	>1	M	C	14	37	2	0	0	0
Medbourne	SP800930	SE	1	S	13.0	>1	M	C	51	54	0	2	1	1
M.Mowbray	SK748199	E	1	B	7.0	*	M	C	141	203	5	7	1	0
M.Mowbray	SK748199	NE	1	B	13.2	*	M	C	20	26	10	29	0	0
Narborough	SP540984	SW	1	B	4.0	1	M	C	1	1	0	0	0	0
Narborough	SP540984	SW	1	B	00.0	*	M	C	8	9	0	0	3	1
Narborough	SP540984	SW	1	B	18.0	>1	M	C	11	5	0	0	0	0
Narborough	SP540984	SW	1	B	25.0	>1	M	C	84	164	6	0	9	3
Narborough	SP540984	SW	1	B	6.9	>1	M	C	0	1	0	0	0	0
New.H'cort	SP638971	N	2	B	5.8	1	M	NC	8	22	13	13	10	8
New.H'cort	SP638971	S	2	B	31.0	1	M	NC	29	65	1	5	2	4

Table 3:1 continued.

New.H'cort	SP638971	SE	1	PD	8.0	>1	M	NC	0	3	0	0	0	0
Oadby	SP628999	S	2	PD	15.0	*	M	NC	5	4	0	0	3	8
Oadby	SP622998	E	2	P	0.6	1	M	NC	0	0	6	3	0	0
Oadby	SP622998	E	2	P	51.0	1	M	NC	34	74	0	0	13	13
Oadby	SP631993	SW	2	B	48.0	>1	M	C	187	243	10	16	37	25
Oadby	SP631993	NW	2	B	22.0	1	M	C	0	0	0	0	0	0
Oadby	SP631993	NW	2	B	3.0	1	M	C	50	45	2	1	19	21
Oadby	SP631993	NW	2	B	24.0	1	M	C	60	98	0	0	27	32
Oadby	SP631993	SE	2	B	15.0	1	M	NC	114	145	2	1	28	22
Oadby	SP631993	NW	2	PD	3.0	1	M	NC	53	65	3	0	12	3
Oadby	SP632993	E	2	B	4.0	1	M	NC	15	28	0	0	6	0
Oadby	SP632002	SW	2	PD	98.8	>1	M	NC	14	32	0	0	39	69
Oadby	SP629003	W	1	B	00.0	*	D	NC	4	4	0	0	1	0
Oadby	SP624998	S	1	B	00.0	1	M	NC	10	14	0	0	2	7
Oakham	SK861091	SE	1	B	10.0	1	M	NC	0	0	3	6	0	0
Packington	SK360146	E	2	B	00.0	1	T	NC	0	1	0	1	0	0
Packington	SK358147	S	1	B	2.6	1	M	NC	54	95	2	2	0	0
Packington	SK361145	E	2	B	22.4	1	M	NC	37	49	5	4	3	2
Packington	SK361145	SW	1	B	73.0	1	M	NC	46	75	5	6	5	10
Queniboro	SK649120	E	2	B	46.5	>1	S	NC	11	31	1	1	4	3
Queniboro	SK640122	N	2	B	12.4	1	M	NC	79	140	26	28	1	6
Queniboro	SK649120	NE	2	p	36.0	>1	S	NC	1	1	12	16	0	0
Quorn	SK564166	E	1	PD	30.0	>1	S	C	5	7	0	0	0	0
Quorn	SK564166	E	1	PD	11.0	*	M	C	85	110	11	18	0	0
Quorn	SK564166	E	1	PD	00.0	*	M	C	69	84	19	13	0	0
Quorn	SK564166	E	1	PD	8.0	*	M	C	45	46	0	0	1	2

Table 3:1 continued.

Quorn	SK564166	E	1	B	42.0	1	S	C	120	156	10	27	0	0
Quorn	SK564166	S	1	PD	13.0	>1	S	NC	0	0	1	1	1	0
Rearsby	SK651142	NE	1	B	4.0	1	M	C	69	123	6	8	7	10
Rearsby	SK651142	NE	1	B	11.0	>1	M	C	150	202	1	0	37	61
Rearsby	SK651142	NE	1	B	20.0	>1	M	C	6	8	0	0	1	3
Rothley	SK576124	SE	1	B	54.0	1	S	NC	142	214	11	4	0	0
Rothley	SK576124	S	3	PD	1.0	1	M	C	0	0	3	4	0	0
Rothley	SK576124	S	3	PD	10.0	1	M	C	77	143	0	6	0	0
Sharnford	SP483920	NE	2	B	83.6	>1	M	C	23	25	75	107	0	0
Sharnford	SP483920	NE	2	B	24.8	1	M	C	42	103	2	0	0	0
Sileby	SK610152	SE	1	S	00.0	1	M	C	8	7	1	2	0	0
Sileby	SK610152	SE	1	S	3.0	1	M	C	16	24	8	16	0	0
Sileby	SK610152	SE	1	S	4.0	1	M	C	2	0	0	0	0	0
Sileby	SK610152	SE	1	S	4.0	1	M	C	11	25	0	0	2	0
Sileby	SK610152	SE	1	S	30.0	1	M	C	11	20	0	0	0	0
Sileby	SK610152	SE	1	S	2.4	1	M	C	9	8	2	9	0	0
Sileby	SK610152	SE	1	S	12.8	1	M	C	10	17	1	1	0	0
Stoughton	SK641022	S	4	B	47.1	*	M	NC	0	0	2	12	0	0
Stoughton	SK641022	SE	3	PB	58.0	*	S	C	1	1	0	0	0	0
Stoughton	SK641022	SE	3	PB	13.0	*	M	C	0	0	0	0	0	0
Stoughton	SK642022	NW	3	PB	00.0	*	M	NC	1	2	1	1	0	0
Stoughton	SK641022	S	1	B	50.0	1	M	C	24	40	10	4	4	11
Stoughton	SK641022	S	1	B	20.8	>1	M	C	0	2	0	0	0	0
Stoughton	SK643022	SE	3	PB	8.8	1	M	NC	16	26	2	2	3	9
Stoughton	SK642022	SE	3	PD	25.0	>1	S	NC	0	0	0	0	0	0
Stoughton	SK642022	SE	3	PB	12.0	*	S	NC	0	0	0	0	0	0

Table 3:1 continued.

Stoughton	Sk643022	NW	3	PB	3.2	1	M	NC	2	15	0	0	0	5
Sutt Bonn	SK504254	E	3	B	9.8	1	M	NC	152	233	6	3	0	0
Sutt Bonn	SK505253	SW	1	B	4.0	1	M	C	16	15	6	4	0	1
Sutt Bonn	SK505253	SW	1	B	6.2	1	M	C	1	3	7	10	0	0
Sutt Bonn	SK504255	NW	1	B	17.0	1	M	C	167	220	1	0	0	0
Sutt Bonn	SK504255	SE	1	B	18.0	1	M	C	305	344	2	2	4	2
Sutt Bonn	SK504255	SE	1	B	2.1	1	M	NC	41	70	0	0	5	2
Sutt Bonn	SK504255	SE	3	PB	22.0	1	M	NC	64	123	0	2	4	2
Sutt Bonn	SK504255	SE	1	S	2.0	1	M	NC	11	20	0	0	0	0
Sutt Bonn	SK504255	SE	1	B	30.0	>1	M	C	0	0	0	0	0	0
Sutt Bonn	SK504255	SE	1	B	12.0	1	M	C	33	51	31	33	2	3
Sutt Bonn	SK504255	SE	1	B	20.0	1	S	C	279	419	95	109	0	1
Sutt Bonn	SK504255	SE	1	PB	11.0	1	M	NC	0	0	0	0	0	0
Sutt Bonn	SK504255	SW	2	PD	6.5	1	M	NC	12	12	0	0	3	6
Swithland	SK553130	NW	1	B	6.0	>1	M	C	4	17	0	4	0	0
Swithland	SK553130	NW	2	B	4.0	1	M	C	0	1	0	2	0	0
Thurcaston	Sk567107	SE	2	B	30.0	>1	S	NC	0	0	1	7	0	1
Thurnby	SK646039	N	1	B	8.0	>1	M	NC	171	121	1	0	1	0
Thurnby	SK646039	N	1	B	30.0	>1	M	NC	16	32	6	6	9	6
Thurnby	SK646039	N	1	B	10.0	>1	M	C	174	223	29	43	21	24
Thurnby	SK646039	N	1	B	00.0	1	M	C	8	20	2	4	0	0
Thurnby	SK647039	N	1	B	17.0	1	S	C	247	293	0	0	20	10
Thurnby	SK646045	SE	3	PB	00.0	*	M	NC	0	0	0	0	0	0
Whetstone	SP556976	S	2	B	28.3	*	S	NC	3	14	4	7	1	1
Whetstone	SP556974	S	1	B	41.0	1	M	C	157	215	120	131	32	18
Whetstone	SP556974	S	1	B	5.0	1	M	C	17	32	7	8	0	0

Table 3:1 continued.

Whetstone	SP556974	S	1	B	00.0	1	M	C	165	247	1	11	35	75
Whetstone	SP556974	S	1	B	15.0	1	M	C	110	140	5	5	76	67
Whetstone	SP556974	S	1	B	00.0	1	M	C	19	40	10	4	7	4
Whetstone	SP556974	W	1	B	8.0	*	M	C	19	39	10	4	7	4
Whetstone	SP556974	W	1	B	21.0	1	M	C	0	1	0	1	0	0
Whetstone	SP556976	W	1	B	14.0	>1	M	C	37	71	2	1	30	45
Whetstone	SP556976	W	1	B	13.0	>1	M	C	20	36	0	0	18	31
Whetstone	SP556976	W	1	B	40.0	>1	M	C	37	93	2	0	68	40
Whetstone	SP556973	N	2	PD	10.0	>1	M	NC	35	50	3	5	15	15
Whetstone	SP556973	S	2	PD	00.0	*	M	NC	448	649	26	36	179	123
Whetstone	SP556976	W	1	B	12.0	>1	M	NC	24	41	1	0	52	103
Whetstone	SP556973	N	1	B	10.0	*	M	NC	160	247	30	52	29	48
Wing	SK894029	W	1	B	8.6	1	M	C	0	0	0	0	0	0
Wing	SK894029	W	1	S	6.0	1	M	C	22	29	0	0	0	0
Wing	SK894029	W	1	S	3.0	1	M	C	2	1	3	1	0	0
Wing	SK894029	W	1	S	58.0	1	M	C	0	0	0	0	0	0
Wing	SK894029	W	1	S	30.0	1	M	C	16	28	0	0	0	0
Wing	SK894029	W	1	B	5.6	1	M	C	0	0	0	0	0	0
Wing	SK894029	W	1	S	12.0	1	M	C	4	19	2	3	0	0
Wing	SK894029	NE	1	B	30.0	>1	M	C	0	0	0	1	0	0
Wing	SK894029	SW	1	PD	00.0	1	D	NC	0	1	0	0	0	0
Wigston	SP604989	S	3	PD	19.0	1	M	C	226	370	5	15	359	277
Wigston	SP604989	S	3	PD	2.6	1	M	C	93	129	2	13	100	133

Table 3:1 continued.

Wood Hse E	SK531139	NW	1	B	12.0	>1	S	C	6	28	0	0	0	2
Wymeswold	SK605233	W	1	B	12.0	1	M	C	0	0	4	0	0	0
Wymeswold	SK605233	W	1	B	6.0	1	M	NC	0	3	5	3	0	0
Wymeswold	SK605233	E	1	PD	00.0	*	M	NC	0	0	0	0	1	0
Wymeswold	SK605233	E	1	B	00.0	>1	T	NC	0	0	0	0	0	0

Table 3:2.

Totals of fleas for the Leicestershire 1974 collection.

Species	Male	Female	Total
C.hirundinis	7258	10391	17649
C.farreni	831	1160	1991
C.rusticus	1430	1481	2911
Total martin fleas	9519	13032	22551
C.gallinae	33	45	78
C.fringillae	35	59	94
Total sparrow fleas	68	104	172
Grand total	9587	13136	22723

of each species.

The sex ratios are in good agreement with those found by other workers which shows an imbalance in favour of females (see, for example, Rothschild (1947) and Dunnet & Allan (1955).

3.2.1 Multiple regression analysis.

Stepwise multiple regression analysis was used to investigate the relationship, if any, between the numbers of one species of martin flea, and the numbers of the other two species. The weight of nest lining materials was included in the analyses since this was the only other continuous variable recorded. The other recorded habitat characteristics are at best discontinuous. The values for numbers of each species of flea in a nest were clearly aggregated, and hence all flea data not only for regression analysis but for all other parametric analyses were transformed to logarithms.

The results of the multiple regression analyses are set out in Table 3:3. With *C.hirundinis* as the dependent variable the analysis first extracted *C.rusticus* (33% of variation) followed by *C.farreni* which accounted for a further 13% of variation. Weight of lining material did not contribute significantly.

C.farreni when used as the dependent variable correlated only with *C.hirundinis* which accounted for 23% of variation.

Both *C.hirundinis* and weight of lining

material correlated with *C.rusticus* as the dependent variable with *C.hirundinis* accounting for 33% of variation and weight of lining material accounting for only a further 2%. The weak correlation between *C.rusticus* and weight of lining material suggests that there is a tendency for higher numbers of this species to occur in nests with more lining material.

Positive correlations between the three species of flea indicate a general trend for high numbers to occur in the same nest as high numbers of the other two species and suggests that they may be responding to the same or similar conditions of the nest. It was therefore decided to examine the relationship between each species and the abiotic variable weight of nest lining without the other species as independent variables using regression analysis. No correlations were obtained for any species. The weight of nest lining material was correlated with the total flea number of fleas but accounted for only 3.24% of variation (R=0.18) which however was significant (Table 3:3).

3.2.2 Analysis of remaining parameters.

The remaining parameters were either discontinuous or, in the case of orientation, non-linear. The numbers of fleas were tested for differences between (i) different eaves shapes, (ii) orientation, and (iii) surface texture of the building, using a one-way analysis of variance in each case. The number of nests collected from each of these variables

Table 3:3.

Results from the multiple regression analysis for each species against the physical parameters of the nest location for 123 martin occupied nests collected in Leicestershire 1974 and the other two species of flea. Only the significant coefficients are shown. The variables used are Weight of nest lining material (Tot weight), *C.hirundinis*, *C.farreni* and *C.rusticus*.

Dependent variable	Intercept	B_1	Variable$_1$	B_2	Variable$_2$	R^2	DF
C.hirundinis	1.07381	0.69833	*C.rusticus*			0.33325**	1,121
	0.78034	0.59100	*C.rusticus*	0.53788	*C.farreni*	0.46036***	2,120
C.farreni	0.17071	0.33154	*C.hirundinis*			0.23560**	1,121
C.rusticus	-0.11894	0.47721	*C.hirundinis*			0.33325**	1,121
	-0.19566	0.46635	*C.hirundinis*	0.00662	Tot weight	0.35582**	2,120
Total fleas	2.47232	0.1977	Tot weight			0.03541*	1,121
Multiple regression with *C.rusticus* as the dependent variable excluding nests with no *C.rusticus*.							
C.rusticus	0.34420	0.4269	*C.hirundinis*			0.14572**	1,59

* = 0.01<P<0.05

** =0.001P<0.01

***= P<0.001

B_1,B_2 = Regression coefficients.

are given in (Table 3:4).

As already stated the numbers of fleas were markedly aggregated and the log transformations used should more or less normalize these data. However, comparing the variances for each species and total number of fleas between the variables in each parameter showed quite large differences for some of them. A Bartlett's test for homogeneity of variance on log transformed data revealed that *C.hirundinis* and total number of fleas in the data for surface texture, and for *C.rusticus* in the data for orientation were non-homogeneous. Therefore the non-parametric Kruskal-Wallis one-way analysis of variance was applied to all data as well as the parametric analysis since the two are not mutually exclusive. However, when the two gave the same results only the parametric test is reported.

Eaves Shape.

As dicussed in the previous chapter the shape of the eaves may influence the amount of mud needed to build an enclosed nest and therefore the size of the nest. A parametric and Kruskal-Wallis one-way analysis of variance on the numbers of each species and total number of fleas associated with each eaves shape showed there to be no significant difference between the means *C.hirundinis*, $F=1.5216$; *C.farreni*, $F=1.300$; *C.rusticus*, $F=2.3642$; total number of fleas, $F=1.1525$; $P>0.05$, DF 3,119 in all cases).

Table 3:4.

Number of nests collected and their use in 1974 for the number of buildings, orientation, wall material, colonial and non-colonial nests.

Eaves type	Martin occupied nests	Sparrow occupied nests	Derelict/ temporary nests
1	82	10	3
2	23	5	1
3	14	3	1
4	4	0	0
Total	123	18	5
Orientation			
North	12	2	0
Northeast	13	1	0
Northwest	11	2	0
East	12	4	2
West	17	0	1
South	17	3	0
Southeast	28	5	1
Southwest	13	1	1
Total	123	18	5

Table 3:4 continued.

Wall material	Martin occupied nests	Sparrow occupied nests	Derelict/ temporary nests
Brick	70	10	3
Painted brick	7	3	0
Painted dash	18	4	2
Stone	26	0	0
Plaster	2	1	0
Total	123	18	5
Colonial	76	5	0
Non-clonial	47	13	5
Total	123	18	5
New nests	78	8	1
Old nests	32	3	1
Total	101	11	2

Total number of 89 buildings.

Direction.

The direction (orientation) that the nests faced may affect the micro-climate in the nest and therefore their suitability for the fleas. The results for both parametric and Kruskal-Wallis one-way analysis of variance however showed there to be no significant difference between the means for any species or the total number of fleas (*C.hirundinis*, F=1.3257; *C.farreni*, F= 1.6202; *C.rusticus*, F= 1.2402; total fleas F= 1.1472 P>0.05 DF 7,115 in all cases).

3.1.4 Wall material.

Different wall materials to which the nests were attached may also affect the micro-climate in the nest, and the rougher surfaces may increase the living area/sheltering places for all stages of fleas. Three main types of surface were recorded, brick, painted dash and stone. Nests from two other surfaces, painted brick (7 nests) and plaster (3 nests), were omitted as they were too few for meaningful analysis. Using a Kruskal-Wallis one-way analysis of variance,ranking the values from least to greatest, gave significant differences for all three species and total flea population with surface texture. On inspection of the mean ranks it was apparent that all three species populations were considerably lower in nests on stone surfaces (Table 3:5). Mann-Whitney U tests for each species and total number of fleas between brick and

Table 3:5.

Results of the Kruskal-Wallis one-way analysis of variance for each species of flea and total flea population with surface texture.

Species	Surface texture	Mean rank	Chi-Square	Probability
C.hirundinis	Brick	59.33		
	Stone	42.92		
	Painted dash	69.61		
			7.3206	0.01<P<0.05
C.farreni	Brick	61.72		
	Stone	42.21		
	Painted dash	61.03		
			6.7174	0.01<P<0.05
C.rusticus	Brick	60.36		
	Stone	38.04		
	Painted dash	72.00		
			14.1957	0.001<P<0.01
Total fleas	Brick	61.45		
	Stone	37.40		
	Painted dash	68.50		
			11.9059	0.01<P<0.05

Table 3:6.

Results of the Mann-Whitney U tests for *C.hirundinis*, *C.farreni*, *C.rusticus* and total numbers of fleas between different wall materials.

C.hirundinis

	Mean Rank	z	P
Brick	43.93		
Painted Dash	51.78	1.14	P>0.05
Brick	51.90		
Stone	38.29	2.07	0.01<P<0.05
Painted Dash	27.33		
Stone	17.13	2.67	0.001<P<0.01

C.farreni

Brick	45.65		
Painted Dash	44.89	0.11	P>0.05
Brick	52.56		
Stone	36.31	2.51	0.01<P<0.05
Stone	18.40		
Painted Dash	25.64	1.96	0.01<P<0.05

Table 3:6 continued.

Table 3:6 continued.

C.rusticus			
Brick	43.67		
Painted Dash	52.83	1.38	P>0.05
Brick	53.19		
Stone	34.42	3.13	0.001<P<0.01
Stone	16.13		
Painted Dash	28.67	3.63	0.001<P<0.01
Total numbers of fleas			
Brick	43.90		
Painted Dash	51.92	1.16	P>0.05
Brick	52.81		
Stone	35.58	2.62	0.01<P<0.05
Stone	16.42		
Painted Dash	28.28	3.10	0.001<P<0.01

painted dash surfaces showed no significant difference between the two, but in all cases brick and painted dash were significantly different to stone (Table 3:6).

Nest lining.

Only the numbers of *C.rusticus* were correlated with the amount of lining material in the regression analysis, and then only very weakly. To investigate the possible effects of lining material a further comparison of each flea species and the total flea population between nests with lining (108 nests) and those without (15 nests) was made. These showed no significant differences between the means (*C.hirundinis* t=0.77: P>0.05, *C.farreni* t=0.42: P>0.05 *C.rusticus* t=0.36: P>0.05) (see Table 3:7).

A further comparison was made between the major lining materials. Three major constituents of the lining material were identified: 'grass' comprising cuttings of grass leaves; 'feathers' from a number of bird species; and 'straw' being the thick stems of cereals. More than one of these components could occur in any one nest and were not weighed individually. The mean densities for each flea species in the presence and absence of each component of the lining material were therefore compared using t-tests on log transformed data (Table 3:8).

All three species were significantly more

Table 3:7.

Results of t-tests for each species of martin flea and total number of fleas between nests containing nest lining material and those without.

Species	Mean±SE		Difference ±SE	t	Probability
	Lining	No lining			
C.hirundinis	1.5460 ± 0.863	1.3613 ± 0.926	0.1847 ± 2398	0.77	P>0.05
C.farreni	0.6780 ± 0.059	0.6068 ± 0.169	0.0712 ± 0.169	0.42	P>0.05
C.rusticus	0.6104 ± 0.027	0.5309 ± 0.207	0.0795 ± 0.220	0.36	P>0.05
Total fleas	1.7110 ± 0.078	1.4548 ± 0.242	0.2562 ± 0.253	1.01	P>0.05

Table 3:8

Comparison of the log means of *C.hirundinis*, *C.farreni* and *C.rusticus* from nests containing/lacking various lining materials.

Species	Feathers			
	Absent ± SE (n=49)	Present ± SE (n=57)	Difference ± SE	Probability
C.hirundinis	1.07 ± 0.123	1.81 ± 0.096	0.746 ± 0.156	0.001<P<0.01
C.farreni	0.47 ± 0.078	0.74 ± 0.008	0.263 ± 0.113	0.01<P<0.05
C.rusticus	0.23 ± 0.071	0.77 ± 0.102	0.532 ± 0.124	0.001<P<0.01

	Grass			
	Absent ± SE (n=57)	Present ± SE (n=51)	Difference ± SE	Probability
C.hirundinis	1.22 ± 0.116	1.77 ± 0.114	0.541 ± 0.162	0.001<P<0.01
C.farreni	0.44 ± 0.067	0.87 ± 0.104	0.431 ± 0.118	0.001<P<0.01
C.rusticus	0.33 ± 0.740	0.78 ± 0.119	0.458 ± 0.138	0.001<P<0.01

	Straw			
	Absent ± SE (n=86)	Present ± SE (n=22)	Difference ± SE	Probability
C.hirundinis	1.49 ± 0.098	1.37 ± 0.166	0.144 ± 0.193	P>0.05
C.farreni	0.65 ± 0.074	0.52 ± 0.088	0.129 ± 0.105	P>0.05
C.rusticus	0.56 ± 0.082	0.45 ± 0.142	0.109 ± 0.164	P>0.05

abundant in nests containing feathers than those that did not. Similarly, nests containing grass yielded significantly more fleas than those without. Straw showed no significant differences from nests without straw and all three species populations were marginally less abundant in nests containing straw than in those lacking it.

A comparison of the weights of lining material between old and new martin occupied nests, again using a t-test, showed that there was significantly more lining material in the old nests ($t=2.57$ $0.01<P<0.05$) (see Table 3:9) indicating that additional material was added in nests older than one season.

The flea populations in new (one season old, 78) and nests older than one season (32) may vary; therefore they were compared using t-tests on log transformed data. No significant differences were found between the means for any flea species or the total flea population. The results are given in Table 3:10 and suggests that the increase in lining material in older nests is having no effect on the numbers of fleas and in fact the mean number in old nests was less than new nests except for *C.rusticus*.

Flea populations in Colonial/non-colonial nests.

It is assumed in the above analyses that all nests are equally susceptible to colonization by fleas. Differential rates of movement between nests could well occur and, in particular, there could be a greater interchange between colonial (76 nests) than non-

Table 3:9.

Results of t-tests for the comparison of weight of nest lining material between old and new martin nests and martin and sparrow nests.

New and old martin nests.

Mean ± SE		Difference	± SE	t	Probability
New	Old				
12.2515 ± 1.734	22.0806 ± 4.212	9.8291	± 3.8245	2.57	0.01<P<0.05

Martin and sparrow nests.

Mean ± SE		Difference	± SE	t	Probability
Martin	Sparrow				
14.2585 ± 1.522	31.9611 ± 3.570	17.7026	± 4.2048	4.21	P<0.001

Table 3:10.

Comparison of flea populations in martin occupied nests between new nests (one season old) and nests older than one season in Leicestershire 1974 using t-tests on log transformed data.

Species	New (68)	Old (32)	Difference ± SE	t	Probability
C.hirundinis	1.5571 ± 0.107	1.5458 ± 0.145	0.0113 ± 0.1614	0.07	P>0.05
C.farreni	0.7262 ± 0.070	0.5489 ± 0.113	0.1773 ± 0.1323	1.34	P>0.05
C.rusticus	0.5893 ± 0.087	0.7036 ± 0.145	0.1143 ± 0.1609	0.71	P>0.05
Total fleas	2.8726 ± 0.103	2.7983 ± 0.164	0.0743 ± 0.3970	0.24	P>0.05

Twentytwo of the martin occupied nests collected could not be aged with certainty and were therefore not used in the analyses.

colonial (47) nests. (Nests were considered colonial if they were on the same building).

As colonial nests may have related densities which would disrupt any attempt to normalize the data by log transformation, it seemed safer to use a non-parametric test for any comparison of flea populations between them. A Mann-Whitney U test for each species and total flea populations with the lowest number ranked at 1 between colonial and non-colonial nests showed a significant difference for *C.rusticus* only. The mean ranks showed that fewer *C.rusticus* occurred in colonial nests (Table 3:11).

Although overall no significant differences were found between new and old nests it was decided to re-run the Mann-Whitney U tests between colonial and non colonial nests this time separating them into the two age catagories. No significance difference was found for any species between one year old colonial and non-colonial nests. When colonial and non-colonial nests older than one year were compared only *C.rusticus* showed a significant difference (Table 3:11). It should be noted, however, that of the 32 nests more than one year old, only seven were non-colonial.

The greatest number of nests found in a colony was eight at Wing (SK894029) while three colonies with seven nests (Medbourne SP800930, Sileby SK610152, Whetstone SP556974) were recorded. If any interchange of fleas was taking place between nests in these larger colonies the variance between nests for the numbers of

each flea species would be significantly less than the overall variance for non-colonial nests. In these colonies only *C.hirundinis* occured in sufficient numbers for analysis. The variances obtained for *C.hirundinis* and total flea numbers in each colony are given in Table 3:12. When these variances were compared with the variance for *C.hirundinis* in non-colonial nests only Sileby was significantly different.

The variance for the total number of fleas in nests from these colonies were then compared with the variance of the total number of fleas in non-colonial nests. This time no significant result was obtained for any colony.

These results, taken together suggests that little interchange of fleas takes place between nests in colonies.

House sparrow (*Passer domesticus*) occupying martin nests.

When martin nests are occupied by house sparrows for winter roosts they usually introduce large amounts of nest lining material. A comparison of the weight of lining material between nests occupied by martins (123) and 'martin' nests occupied by sparrows (18) confirmed this impression ($t=4.21, P<0.001$) (Table 3:9) showing that there was significantly more lining material in the sparrow occupied nests. The introduction of a large quantity of lining material and the

Table 3:11.

Abundance of individual flea species in colonial (76 nests) compared with non-colonial (47nests) using a Man-Whitney U test on log transformed data for martin occupied nests only, Leicestershire 1974.

All nests(123)

Species	Colonial (76) Mean rank	Non-colonial (47) Mean rank	z	Probability
C.hirundinis	60.94	63.77	0.4264	P>0.05
C.farreni	61.72	62.47	0.1143	P>0.05
C.rusticus	56.73	70.82	2.2705	0.001<P<0.01
Total fleas	59.89	65.41	0.8357	P>0.05

One year old nests.

Species	Colonial (39)	Non-colonial (29)	z	Probability
C.hirundinis	32.62	37.03	0.9123	P>0.05
C.farreni	34.86	34.02	0.1754	P>0.05
C.rusticus	31.63	38.36	1.4853	P>0.05
Total fleas	32.09	37.74	1.1658	P>0.05

Table 3:16 continued.

Table 3:11 continued.

Greater than one year old nests.

Species	Colonial (25)	Non-colonial (7)	z	Probability
C.hirundinis	16.72	15.71	0.2509	P>0.05
C.farreni	16.74	15.64	0.2816	P>0.05
C.rusticus	14.96	22.00	1.8530	0.01<P<0.05
Total fleas	16.08	18.00	0.4789	P>0.05

Table 3:12.

Numbers and log variances for *C.hirundinis*, *C.farreni*, *C.rusticus* and total number of fleas in the largest colonies from Leicestershire 1974.

		C.hirundinis				Total number of fleas			
Locality	Number of nests	Number of individuals	s^2	F	P	Number of individuals	s^2	F	P
Wing	8	122	0.6236	1.29	P>0.05	254	0.5955	1.02	P>0.05
Medbourne	7	446	0.2687	2.85	P>0.05	520	0.3038	1.90	P>0.05
Sileby	7	168	0.1521	5.05	0.01<P<0.05	224	0.1780	3.25	P>0.05
Whetstone	6	1159	0.6681	1.14	P>0.05	1788	0.6545	1.12	P>0.05

Variance for C.hirundinis in non-colonial nests = 0.7665 (N=47).

Variance for total number of fleas in non-colonial nests = 0.5799 (N=47).

disturbance, at a time of year when the fleas would normally be in a quiescent state, may affect their numbers.

The numbers of martin fleas were therefore compared between the 18 sparrow occupied martin nests and 123 martin occupied nests using a one-tailed Mann-Whitney U test. This test was used on these data as the variances were found to differ significantly between 'martin' and 'sparrow' occupied nests for *C.rusticus*. It therefore seemed better to use a non-parametric test for all these data. A one-tailed test was used to see if there was a reduction in the numbers of fleas in the sparrow occupied nests.

Significant differences were found between mean ranks for *C.hirundinis* and the total flea population only. The results of the Mann-Whitney tests are given in Table 3:13. This suggests that the presence of house sparrows is affecting the most abundant species, *C.hirundinis*. The result for total flea numbers is probably due to the large number of *C.hirundinis* contained in it. The numbers of species occuring in sparrow nests and the number of nests are given below.

Species	Number of fleas	Number of sparrow occupied martin nests
C.hirundinis	1,983	12
C.farreni	323	10
C.rusticus	20	7

Table 3:13.

Results of Mann-Whitney U tests for *C.hirundinis*, *C.farreni*, *C.rusticus* and total numbers of fleas between martin and house sparrow occupied nests.

Total martin nests (123).

Species	Mean Rank		z	Probability
	Martin	Sparrow		
C.hirundinis	73.11	51.59	2.12	0.001<P<0.01
C.farreni	70.76	68.62	0.20	P>0.05
C.rusticus	71.93	60.18	1.20	P>0.05
Total fleas	72.94	52.82	1.91	0.01<P<0.05

Multiple regression analyses using each species of flea as the dependent variable with the other two species as independent variables on the flea populations in each sparrow occupied nest gave no significant correlations. The loss of correlation between *C.hirundinis* and the other two species was presumably caused by the overall reduction in numbers and the fewer observations.

The flea populations of temporary (3 nests) and deserted (3 and 2 nests respectively) were examined separately. Fleas were found in only one nest of each type; 1♀ *C.hirundinis* in a temporary nest, and 4♂ and 4♀ *C.hirundinis,* and 1♀ *C.farreni* in a deserted one. The presence of the host for only a short period of time would account for this paucity.

Both *C.gallinae* and *C.fringillae* occurred in a few nests,the highest numbers occurring in sparrow occupied nests. In only one nest were more than 20 individuals encountered with 22♂ 30♀ *C.gallinae* and 12♂ 16♀ *C.fringillae*. Because of the paucity of these species they were not used in any of the analyses.

A few likely predators namely staphylinid beetles, spiders and mesostigmatig mites, were encountered in some nest, but were too few for any statistical analysis. The variety of arthropods associated with house martin nests is well documented (see Hicks 1971). The only non-predatory taxon which may affect the flea populations were the larvae of Lepidoptera, all *Tinea* sp., which may chew the flea cocoons (George *pers. comm.*). These were encountered in

most nests, but a Kendall's tau rank correlation test showed no correlation between them and the abundance of the fleas (tau=0.0038117 ;P>0.05). All other arthropods collected with the fleas are listed in appendix 1.

3.3 Discussion.

The results of this initial survey confirm previously published data (eg. Dunnet & Allan, 1955) that the bulk of the flea populations remain in the nest throughout the year.

A relationship that allows for three congeneric and monoxenous species of flea to share the same host and inhabit the same nest suggests that either intra-specific control is sufficiently strong to minimize inter-specific competition, or coexistence is permitted either by sufficient niche segregation or through extrinsic controls, e.g. predation. The lack of inter-specific competition is certainly supported by the results of the multiple-regression analyses (Table 3:3) which show positive relationships for *C.hirundinis* with both *C.farreni* and *C.rusticus*. This relationship suggests that conditions favourable for *C.hirundinis* are also favourable for both the other species, while the lack of any correlation between these latter two species may be due to their relatively low numbers, and particularly in *C.rusticus*, the marked aggregation of their numbers in the data.

Amongst nests on man-made structures the

important features appear to be the nest lining material, and the texture of the surface to which the nest was attached. Both Jurik (1974) in Czechoslovakia and Darskaya (1964) in USSR commented on nest lining material but did not attempt a critical appraisal, nor did either give sufficient detail for satisfactory comparisons.

The results of the analyses on individual nest lining materials (Table 3:8) indicate that all three species are affected by the components of the nest lining. Both feathers and grass compact much more than straw and this may affect the micro-climate of the nest although no significant differences were found in the abundance of the three flea species between nests with lining and those without. Similarly the very weak correlations obtained for *C.rusticus* and for the total number of fleas, and the lack of any correlation for the other two species, with the quantity of nest lining material in the regression analysis further suggests that quantity of material is of little importance in controlling flea numbers. The results overall for nest lining material therefore suggest that these species are able to tolerate a wide range of nest linings and nest conditions.

The relation between each species and wall material is difficult to explain. The characteristics of these materials may influence humidity and thermal insulation in the nest. Wall material may also vary in

texture, rougher surfaces perhaps offering more sheltering places than smoother ones thereby increasing the available living space. Certainly on inspection of nest sites brick and painted dash appeared to have rougher surfaces than stone which had been faced and were smooth.

No significant effect of orientation of the nests were detected in any species. This suggests that the degree of exposure to which the nest or nest site is subjected is not influencing the flea populations significantly.

Although many fleas associated with birds nests are known to emigrate (eg. Bates, 1962; Darskaya, 1964; Jurik, 1974), in this study, the only detectable difference between 'colonial' and 'non-colonial' nests was that *C.rusticus* was more abundant in non-colonial nests, although in all species the mean ranks were greater for non-colonial nests. These results suggest that there is little movement between nests in colonies and that colonization of new nests, and any re-colonization of old nests, relies on transportation by the martins.

The time at which each species reaches the nest and becomes established is likely to affect the composition of the nest community and consequently the autumn nest densities would vary considerably. Thereafter the densities are likely to be affected by a variety of factors including the availability of the

host, the characteristics of the nest and the associated nidicoles.

The result of the comparison between new and old nests was perhaps a little surprising. It is clear from these data that considerable numbers of fleas are present in nests in the autumn and that these overwinter and form the breeding population in the next spring. The colonization of new nests on the other hand relies on the transportation of fleas by the martins. The few records that exist for the numbers of fleas carried by the martins (eg. Rothschild 1952) show that very few are usually transported at one time and therefore one assumes that the starting population in a newly constructed nest is small. If this is the case one would have expected that the older nests with the larger starting populations would have had a much larger autumn population than a nest in its first season. This of course assumes that the bulk of the overwintering community survives the winter and is fecund in the following spring. Unfortunately no information is available on this aspect or the length of the life cycle for these species. Other species of bird flea, for example *C.gallinae* and *C.styx* have been observed moving away from blue tit and sand martin nests respectively in the spring (Bates *op. cit.* and Humphries 1969) indicating that at least part of the overwintering population had survived the winter.

The occupation of martin nests by sparrows had

a significant effect on *C.hirundinis* and the total flea population. The reduction in this species may be due to the general disturbance of the nest in the autumn, a time when all three species are in an inactive state. The presence of sparrows would presumably cause the fleas to become active and perhaps seek a blood meal, although there was no evidence of fleas collected from sparrow occupied nests having fed recently. It is surprising that *C.farreni* and *C.rusticus* are not apparently similarly affected. They are, however, less abundant overall than *C.hirundinis* and although individually may not show a significant drop in numbers in sparrow occupied nests may contribute to the overall reduction in the total flea populations.

The results of this initial survey suggest that a few of the abiotic factors are operating to influence the flea populations. These collections were all made in the autumn soon after the martins had left the nests and so the samples represent the range of species composition which can exist at one time in one geographical location. These collections, however, give no clue as to how each species density changes through the year or is affected by biotic controls (for example, the effects of the martins themselves).

Day *et al.* (*op. cit.*) consider that fleas have three major mechanisms to avoid competition. First, some species separate spatially while feeding. Prasad (1972)

showed that two rat fleas *Xenopsylla cheopis* and *X.astia* prefer different feeding sites on the host, *X.cheopis* feeding on the posterior portion with *X.astia* on the anterior part of the body.

The second mechanism is sensitivity to micro-habitat selection. Day *et al.* (*op. cit.*) noted several species in which the external environment surrounding the host and its nest was as important as the nest itself. George (1959) examined the numbers of the fleas *C.gallinae* and *Dasypsyllus gallinulae (Dale)* in nest boxes used by the pied flycatcher *Muscicapa hypoleuca*. When comparing the number of fleas between the different directions the nest boxes faced, he found that nest boxes facing between southwest and south yielded more than four times as many fleas as those facing northwest and southeast. Prevailing winds in the study area (Forest of Dean, Gloucestershire) were southerly and westerly. George took this as an indication that the direction in which the nest box faced affected the microclimate in it. *D.gallinulae* tends to be associated more with nests near to the ground, in wet habitats. It was unusual therefore to find this species in the drier conditions usually associated with nest boxes. *Dasypsyllus* is a tropical genus and George considered that under adverse conditions this species would do less well than *C.gallinae*, which is recorded from a much wider range of passerine nests. On comparing the ratios of the numbers

of *gallinulae* to *gallinae* in the south west and south facing nests the ratio was 1:12 whilst in the north west and south east facing nests the ratio was 1:54. The reduction of a more sensitive species, George considered, was further evidence that micro-climate was affected by direction.

Thirdly, Day *et al.* (*op. cit.*) considered that if intense inter-specific competition takes place between a number of species it may result in temporal species separation. They investigated this aspect with four species of flea *Conorhinopsylla stanfordi* Stewart, *Epitedia faceta* (Rothschild), *Opisodasys pseudarctomys* (Baker) and *Orchopeas howardii howardii* (Baker) in the nest of the American Flying Squirrel (*Glaucomys volans volans*). They found that the breeding cycles of these four species were staggered so that only the adults of one species predominated in the nest during a given month of the year.

Of these three considerations for avoiding inter-specific competition the results from this initial survey suggest that the response to different wall materials and nest lining materials shown by *C.hirundinis*, *C.farreni* and *C.rusticus* may possibly be connected with differences in environment with different materials. As previously stated the direction the nest faced does not seem to affect any of these species.

It seems unlikely that each species is breeding at a different time as the martins' breeding season

covers such a short period of the year. Further there is little evidence that these species of flea breed outside the martins' breeding season although Gordeyeva (1969) found engorged *C.hirundinis* in sparrow occupied martin nests in the spring before the return of the martins. Spatial distribution of adults of these species on the host has not been investigated.

Chapter 4.

Analysis of further collections from Leicestershire, Derbyshire and Cornwall.

4.1 Introduction

The analysis of the initial survey indicated that some abiotic factors were affecting the flea populations. This was of course only in one geographic locality, Leicestershire, at one time. Dunnet & Allan (1955) in Scotland found that over a few years the species composition and abundance of martin fleas varied between localities and, where collections were made at the same localities over successive years the differences in species composition and abundance were maintained. They also found at one site annual differences in the flea populations. Rothschild (1947 & 1963) made two collections with sixteen years between them (1946 & 1962) and found that the species composition had completely changed from one dominated by *C.hirundinis* and *C.rusticus* to one dominated by *C.farreni*.

The evidence suggests therefore that if a species is common in one area it is likely to remain so for a short while even though the nests may be destroyed each year (which Dunnet *et al.*(*op.cit.*) had to do in order to determine the species present). Presumably in this situation there were enough nests left untouched in the area, forming a reservoir of fleas that could be picked up by martins visiting the older nests in the spring, roosting in them, and then moving on to build

new nests and incidentally taking some of the fleas with them. The dominant flea species therefore would be likely to remain the dominant species in that area. In the situation where the colony is more isolated and where the nests are destroyed each year, the species composition may be expected to be less stable between years.

If the composition of the nest lining material is playing a part in determining how well a particular species does, and there was some suggestion of this in the results from 1974, particular materials may remain stable in one area over a few years, but may change over a much longer period of time, perhaps due to a change in land use in the surrounding area, eg. pasture to arable.

To see whether flea population densities vary temporally and geographically further collections were made in Leicestershire in 1977, 1978, 1984 and 1985 as far as possible from the same areas as the 1974 collection. Collections were also made in the county of Cornwall on the Lizard peninsula in 1978, 1979 and 1980 to examine temporal effects in a different locality.

In the 1974 data, no significant difference in flea population size was found between nests that were one season old and those older than one season. As discussed in the previous chapter this was a surprising result assuming that the bulk of the fleas survived the winter to form a much larger breeding population in the spring than in newly built nests.

To investigate this aspect nest collections

were made in Leicestershire in October and December 1977 and March 1978, and again in October 1984 and then in January and April 1985. One problem encountered was that as the winter progresses more martin nests are taken over by house sparrows and many nests are removed by the householders, making it difficult to obtain a large sample of nests in the spring. All the nests from Cornwall were collected in the autumn.

In order to see whether the fleas overwinter in their cocoons ethyl acetate on a piece of cotton wool was intoduced into the nests before collection to kill the fleas *in situ*. This was done in the Leicestershire 1977/78 collection only.

In the initial survey it was felt that the shape of the eaves might be important as this may dictate the size of the nest and therefore the living area inside. The eaves were classified 1-4 depending on the size of the angle they produced. An analysis of variance on the flea populations with eaves shape failed to show any significant differences between eaves type. In these collections the volume of mud in the wall of the nest was measured in a measuring cylinder, after all the fleas had been extracted from the nest, by crumbling it into a fine powder. This gave a rather more precise measure of the volume of mud in the nest wall and, as the thickness of the walls between nests are similar (see McNeil & Clark 1977) indicated changes in the size of the nest lumen. The volume of mud was included in the

regression program. Using this method it was found that the assumption that the greater the angle of the eaves the more mud would be required to build a nest was false, as often less mud had been used to construct a nest on eaves with a large angle than one with a smaller angle, see Table 4:1.

In addition to these collections from house eaves, a small collection of nests was made from inland cliffs at Cheedale in Derbyshire in October 1979 and 1980 and maritime cliffs in Cornwall, in October 1979. These were used as a comparison with the flea populations in nests on buildings.

Little data are available for flea populations in nests on inland cliff sites. Dunnet *et al.* (*op. cit.*) examined three nests from a quarry in Aberdeenshire and found only *C.hirundinis* in 'large numbers' (*sic*). They also examined nests from sea cliffs in NE Scotland and found that *C.rusticus* was by far the most abundant flea in this situation. In collections made from sea cliffs in SW Ireland (Claassons 1965), and the Isle of Man (Roberts 1975) found that again *C.rusticus* was the most abundant species, although it should be noted that in both the NE Scotland and the Isle of Man collections both *C.hirundinis* and *C.farreni* were present albeit in small numbers. In SW Ireland no *C.hirundinis* was found in cliff nests (Claassons *op. cit.*). Cliff sites as opposed to eaves on buildings are generally thought of as being a more exposed and wetter habitat (George *pers. comm.*), and this may be a factor which favours the occurence of *C.rusticus*.

To test whether the moisture content was significantly different between nests on buildings, inland and sea cliffs, a strip of cobalt thiocyanate paper was sealed in the polythene bags with the nests on collection. This was done with all nests collected from cliffs and seventeen of the nests collected from house eaves in Leicestershire 1977/1978 and Cornwall 1978-80. The nests were stored in a constant temperature room at approximately the same temperature as the ambient when collected until sorted for fleas, usually between three days and one week later. The cobalt thiocyanate paper was then subjected to the procedure described in chapter 2.

The nests in these collections were sorted for fleas in the same way as the 1974 collection, and all statistical tests using numbers of fleas were performed on log transformed data, using both parametric and non-parametric tests. Where these gave identical results the results from the parametric test only are given.

Results.

4.2 Leicestershire 1977 and 1978.

The data for the nests collected in the period October 1977 to March 1978 are set out in Table 4:1 which shows all the parameters recorded. The flea data are clearly dominated by *C.hirundinis* while *C.farreni* was recorded at low densities in only 13 nests (range 1-52) whilst *C.rusticus* was found in only three nests. This species was not used as a dependent variable

Numbers of each species of martin flea with all variables recorded for Leicestershire 1977/78 collections.

N= north, NE= northeast, NW= northwest, W= west, B= brick, PD= painted dash, PB= painted brick, NF= feathers, NG= grass, NS= straw.

M= martin occupied, S= sparrow occupied, C= colonial, NC= non-colonial, C.h= *C.hirundinis*, *C.f= C.farreni*, *C.r= C.rusticus*.

Location	Grid ref	Dir	Eaves shape	Wall material	Volume of Mud	Weight of lining			Nest age	Nest use	Colony/ non Colonial	C.h		C.f		C.r		Date
						NF	NG	NS				♂	♀	♂	♀	♂	♀	
October 1977																		
Cosby	SP547947	W	1	PD	475	0	4	0	1	M	C	32	35	0	0	0	0	
Cosby	SP547947	W	1	PD	600	0	36	0	1	M	C	9	140	0	0	0	0	
Cosby	SP547947	W	1	PD	450	0	20	0	1	M	C	84	94	0	0	0	0	
Cosby	SP547947	W	1	PD	280	0	26	0	1	S	C	0	0	0	0	0	0	
Cosby	SP547947	W	1	PD	450	0	96	0	1	S	C	0	0	0	0	0	0	
Hoby	SK671176	NE	1	PD	350	0	22	0	1	M	NC	37	49	5	5	0	0	
Hoby	SK671175	NE	1	B	450	0	50	0	>1	M	C	1	3	1	6	0	0	
Hoby	SK671175	NE	1	B	350	2	0	26	>1	M	C	223	308	0	4	0	0	
Leicester	SK594021	NW	1	PD	350	0	2	0	>1	M	C	1	2	0	0	0	0	
Leicester	SK594021	NW	1	PD	370	2	0	0	1	M	C	17	30	0	0	0	0	
Leicester	SK594021	NW	1	PD	250	0	80	0	>1	S	C	0	1	0	0	0	0	
Leicester	SK594021	NW	1	PD	200	0	0	0	>1	S	C	0	0	0	0	0	0	
Leicester	SK565044	NW	1	PD	350	0	5	0	1	M	C	14	7	0	0	0	0	
Leicester	SK565044	NW	1	PD	180	1	81	0	>1	S	C	0	1	0	0	0	0	
Queniboro	SK649120	NE	1	B	650	1	18	0	>1	M	C	55	77	8	20	0	0	
Queniboro	SK649120	NE	1	B	475	3	19	0	>1	M	C	194	271	4	2	0	0	

Table 4:1 continued.

Location	Grid ref.	Dir	Eaves shape	Wall material	Volume of mud	Weight of lining			Nest age	Nest use	Colony/ non colonial	C.h		C.f		C.r	
						NF	NG	NS				♂	♀	♂	♀	♂	♀
Whetstone	SP556976	NW	1	B	355	1	17	0	1	M	NC	132	187	10	12	0	0
Whetstone	SP556976	W	1	B	200	1	10	0	1	M	NC	97	73	1	0	0	0
Whetstone	SP558971	W	2	B	380	0	22	0	1	M	NC	7	3	0	0	0	0
December 1977																	
Oadby	SP697998	N	2	PD	160	4	20	0	1	M	NC	162	242	2	0	0	0
Oadby	SP697998	N	2	PD	200	0	20	0	1	M	NC	368	504	44	8	0	0
Oadby	SP630994	N	2	B	450	1	9	0	1	M	NC	438	586	8	5	4	1
Oadby	SP630994	N	2	B	280	0	5	0	>1	M	NC	50	58	0	0	0	0
Stoughton	SK642023	W	3	PD	510	3	18	0	>1	M	C	346	368	0	0	0	0
March 1978																	
Stoughton	SK642023	W	3	PD	400	7	10	0	>1	M	C	117	123	8	0	0	0
Oadby	SP633994	N	2	PD	360	0	10	0	1	M	NC	46	50	0	0	0	0
Oadby	SP633993	N	2	B	410	0	23	0	1	M	NC	632	534	6	0	0	0
Oadby	SP634992	N	2	B	360	0	19	0	1	M	NC	12	8	0	0	1	0
Oadby	SP629997	N	2	PB	295	1	27	0	>1	M	C	432	378	0	2	10	14
Oadby	SP629997	N	2	PB	380	0	11	0	>1	M	C	100	106	6	4	0	0

in the regression analysis or any of the other analyses. *C.gallinae* was found in two nests.

4.2.1 Multiple Regression Analysis (Table 4:2).

Multiple regression analyses were only performed on the twenty five martin occupied nests with all the environmental variables which approximated to a continuous distribution ie. volume of mud in the nest wall, nest lining (both as total mass and as the separate constituents). These were tested over all three months of collection ie. October, December and March, and for the individual collections where there were sufficient data. The dependent variables were taken initially as the total flea populations, but then both *C.hirundinis* and *C.farreni* were taken separately as the dependent variable with the other species as the independent variable.

Total fleas over the period.

When regressed on all variables with nest lining taken as a whole, no correlations were obtained. Similarly none was obtained when the program was re-run with the nest lining components separated.

Species of flea only.

A regression with *C.hirundinis* as the dependent variable with *C.farreni* as the only independent variable gave a significant positive result,

accounting for 19% of variation with R=0.4370 (0.01<P<0.05).

Individual species with abiotic variables.

The multiple regressions were re-run this time using each individual flea species as the dependent variable against the physical variables and the other two species. In the regressions with the weights of nest lining components combined, *C.hirundinis* as the dependent variable was positively correlated with *C.farreni* and as before accounted for 19% of variation. *C.farreni* when used as the dependent variable again only correlated with *C.hirundinis*. Re-running the program with the nest lining components separated gave a positive correlation for *C.hirundinis* as the dependent with *C.farreni* as the first correlate (19% of variation) and the lining material 'feathers' as the second correlate accounting for a further 13.7% of variation (R=0.5734;0.001<P<0.01). *C.farreni* as the dependent variable, again correlated only with *C.hirundinis*.

So far all of the regressions, except for those with total number of fleas as the dependent variable, have had the species of flea included with the abiotic variables as independent variables. *C.hirundinis* and *C.farreni* were positively correlated in the regressions where only fleas were used as variables as well as with abiotic variables. To see if the presence of the fleas as independent variables were in any way

Table 4:2.

Multiple regression analysis for each species against the physical variables of the nest location for 25 martin occupied nests and the other two species of flea from Leicestershire 1977/78 collection. Only the significant correlatons at 5% probability or better are shown.

The variables used were Weight of nest lining material (WTL) both as seperate components and combined(Feathers (NF), Grass(NG), and Straw(NS), Volume of mud(VM), *C.hirundinis*(C.h), *C.farreni*(C.f).

Dependent variable	Intercept	B_1	Var_1	B_2	Var_2	DF	R^2
With fleas only.							
C.hirundinis	1.86983	0.51887	C.f			1,23	0.19104
C.farreni	-0.27066	0.36819	C.h			1,23	0.19104
With nest lining components combined.							
C.hirundinis	1.86983	0.51887	C.f			1.23	0.19104
C.farreni	-0.27066	0.36819	C.h			1,23	0.19104
With nest lining components separated.							
C.hirundinis	1.86983	0.51887	C.f			1,23	0.19104
	1.66278	0.59707	C.f	0.15398	NF	2,22	0.32888
C.farreni	-0.27066	0.36819	C.h			1,23	0.19104
Multiple regression with the species of flea and time as the independent variables.							
C.hirundinis	2.63882	0.61907	T			1,23	0.27663
	2.21880	0.54009	T	0.75283	C.f	2,22	0.44554

affecting which abiotic variables were extracted the regressions were run again with just the abiotic variables against each species as the dependent variable on the data treated as one collection. No change in the abiotic correlates was observed, indicating that the regression was treating each variable separately.

The data have so far been considered as a single sample but comprise three samples collected at different times ie. 14 nests collected in October 1977, 6 in December and 5 in March 1978. When the effect of time of collection was introduced as a component,with each species as the dependent variable and the other as an independent variable, *C.hirundinis* showed a strong positive correlation with time (27.7% of variation; $R=0.5259$; $0.001<P<0.01$),with *C.farreni* as the second correlate (a further 17%).. The data for *C.farreni* in both December and March were too few for any useful results to be expected and no correlations were obtained.

4.2.2 Analysis of the other variables.

The remaining parameters were either discontinuous or in the case of orientation (direction), non-linear. The populations associated with orientation, were not considered worth analysing as only four directions were involved all falling within an arc of 130^{o}.

Nests were collected from three surfaces only brick (11), painted dash (12) and painted brick (2).

This last category was ommited from the analyses. The flea populations in nests from brick and painted dash surfaces were compared using a t-test. The populations for *C.hirundinis*, *C.farreni* and total number of fleas were not significantly different between the two surfaces ($t=0.29; P>0.05$; $t=1.82$ and $t=1.14; P>0.05$ respectively see Table 4:3).

The populations associated with nests in colonial or non-colonial nests were compared using Mann-Whitney U tests. Although little evidence was found in the 1974 data to suggest that nests in colonies had related densities of fleas it seemed safer to continue using a non-parametric test for comparing colonial with non-colonial nests. The flea populations between new or old nests were compared using t-tests. The numbers of nests associated with each of these variables is given in Table 4:4.

The populations associated with nests in colonial and non-colonial nests were compared using a Mann-Whitney U test. The results of the Mann-Whitney U test between colonial and non-colonial nests are given in Table 4:5 and show no significant differences between the two for either species or total number of fleas. As the number of nests in each colony was small a comparison between individual colony variances with the overall variance for non-colonial nests was not worth attempting.

Table 4:3.

Results of t-tests for *C.hirundinis*, *C.farreni* and total number of fleas between the wall materials brick and painted dash Leicestershire 1977/78.

Species	Mean ± SE		Difference ± SE	t	Probability
	Brick	Painted dash			
C.hirundinis	2.1310 ± 0.198	2.0589 ± 0.233	0.0889 ± 0.3004	0.29	P>0.05
C.farreni	0.6870 ± 0.178	0.2517 ± 0.150	0.4353 ± 0.2336	1.82	P>0.05
Total fleas	2.6128 ± 0.383	2.2895 ± 0.304	0.5233 ± 0.4879	1.14	P>0.05

Table 4:4.

Number of nests collected and their use in Leicestershire 1977/78 for the number of buildings, orientation(direction), surface texture(wall material) colonial and non-colonial nests.

Orientation	Martin occupied nests	Sparrow occupied nests
North	9	0
Northeast	5	0
Northwest	4	3
West	7	2
Total	25	5
Wall material		
Brick	11	0
Painted dash	12	5
Painted brick	2	0
Total	25	5
Eaves type		
1	13	5
2	10	0
3	2	0
Total	25	5

Table 4:4 continued.

Table 4:4 continued.

Colonial	14	5
Non-colonial	11	0
Total	25	5
New nests	15	2
Old nests	10	3
Total	25	5

Total number of buildings = 17

Table 4:5.

Results of the Mann-Whitney U tests for *C.hirundinis*, *C.farreni* and total number of fleas between colonial and non-colonial nests for Leicestershire 1977/78.

Species	Mean Rank		z	Probability
	Colonial	Non-colonial		
C.hirundinis	12.29	13.91	0.5474	P>0.05
C.farreni	11.50	14.91	1.2191	P>0.05
Total fleas	11.86	14.45	0.8759	P>0.05

The flea populations in new and old nests were compared using t-tests. No significant differences were found for any species or the total number of fleas. *C.hirundinis* ($t=0.008; P>0.05$, *C.farreni* $t=0.35; P>0.05$ and total fleas $t=0.16; P>0.05$ (see Table 4:6)).

Comparison of lining materials.

The lining materials comprised mainly cut grass and feathers, and straw occurred in only one nest. In thirteen of these nests feathers were absent and in only two nests was grass absent. All nests collected contained some lining material.

The 1974 results for type of nest lining material indicated that individual nest lining components and total weight of lining material as affecting the flea populations. In the regression analysis for Leicestershire 1978/79 collections no significant correlations were obtained for total weight of lining material. When the nest lining components were separated, however, *C.hirundinis* was positively correlated with the weight of feathers.

As the majority of nests contained both feathers and grass in combination no comparison of flea population densities could be made on a presence/absence basis between them.

The total weights of nest lining material were compared between new and old martin occupied nests using a Mann-Whitney U test which showed no significant

Table 4:6.

Results of t-tests for *C.hirundinis*, *C.farreni* and total number of fleas between new and old martin nests Leicestershire 1977/78.

Species	Mean ± SE		Difference ± SE	t	Probability
	New	Old			
C.hirundinis	2.1274 ± 0.162	2.1317 ± 0.267	0.0024 ± 0.292	0.008	P>0.05
C.farreni	0.4597 ± 0.155	0.5428 ± 0.167	0.0830 ± 0.2348	0.35	P>0.05
Total fleas	2.1367 ± 0.162	2.1811 ± 0.243	0.4440 ± 0.2810	0.16	P>0.05

difference between the two (z= 0.4079;P>0.05), which is contrary to the results for the 1974 collection where there was significantly more lining material in the old nests.

Other Arthropods.

A similar variety of arthropods was encountered in this collection to those found in 1974. Most nests contained the larvae and pupae of Tineidae and puparia of the hippoboscid *Crataerina hirundinis*. A few nests contained Aranea, Acari and Coleoptera but all were too few for any analysis with flea populations. A Kendalls tau rank correlation between numbers of each species of flea and tineids gave a tau-value of 0.248843;P>0.05). (All the arthropods collected are listed in appendix 1).

Comparison of fleas between the three collections.

In the multiple regressions *C.hirundinis* showed a strong positive correlation with time. This indicated that there was higher numbers in the winter and spring collections. This increase in numbers could be due to larvae pupating during the winter months although very few larvae were encountered in the autumn collection. What this result does show, however, is that there is no significant decrease in the numbers of

C.hirundinis between October and March.

The numbers of *C.hirundinis* were further analysed between collections using a one-way analysis of variance. No significant difference was obtained indicating that mortality is not having a major effect on overwintering fleas, at least until March ($F=3.3846_{2,22}$; $P>0.05$). In the nests treated with ethyl acetate prior to collection the majority of fleas were contained in cocoons or were in the process of breaking out of them (see Plate 7). Presumably the disturbance caused by the introduction of the ethyl acetate soaked cotton wool was sufficient to cause emergence. This shows that the vast majority overwinter in their cocoons. This agrees with observations on other species of bird fleas for example *C.gallinae* and *C.s.styx* (Bates 1962).

House sparrow occupied nests.

Two of the five nests which had been occupied by sparrows contained fleas: in both cases 1♂ *C.hirundinis*. The low numbers of fleas in these nests is more dramatic than in the 1974 data and, despite the small sample, is a further indication that the presence of sparrows has a deleterious effect on the populations of martin fleas.

In the 1974 data a significant increase in the amount of lining material was found in sparrow occupied nests compared to all the martin nests. In this

collection it was surprising to find one sparrow occupied nests with no lining material although the other four nests appeared to have more lining material than the martin nests. A Mann-Whitney U test confirmed that there was a significant increase overall in the sparrow nests. The results are given in Table 4:7.

4.2.3 Discussion

This collection, although much smaller than that of 1974, shows some similarities. *C.hirundinis* was again the most abundant species but *C.farreni was* the next most abundant and only a very few *C.rusticus* were recorded. In the 1974 data, the abundance of these last two was reversed. Comparing the numbers of *C.hirundinis* between 1974 and 1977 using a Mann-Whitney U test showed that it was significantly more abundant in this collection than in 1974. The numbers of *C.farreni* were not significantly different between the two years but there were significantly fewer *C.rusticus* in this collection. The results of the Mann-Whitney test are given in Table 4:8.

In the 1974 data *C.rusticus* was positively correlated with *C.hirundinis* accounting for 33% of variation. With this result in mind it would seem unlikely that the low numbers of *C.rusticus* in this collection were due to the larger populations of *C.hirundinis* out-competing *C.rusticus*. This is of course unless there is a critical density at which one species

Table 4:7.

Results of the Mann-Whitney U tests for the weight of nest lining material between martin and sparrow ocupied nests Leicestershire 1977/78.

Total martin nests.

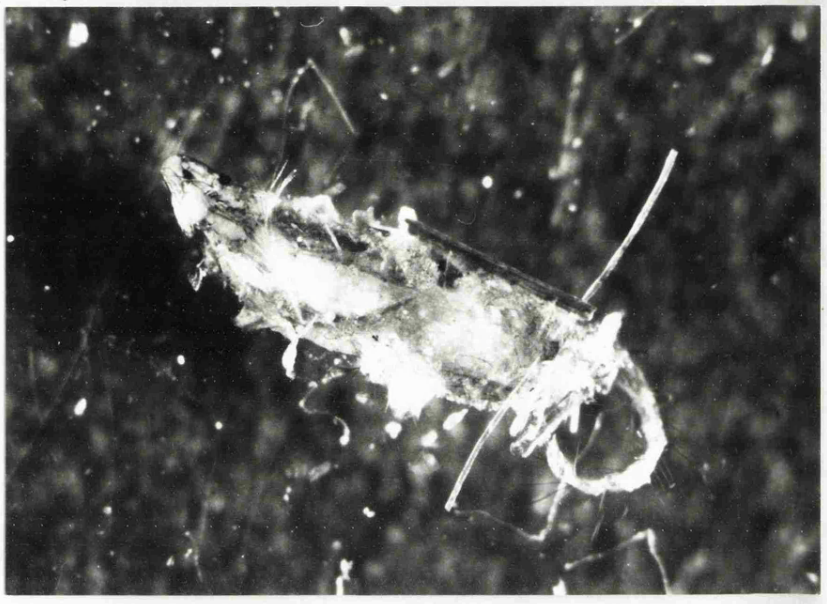
Mean Ranks		z	Probability
Martin(25)	Sparrow(5)		
14.2	22.40	1.9203	0.01<P<0.05

Table 4:8.

Comparison of flea populations between 1974 and 1977/78 collections.

Species	Mean Rank		z	Probability
	1974	1977		
C.hirundinis	69.04	101.34	3.4375	0.001<P<0.01
C.farreni	76.26	65.82	1.1348	P>0.05
C.rusticus	79.37	50.56	3.4026	0.001<P<0.01

Plate 7.



C.hirundinis killed with ethyl acetate in the act of emerging from its cocoon.

will out-compete another. Unfortunately with so few *C.rusticus* present in Leicestershire 1977/78 no analyses were possible.

In the regressions described earlier, *C.hirundinis* was positively correlated with *C.farreni*, which was also the case in the 1974 data. This again suggests that conditions suiting one species are also suitable for the others if they are in sufficient numbers to colonise a nest in the first place. This relationship further suggests that there is no inter-specific competition between them at the densities encountered. But although quite strongly correlated (R=0.4370), the correlation accounted for only 19% of variation in this collection and 13% of variation in 1974 leaving a large amount of variation unaccounted for. The very low numbers of *C.rusticus* encountered in the Leicestershire 1977/78 collection is difficult to explain. Temporal differences have been demonstrated for the same site between collections a number of years apart (Rothschild 1947 and 1963), but this was for all three species. However, whatever factors influence their distribution, the species may be affected differentially.

The nest lining materials were the same as those found in the 1974 collection. In the regression analysis *C.hirundinis* was the only species to correlate with lining material extracting feathers as the only correlate. This accounted for a significant amount of variation in the equation and, as with the 1974 data,

suggests that individual lining materials can affect the flea populations. No differences were found in the amounts of lining material between new and old nests, with also no differences in the flea populations between the two. In the 1974 collection significant differences in the amount of lining materials were found between new and old nests. In this collection although no significant difference was found between the two, on average nests older than one season had 37% more lining than those built in the year of collection.

It is easy to see that nests being used in a second season are likely to have new lining material added to that left from the previous season. This would then lead to an increase in the weight of lining material in nests older than one season.

The result of the regression with time included produced a significant positive correlation with *C.hirundinis* suggesting an increase in its numbers through the winter months. As discussed earlier this apparent increase may have been due to the few remaining larvae in the autumn pupating and adding to the number of adults found in the spring. However, such a large increase in its numbers between October and March is unlikely based on the few larvae encountered in autumn nests. The numbers of nests collected in December and March were small (6 and 5 respectively). In each of these collections there are a few nests (3 and 2 respectively) that have very high numbers. It seems likely therefore that these few nests with high numbers

were collected by chance from two suburbs of Leicester not sampled in October, and therefore the correlation between *C.hirundinis* and time is not meaningful. This result, however, does suggest that there is no significant mortality in overwintering fleas. This result was further confirmed by the comparison between the three collections by a one-way analysis of variance which showed no significant differences between the three collections.

These data suggest that large numbers of fleas survive the winter. As only a few fleas are apparently carried to new nests on the martins, old nests are likely to have larger starting populations in the spring. Assuming the fleas that survive over winter are fecund, larger autumn populations would be expected, which is not the case in this or the 1974 collection in nests older than one season. It may be possible if the life cycle is short for the populations to achieve a maximum for any one nest within one season.

The results for each species with wall texture produced no significant results for species or total number of fleas. The same result was obtained between the same surfaces in the 1974 data.

No significant difference in flea populations were found between colonial and non-colonial nests. This is in agreement with the 1974 collection and further suggests that the proximity of other nests does not influence the size of the flea populations significantly. The size of the nest would also seem to

be of no importance within the sizes recorded.

A similar variety of other arthropods was encountered in this collection to those found in 1974 (see appendix 1). But were too few in number for any analyses with the flea populations.

In this survey fewer abiotic factors appear to be influencing the flea populations compared with those in the 1974 data. The comparisons between the two collections shows that the abiotic variable nest lining material has a variable effects on the fleas which changes with time. The other abiotic variables wall texture, volume of mud, nest age, coloniality and presence of sparrows are more constant.

4.3 Cornwall 1978,1979,1980.

The data for the nests collected in the period October 1978 to October 1980 are set out in Table 4:9 which shows all the parameters recorded. The data for *C.hirundinis* and *C.farreni* are similar for each years collection. *C.rusticus* was more abundant in the first year's collection but overall is a scarce species.

As with the Leicestershire collections, multiple regression analyses were performed using all three species of flea, volume of mud and the weight of nest lining material, both as individual components and combined. These were initially tested over all three years by firstly taking as the dependent variable the total number of fleas in each nest with the abiotic variables as independent, and then each separate species

Table 4:9.

Numbers of each species of martin flea with all variables recorded for Cornwall 1978/79/80.

E= east, SE= southeast, PD= painted dash, ST= stone, PB=painted brick, NF= feathers, NG= grass, NS= straw, M= martin, C= colonial

Ch= C.hirundinis, C.f= C.farreni, Cr= C.rusticus.

Location	Dir	Eaves shape	Wall material	Volume of mud	Weight of lining			Nest age	Nest use	Colony/ non colonial	C.h		C.f		C.r	
					NF	NG	NS				♂	♀	♂	♀	♂	♀
October 1978																
Coverack	SE	2	PD	350	1	0	29	>1	M	C	0	0	10	11	1	0
Coverack	SE	2	PD	350	25	0	6	>1	M	C	0	0	5	5	0	0
Coverack	SE	2	PD	390	2	0	0	>1	M	C	0	0	5	3	1	0
Coverack	SE	2	PD	300	4	0	20	>1	M	C	0	0	12	16	5	4
Coverack	SE	2	PD	320	0	0	0	>1	M	C	0	0	38	34	30	28
Coverack	E	1	St	320	0	0	10	>1	M	C	20	18	31	82	4	16
Coverack	E	1	St	380	0	0	6	>1	M	C	3	4	14	16	4	15
Coverack	E	1	St	290	2	0	4	>1	M	C	0	0	4	14	0	4
Coverack	E	1	St	330	1	0	15	>1	M	C	1	6	22	0	0	0
Mullion	S	2	PD	360	1	0	12	>1	M	C	42	56	4	2	16	8
Mullion	S	2	PD	440	0	0	6	>1	M	C	44	28	6	8	30	24
Mullion	S	2	PD	380	1	0	16	>1	M	C	106	148	48	24	18	10
October 1979																
Coverack	SE	2	PD	300	0	0	0	1	M	C	0	0	3	9	0	0

Table 4:9 continued.

Location	Dir	Eaves	Wall material	Volume of mud	Weight of lining			Nest use	Nest age	Colony/ non colonial	C.h		C.f		C.r	
					NF	NG	NS				♂	♀	♂	♀	♂	♀
Coverack	SE	2	PD	390	0	1	0	1	M	C	38	56	2	4	0	0
Coverack	SE	2	PD	330	6	16	0	1	M	C	21	21	2	2	0	0
Coverack	SE	2	PD	360	0	11	0	1	M	C	7	9	0	2	0	1
Coverack	SE	2	PD	340	16	17	0	1	M	C	26	58	24	22	0	0
Coverack	SE	2	PD	320	3	0	0	1	M	C	11	17	4	9	1	3
Coverack	SE	2	PD	650	16	17	0	1	M	C	44	50	2	8	0	0
Coverack	SE	2	PD	400	4	7	0	1	M	C	28	32	9	32	0	0
Coverack	E	1	ST	340	2	0	0	1	M	C	10	8	18	17	0	0
Coverack	E	1	ST	360	0	0	0	1	M	C	6	6	11	8	0	0
Coverack	E	1	ST	280	0	0	0	1	M	C	54	66	174	144	3	0
Coverack	E	1	ST	320	0	2	0	1	M	C	4	1	1	0	0	0
October 1988																
Coverack	SE	2	PD	270	0	2	0	1	M	C	61	74	12	15	0	0
Coverack	SE	2	PD	360	0	2	0	1	M	C	20	28	24	31	0	0
Coverack	SE	2	PD	420	1	2	0	1	M	C	0	13	6	17	0	0
Coverack	SE	2	PD	290	1	0	5	1	M	C	1	0	1	1	0	0
Coverack	SE	2	PD	310	0	1	0	1	M	C	31	43	5	16	0	0
Coverack	SE	2	PD	420	3	0	0	1	M	C	4	6	14	0	0	0
Coverack	SE	2	PD	480	2	0	0	1	M	C	2	7	1	9	0	0
Coverack	E	1	ST	260	1	5	0	1	M	C	4	7	3	10	4	2
Coverack	E	1	ST	320	0	5	0	1	M	C	16	27	11	20	3	8
Coverack	E	1	ST	380	2	1	0	1	M	C	56	100	148	280	1	1
Coverack	E	1	ST	370	24	0	0	1	M	C	7	16	21	28	0	0

in turn as the dependent variable against the abiotic variables and the other two species.

4.3.1 Multiple regression analysis.

Total fleas over the period.

When regressed on all variables with nest lining as a whole and with the the nest linings separated the total number of fleas collected gave no significant correlations.

Individual species over the period.

The multiple regressions using each species as the dependent variable against the other two species again produced no correlations. Re-running the regressions this time with the abiotic variables included similarly revealed no significant correlation for any of the flea species.

Running the program with the nest lining components separated yielded no significant results for *C.hirundinis* or *C.farreni*. *C.rusticus* as the dependent variable correlated only with the nest lining material straw as a positive component accounting for 11.4% of variation ($R=0.3383, 0.01<P<0.05$)(Table 4:10). Multiple regression analyses using each flea species as the dependent variable against the other two species showed there to be no correlation betwen them.

The majority of nests in the Cornwall collection were taken at Coverack (32 nests). Only three

nests were collected outside of this locality and these were all at Mullion in the 1978 collection. These three nests all contained relatively high numbers of all three species of flea; it was therefore decided to re-analyse the data excluding the nests from Mullion (Table 4:11).

Total fleas over the period at Coverack.

When regressed on all variables with nest lining components combined or separated the total number of fleas collected gave no significant correlations.

Individual species over the period at Coverack.

Multiple regressons using each species of flea as the dependent variable with the other two species as independent variables yielded no correlation with *C.hirundinis*. *C.farreni* extracted first *C.rusticus* as a positive correlate accounting for 14.4% of variation ($R=0.3794, 0.01<P<0.05$) with *C.hirundinis* as the second correlate which was also positive and accounted for a further 19% of variation ($R=0.5787, 0.001<P<0.01$). *C.rusticus* when used as the dependent variable correlated first with *C.farreni* as a positive correlate accounting for 14.4% of variation with *C.hirundinis* as the second correlate extracted as a negative component and accounted for a further 13% of variation ($R=0.5262, 0.001<P<0.01$).

The lack of correlation between *C.hirundinis* and either of the other two species is slightly surprising since *C.hirundinis* is extracted as a second correlate with both. In the case of *C.farreni* both

Table 4:10. Cornwall collection 1977,1978,1980.

Results from the multiple regression analysis for each species (log) against the abiotic variables of the nest location for 35 martin occupied nests and the other two species of flea. Only the significant correlations at 5% probability or better are shown. The variables used are Weight of nest lining material(WTL), Feathers(NF), Grass(NG) and Straw(NS), Volume of mud(VM), *C.hirundinis*(C.h), *C.farreni*(C.f) and *C.rusticus*(C.r).

Whole collection.

With nest lining components combined.

No significant correlations.

With nest lining components separated.

Dependent variable	Intercept	B_1	Var_1	DF	R^2
C.rusticus	0.3318	0.2863	NS	1,33	0.1145

Table 4:11. Cornwall regressions without Mullion.

Results of the multiple regression analysis for each species (log) against the abiotic variables of the nest location for martin occupied nests and the other two species of flea. Only the significant correlations at 5% probability or better are shown. The variables used are Weight of nest lining material(WTL), Feathers(NF), Grass(NG),and Straw(NS), Volume of mud(VM), *C.hirundinis*(C.h), *C.farreni*(C.f) and *C.rusticus*(C.r).

Whole collection.

Fleas only

Dependent variable	Intercept	B_1	Var_1	B_2	Var_2	DF	R^2
C.farreni	1.2042	0.3916	C.r			1,30	0.1440
	0.8234	0.4885	C.r	0.3086	C.h	2,29	0.3349
C.rusticus	-0.1565	0.3676	C.f			1,30	0.1440
	-0.0376	0.49856	C.f	-0.2601	C.h	2,29	0.2769

With nest lining components combined.

Dependent variable	Intercept	B_1	Var_1	B_2	Var^2	DF	R^2
C.farreni	1.2042	0.3916	C.r			1,30	0.1440
	0.8234	0.4885	C.r	0.3086	C.h	2,29	0.3349
C.rusticus	-0.1565	0.3676	C.f			1,30	0.1440
	-0.0376	0.4985	C.f	-0.2601	C.h	2,29	0.2769

Table 4:11 continued.

With nest lining components separated.

Dependent variable	Intercept	B_1	Var_1	B_2	Var_2	B_3	Var_3	DF	R^2
C.hirundinis	1.27891	-0.0506	NS					1,30	0.2073
	0.56779	-0.0526	NS	0.53708	C.f			2,29	0.3445
	0.19262	-0.0415	NS	0.66517	C.f	0.0605	NG	3,28	0.5045
C.farreni	1.2042	0.3916	C.r					1,30	0.1440
	0.8234	0.4885	C.r	0.3084	C.h			2,29	0.3349
	0.83175	0.4388	C.r	0.4094	C.h	-0.0375	NG	3,28	0.4507
C.rusticus	-0.1565	0.3676	C.f					1,30	0.1440
	-0.0376	0.4985	C.f	-0.2601	C.h			2,29	0.27692

C.hirundinis and *C.rusticus* are positively correlated, and this appears to be a case of complementation. ie. to some extent low numbers of *C.rusticus* balance high numbers of *C.hirundinis* and *vice versa* to produce an overall positive relationship. This is confirmed by a positive correlation ($R=0.5168$, $0.001<P<0.01$) between *C.farreni* and the sum of the other two species.

The regressions were re-run this time with the abiotic variables included. With nest lining components combined the regressions gave the same results as the regressions without the abiotic variables included.

Re-running the regressions with the nest lining components separated and *C.hirundinis* as the dependent variable, extracted first, as a negative component, the lining material straw accounting for 20.7% of variation ($R=0.4553, 0.01<P<0.05$) with *C.farreni* second as a positive correlate accounting for 13.7% of variation ($R=0.5869$, $0.001<P<0.01$) and thirdly grass again as a positive correlate accounting for a further 15.9% of variation ($R=0.7102, 0.001<P<0.01$).

C.farreni as the dependent variable extracted first *C.rusticus* as a positive correlate accounting for 14% of variation with *C.hirundinis* as the second correlate also as a positive component accounting for a further 19% of variation. Thirdly grass was extracted as a negative component accounting for a further 11.5% of variation. *C.rusticus* as the dependent variable gave the same results as the regressions with only the three species included.

The variable, volume of mud, was not extracted as a correlate in any of these regressions indicating that this variable is not influencing the size of the flea conmunity.

Regressions: Separate collections (1978,1979,1980). (Table 4:12).

Total fleas in individual collections.

When regressed on all variables but taking nest lining material as one variable, no correlation was obtained for any of the collections. Re-running the regressions with the nest lining components separated yielded no correlations in the 1978 and 1979 data. For the 1980 data a negative correlation with straw was extracted accounting for 40% of variation ($R=0.6332, P<0.001$). However, with only one nest containing straw in this collection the result is meaningless (Table 4:12).

Individual species.

The regression was re-run with each species of flea in turn as the dependent variable and the other species as the independent variables. With *C.hirundinis* as the dependent variable no correlations were found with the other two species in the 1978 or 1979 collections. In the 1980 collection this species was strongly correlated with *C.farreni* ($R=0.8064, P<0.001$)

accounting for 65% of variation. With *C.farreni* as the dependent variable a strong positive correlation with *C.rusticus* was found in the 1978 data (R=0.8009) accounting for 64% of variation. In the 1979 collection no correlations were obtained. In the 1980 collection this species was, as noted above, positively correlated with *C.hirundinis* accounting for 65% of variation. *C.rusticus* as the dependent variable correlated only with *C.farreni* in the 1978 collection only.

Re-running the program first with the nest lining material combined and then separated gave the same results as the regressions with just fleas except for *C.rusticus* in the 1980 collection, but with only 3 out of 11 nests containing *C.rusticus* the result is meaningless.

As with the Leicestershire 1977/78 data the regressions were re-run without the fleas as independent variables. No change in the abiotic correlates was observed. The results of the multiple regressions for the separate collections are given in Table 4:12.

4.3.2 Analysis of the other variables.

The other variables, as with the other collections, were either discontinuous or non-linear (orientation). Nests from only three directions were recorded, east (8 nests), south (3 nests all at Mullion) and southeast (13 nests). With only three directions represented and with only three buildings involved it

Table 4:12. Separate collections without Mullion.

Results of the multiple regression analysis for each species (log) against the abiotic variables of the nest location and the other two species of flea for each collection at Coverack. Only the significant correlations at 5% probability or better are shown. The variables used are Weight of nest lining material (WTL), Feathers (NF), Grass (NG), Straw (NS), Volume of mud (VM), *C.hirundinis* (C.h), *C.farreni* (C.f) and *C.rusticus* (C.r).

Just fleas

1978

Dependent variable	Intercept	B_1	Var_1	DF	R^2
C.farreni	1.0986	0.4427	C.r	1,7	0.6415
C.rusticus	1.3252	1.4489	C.f	1,7	0.6415

Nest lining components combined and separated gave the same results as the regressions with just fleas.

1979

No Correlations.

1980

C.hirundinis	0.1930	0.8568	C.f	1,9	0.6503
C:farreni	0.3492	0.7589	C.h	1,9	0.6503

1980.

With nest lining components combined.

Dependent variable	Intercept	B_1	Var_1	DF	R^2
C.hirundinis	0.1900	0.8568	C.f	1,9	0.6503
C.farreni	0.3492	0.7589	C.h	1,9	0.6503

Table 4:12 continued.

1980

With nest lining components separated.

Dependent variable	Intercept	B_1	Var_1	DF	R^2
C.hirundinis	0.1930	0.8568	C.f	1,9	0.6503
C.farreni	0.3492	0.7589	C.h	1,9	0.6503
C.rusticus	-0.0644	0.1747	NG	1,9	0.6704
Total fleas	3.2704	-0.5314	NS	1,9	0.4010

seemed of no value analysing flea populations with this variable since orientation would be confounded with buildings and location.

Similarly no analyses were performed for coloniality or nest age. All nests were colonial with all of the 1978 nests older than one year and all new in the 1979 and 1980 collections.

Nests were collected from only two types of wall material. No comparison of the flea populations were made as this variable would also be confounded with building and location.

4.3.3 Flea populations between years at Coverack.

In the Cornwall data nests were collected from two buildings at Coverack and one building at Mullion. To examine the temporal effects on flea populations they were compared between the three collections using a one-way analysis of variance excluding the Mullion data.

The analysis of variance between collections gave significant results for *C.hirundinis* and *C.rusticus*. The Student-Newman-Keuls range test showed that *C.hirundinis* was less abundant in 1978 compared with both 1979 and 1980, while *C.rusticus* was significantly more abundant in the first year. The 1979 and 1980 collections did not differ significantly in either case while *C.farreni* showed no significant change (Table 4:13).

The collections at Coverack came from two

Table 4:13.

Results of the one-way analysis of variance between years for each species and total flea numbers for all nests collected at Coverack, Cornwall.

Species	F	DF	Probability
C.hirundinis	10.1047	2,29	0.001<P<0.01
Variables		1978	1979	1980
Mean		0.3775	1.4375	1.4078
SNK			———————	
C.farreni	0.7522	2,29	P>0.05
C.rusticus	5.5695	2,29	0.01<P<0.05
Variables		1978	1979	1980
Mean		0.7439	0.1335	0.2183
SNK			———————	
Total fleas	0.0046	2,29	P>0.05

buildings 400 meters apart, a stone cottage and the lifeboat station. The analysis of variance was re-run this time comparing the flea populations between collections from the two buildings at Coverack separately (Table 4:14). No significant differences were found between collections from the stone cottage. Also no significant differences were found for *C.farreni* between collections at the lifeboat station. *C.hirundinis* was absent from the lifeboat station in 1978, therefore the 1979 and 1980 collections for this species were compared using a t-test which showed no significant difference between the means. In the lifeboat station collection no *C.rusticus* were found in the 1980 collection. The variances between 1978 and 1979 for this species and between all three collections for total number of fleas were non-homogeneous; therefore the collections for *C.rusticus* were compared using a Mann-Whitney U test and for the total number of fleas using a Kruskal-Wallis one-way analysis of variance (Table 4:14). A significant result was obtained for *C.rusticus* between 1978 and 1979 collections, the larger mean in 1978 indicating that this species was more abundant in that year's collection. However, the non-significant result for the Kruskal-Wallis test with total numbers of fleas showed that overall there was no significant difference in the total flea population between years.

To see how the flea populations differed in the same locality between nests on different buildings,

Table 4:14.

Results of the one-way analysis of variance, Mann-Whitney U test, t-test and Kruskal-Wallace one-way analysis of variance between years for each species and total flea population in nests form the stone cottage and lifeboat station at Coverack Cornwall.

One-way analysis of variance.

Stone cottage.

Species	F	DF	Probability
C.hirundinis	1.6926	2,9	P>0.05
C.farreni	0.2464	2,9	P>0.05
C.rusticus	2.0442	2,9	P>0.05
Total fleas	0.5627	2,9	P>0.05

Lifeboat station.

C.farreni	0.7343	2,20	P>0.05

t-test

Species	Mean±SE		Difference±SE	t	Probability
	1979	1980			
C.hirundinis	1.431±0.2583	1.312±0.2368	0.1887±0.3504	0.33	P>0.05

Table 4:14 continued.

Mann-Whitney U test.

Species	Mean Rank		z	Probability
	1978	1979		
C. rusticus	11.50	5.50	2.6396	0.01<P<0.05

Kruskal-Wallis one-way analysis of variance.

Species	Mean Rank			Chi-square	Probability
	1978	1979	1980		
Total fleas	18.29	17.75	17.95	0.0171	P>0.05

the data were analysed further by comparing the population densities of each species between each building in each year using t-tests. No significant difference between the means were found for *C.farreni* in any collection (Table 4:15). The numbers of *C.hirundinis* and *C.rusticus* were not significantly different between the two buildings in the 1979 collection. *C.hirundinis* was not found in any nests taken from the lifeboat station in 1978 with *C.rusticus* absent from nests taken from this building in 1980.

Nest lining material.

The nest lining material in these collections comprised grass, feathers and straw. Other materials such as seaweed occured in a few nests but as there were only a few pieces in each case they were not considered in any analyses. In three nests, no lining was present.

The type of lining material used varied between years at Coverack. In the 1978 collection straw was present in all but two nests, feathers in all but three and grass in none while one nest contained no lining. In 1979 straw was absent, grass occured in seven nests, feathers in six and in two nests there was no lining material. In the 1980 collection feathers occured in seven nests, grass also in seven with straw in only one.

Although the lining components varied between years on comparing the total weight of lining material, using a Kruskal-Wallis one-way analysis of variance, no

Results of the t-tests for each species between nests on the life boat station and stone cottage at Coverack, Cornwall in each years collection.

1978.

Species	Mean±SE		Difference±SE	t	Probability
	Lifeboat Station	Stone Cottage			
C.hirundinis	None present in nests from the lifeboat station.				
C.farreni	1.3328±0.162	1.5472±0.175	0.214±0.240	0.89	P>0.05
C.rusticus	0.7542±0.306	0.8306±0.312	0.076±0.449	0.17	P>0.05

1979.

	Mean±SE		Difference±SE	t	Probability
	Lifeboat	Cottage			
C.hirundinis	1.4313±0.258	1.4463±0.252	0.015±0.375	0.04	P>0.05
C.farreni	1.0824±0.170	1.3407±0.359	0.258±0.397	0.65	P>0.05
C.rusticus	0.1859±0.101	0.1204±0.120	0.065±0.155	0.42	P>0.05

1980.

	Mean±SE		Difference±SE	t	Probability
	Lifeboat	Cottage			
C.hirundinis	1.3125±0.237	1.5747±0.237	0.2622±0.364	0.72	P>0.05
C.farreni	1.2304±0.151	1.7050±0.330	0.4746±0.362	1.31	P>0.05
C.rusticus	None present in nests from the lifeboat station.				

significant differences were found between collections (Table 4:16).

To see if the total weight of lining material differed between the two buildings at Coverack in the same year they were compared using a Mann-Whitney U test. No significant differences were obtained between the two for 1978 and 1979. In the 1980 collection a significant difference was found between the two, with more lining material occuring in nests on the stone cottage.

The lining materials were examined further by comparing the weights of the individiual lining materials between the two buildings in the same year. In all cases no significant difference was found. It is unclear why significantly more material was used in nests on the stone cottage in 1980. The individual lining materials were the same as those for the life boat station with no significant differences in the individual weights between the two (see Table 4:17).

Other Arthropods

A similar variety of arthropods was encountered in this collection to those found in the other collections. Most nests contained a few larvae and pupae of Tineidae and puparia of the hippoboscid *Crataerina hirundinis* but all were too few for any statistical analysis (see appendix 1).

4.3.4 Discussion

The results from these collections show that over three successive years at the same locality the

Table 4:16.

Results of the Kruskal-Wallis one way analysis of variance for total weight of lining material between years at Coverack.

Mean Rank			Chi-square	Probability
1978	1979	1980		
19.56	15.45	13.64	2.1871	P>0.05

Table 4:17.

Results of the Mann-Whitney U tests for total weight and individual lining materials between nests on the lifeboat station and stone cottage Coverack for each year.

	Mean Rank		z	Probability
	Total weight			
	Lifeboat Station	Stone Cottage		
1978	5.40	4.50	0.4920	P>0.05
1979	7.88	3.75	1.8915	P>0.05
1980	4.50	8.63	0.0424	0.01<P<0.05

Individual lining materials.

1978	Mean Rank		z	Probability
	Lifeboat Station	Stone Cottage		
Feathers	6.00	3.75	1.2566	P>0.05
Grass	None			
Straw	4.90	5.13	0.1235	P>0.05

Table 4:17 continued.

Table 4:17 continued.

1979	Mean Rank		z	Probability
	Lifeboat Station	Stone Cottage		
Feathers	7.56	4.38	1.5441	P>0.05
Grass	7.75	4.00	1.7644	P>0.05
Straw	None			

1980	Mean Rank		z	Probability
	Lifeboat Station	Stone Cottage		
Feathers	5.43	7.00	0.7831	P>0.05
Grass	5.29	7.25	0.9813	P>0.05
Straw	6.29	5.50	0.7559	P>0.05

numbers of *C.hirundinis* and *C.rusticus* varied significantly but *C.farreni* and the total number of fleas did not. The results for the collections on the two buildings at Coverack show that in colonies quite close together the flea populations differ significantly. The composition and abundance of the flea populations on the stone cottage were not significantly different between years. On the lifeboat station the populations of *C.hirundinis* and *C.rusticus* differed significantly over the three years whilst *C.farreni* remained stable.

All the nests in 1978 were older than one year. The results with the data for the two buildings combined suggests that the populations of *C.hirundinis* and *C.rusticus* are affected by the age of the nest. The clearing of nests in 1978 and 1979 would mean that the next season's flea populations in new nests would be starting with fleas which the martins had carried with them. Therefore, the composition of the flea community might change from season to season. However, if that was the case it might be expected that the same would apply to both buildings which is not the case. Also one would have expected the populations of *C.farreni* to be similarly affected, which is also not the case.

One possible explanation for the greater stability in the flea populations associated with the stone cottage is that the facing of the stone to which the nests were attached was heavily weathered with many deep cracks. If a proportion of the flea population

pupated in these cracks and survived until the next spring they would be available to colonise any new nests built in the following season. (A closer inspection of the stone surface of the cottage might have yeilded evidence to support this inference). The nests collected by Dunnet & Allan (1955) in NE Scotland were from granite buildings. If the faces of these were rough and creviced part of the flea population could have been left behind when the nests were collected. In this situation it might explain the annual stability they observed in some colonies. The painted dash surface at the lifeboat station was comparatively smooth and it is unlikely that any of the flea community was left behind.

The results of the regression analyses with the three species of flea varied depending on whether the data were treated as one collection or the three years treated separately. In the data treated as one collection no relationships were found between species. When the data for Mullion were excluded from the regressions, a positive relationship was found between *C.farreni* and each of the other two species. Also in these data *C.rusticus* was positively correlated with *C.farreni* but negatively correlated with *C.hirundinis*. However, the amount of variation accounted for by the regressions was small (<20%). This suggests that overall the presence of one species is not greatly affecting the abundance of the other two at the densities recorded.

Taking the regressions for the separate years, however, produced very strong positive correlations

between *C.farreni* and *C.rusticus* in 1978 and a similar correlation between *C.hirundinis* and *C.farreni* in 1980. No correlations were obtained in the 1979 data although large populations of *C.hirundinis* and *C.farreni* were present. The lack of correlation between these two species was substantiated by using rank correlation which showed no correlation between them. The very strong positive relationships found in the other years suggests that the overall conditions were suitable for both species and that at the densities recorded were not in competition with each other. If this is the case it also suggests that the nest conditions varied over the three years.

Of the abiotic variables measured, the nest lining materials varied significantly between the collections. In the more extensive 1974 data in Leicestershire there seemed to be some interaction between the type of lining material and the fleas. The paucity of *C.hirundinis* in the 1978 collections may have been due in part to the presence of straw. This is supported to some extent by the results of the regressions with the three collections combined where *C.hirundinis* was negatively correlated with straw and positively correlated with grass. But even so these two correlates together accounted for only 30% of the variation. *C.farreni* also responded to the type of lining material and was positively correlated with grass. This also only accounted for a small part of the variation (12%) and suggests that overall the effects of

the lining material on the flea populations is relatively slight.

In the separate years collections only grass and straw were extracted as correlates with *C.rusticus* and total flea numbers respectively in the 1980 collection. However, with only 3 nests containing any *C.rusticus* and only one nest containing straw , these results are meaningless.

As in the two collections from Leicestershire (1974 and 1977) the size of the nest appears to have little effect on the flea populations. Also when the volume of mud was used as the dependant variable with the weights of the individual nest linings separated and combined no correlations were obtained. The size of the nest therefore would appear not to influence the martins in the amount of lining material they use.

In conclusion the hypothesis that a species will remain common in one area over a period of time is supported in these data by *C.farreni* only. The nearest martin nests to those at Coverack from which fleas could have been transported is not known. The nearest buildings known to support a colony of martins was at Mullion, 12km away, which supported large populations of all three species in 1978. At the request of the house owner not all of the nests were collected from this site, therefore a population of fleas would almost certainly have been available there in the spring of 1979. Even so the colonisation of fleas in any new nests at Coverack in 1979 would still have relied upon the

martins visiting these or other nearby nests.

If a proportion of the flea population was left behind in the stone facings of the cottage at Coverack this would of course have been the nearest source of fleas for the colonisation of new nests on both this building and the life boat station. In any event it would seem that a large part of the variation in the flea populations is due to chance transportation on the martins. Thereafter the populations are affected to some extent by the abiotic factors, which seem to vary from one situation to another. The often large amount of variation unaccounted for in the data is presumably due to random variation as well as to biotic or unmearsured abiotic factors.

4.4 Leicestershire 1984 and 1985.

The data for the nests collected in the period October 1984 to April 1985 are set out in Table 4:18 which shows all the parameters recorded. As with the flea data in the 1977 collection *C.hirundinis* is clearly the dominant species of the three, with *C.farreni* and *C.rusticus* second and third respectively. *C.gallinae* occured in only three nests and *C.fringillae* in one. The same variables were used in the multiple regression analysis as for the previous collections.

4.4.1 Multiple regression analysis.

Total fleas over the period.

Using the total number of fleas as the

Table 4:18.

Numbers of each species of martin flea with all variables recorded for Leicestershire 1984/85.

N= north, W= west, S= south, E= east, NW= northwest, NE= norheast, SE= southeast, B= brick, PD= painted dash, PL= plaster, NF= feathers, NG=grass, NS=straw, M= martin, S= sparrow, C= colonial, NC= non-colonial, C.h= C.hirundinis, C.f= C.farreni, C.r= C.rusticus.

Location	Grid ref	Dir	Eaves shape	Wall material	Volume of mud	Weight of lining			Nest age	Nest use	Colony/ non colonial	C.h		C.f		C.r		Date
						NF	NG	NS				♂	♀	♂	♀	♂	♀	
October 1984																		
Walcote	SP567838	W	3	B	280	0	4	0	>1	M	C	186	257	26	14	22	73	
Walcote	SP567838	W	3	B	350	0	2	0	>1	M	C	52	64	12	15	10	20	
Walcote	SP567838	W	3	B	320	1	2	0	>1	M	C	526	672	58	79	67	86	
Walcote	SP567838	W	3	B	290	1	3	0	>1	M	C	20	38	3	7	19	21	
Walcote	SP567838	W	3	B	310	0	4	0	>1	M	C	34	39	71	82	103	194	
Walcote	SP567838	W	3	B	360	1	2	0	>1	M	C	264	302	14	23	126	172	
Walcote	SP567838	W	3	B	300	1	1	0	>1	M	C	29	34	41	63	3	5	
Walcote	SP567838	W	3	B	540	1	3	0	>1	M	C	82	98	4	5	1	7	
Cosby	SP547947	W	1	PD	480	1	3	0	>1	M	C	32	47	0	0	0	0	
Cosby	SP547947	W	1	PD	580	0	2	0	>1	M	C	18	22	19	34	0	0	
Cosby	SP547947	W	1	PD	490	0	3	0	>1	M	C	45	46	5	23	0	0	
Cosby	SP548958	S	2	B	390	1	3	0	>1	M	NC	62	91	13	29	0	0	
Cosby	SP548959	S	2	B	410	0	4	0	>1	M	NC	12	32	43	64	0	0	
Cosby	SP547957	S	2	B	350	1	2	0	>1	M	NC	102	213	38	73	0	0	
Whetstone	SP556976	S	1	B	390	0	1	0	1	M	C	231	298	26	39	20	33	

Location	Grid ref	Dir	Eaves Shape	Wall material	Volume of mud	Weight of lining			Nest age	Nest use	Colony/ non colonial	C.h		C.f		C.r	
						NF	NG	NS				♂	♀	♂	♀	♂	♀
Whetstone	SP556976	S	1	B	410	0	3	0	1	M	C	143	209	7	10	89	134
Whetstone	SP556973	S	2	PD	320	1	2	0	>1	M	NC	94	134	2	16	108	152
Whetstone	SP557972	N	2	B	370	1	3	0	1	M	NC	19	39	5	17	0	0
January 1985																	
Oadby	SP631993	N	2	B	430	1	8	0	1	M	C	23	44	10	8	0	0
Oadby	SP631993	N	2	B	360	1	12	0	1	M	C	37	54	34	28	0	0
Oadby	SP622997	NW	2	B	380	2	4	0	1	M	NC	122	223	64	69	0	0
Oadby	SP632001	NW	2	PD	290	0	18	0	>1	M	NC	63	74	22	31	20	17
Oadby	SP628997	N	2	PD	450	0	19	0	>1	M	C	15	31	19	42	0	0
Oadby	SP628997	N	2	PD	420	1	3	0	>1	M	C	8	25	20	23	0	0
Oadby	SP630988	NW	2	PD	310	1	6	0	1	S	NC	1	16	0	0	0	0
Oadby	SP625998	NW	2	PD	350	2	6	0	1	M	NC	19	36	2	8	0	0
Stoughton	SK642021	W	3	PD	420	1	7	0	>1	M	C	20	21	3	9	1	2
Stoughton	SK642021	W	3	PD	380	2	22	0	>1	M	C	16	27	18	29	8	17
Leicester	SK608052	NW	1	PD	390	1	20	0	>1	M	NC	143	209	61	83	19	32
Leicester	SK608053	NW	1	PD	330	2	4	0	>1	M	NC	230	311	26	49	3	14
Whetstone	SP562978	W	2	B	460	1	10	0	1	M	NC	87	109	16	22	0	0
April 1985																	
Cosby	SP548952	S	2	B	324	2	6	8	>1	S	C	0	0	0	0	0	0
Cosby	SP548952	S	2	B	290	1	5	0	>1	M	C	164	97	63	41	0	0
Whetstone	SP559977	S	2	B	425	2	3	0	>1	M	NC	263	186	26	18	0	0
Whetstone	SP558976	S	2	B	522	5	1	19	1	S	NC	0	0	0	0	0	0
E Goscote	SK644135	E	2	B	420	0	5	0	1	M	C	94	116	9	3	0	0

Table 4:18 continued.

Location	Grid ref	Dir	Eaves shape	Wall material	Volume of mud	Weight of lining			Nest age	Nest use	Colonial/	C.h		C.f		C.r	
						NF	NG	NS				♂	♀	♂	♀	♂	♀
E Goscote	SK644135	E	2	B	335	3	0	23	1	M	C	292	216	12	10	14	10
Oadby	SP634996	SE	2	PD	295	0	6	10	>1	S	NC	2	0	0	0	0	0
St.,Harrold	SK378209	S	3	PL	535	1	1	1	>1	M	C	94	102	3	3	0	0
St.,Harrold	SK378209	S	3	PL	480	1	5	3	>1	M	C	21	19	29	27	0	0
St.,Harrold	SK378209	S	3	PL	560	1	8	1	>1	M	C	17	20	8	5	0	0
ST.,Harrold	SK378209	W	4	B	520	2	10	7	>1	M	C	221	187	33	39	1	3

dependent variable the regressions with both nest lining components combined and treated separately extracted only the volume of mud as a negative component accounting for 31% of variation ($R=0.5574; P<0.001$).

Individual species over the period.

An initial analysis using only fleas in the regression gave a strong positive correlation between *C.hirundinis* and *C.rusticus* ($R=0.4481$; $0.001<P<0.01$) accounting for 20% of variation. Re-running the program with the total lining and with *C.hirundinis* as the dependent variable extracted again only *C.rusticus* (20% of variation). When *C.farreni* was used as the dependent variable it correlated only with the volume of mud as a negative component which accounted for 12% of variation ($R=0.3501; 0.01<P<0.05$). *C.rusticus* correlated first with the volume of mud as a negative component (26% of variation, $R=0.5116; 0.001<P<0.01$), with *C.hirundinis* as the second correlate accounting for a further 10% of variation, ($R=0.6007$; $0.001<P<0.01$) as a positive component.

Re-running the regression with nest lining components separated gave the same results as the regressions with the nest linings combined, (see Table 4:19).

Regressions with individual collections.

As in the previous collections the data so far have been treated as one sample but in fact are the results of three separate collections (October 1984, January 1985 and April 1985). Adding the variable time to the regressions and re-running the program with each species of as the dependent variable gave no significant correlations with this variable. In the data for April 1985 there were too few *C.rusticus* for inclusion in the regressions.

Total fleas.

The only significant correlation extracted with the total number of fleas as the dependent variable was feathers as a positive component accounting for 64.4% of variation ($R=0.8025; P<0.001$) in the April collection.(Table 4:21).

Individual species.

Running the regressions with each species of flea as the dependent variable with the other two species as independent variables produced a significant positive correlation between *C.hirundinis* and *C.rusticus* in the October 1984 collection accounting for 33% of variation ($R=0.5727; P<0.001$). In the regressions for the January 1985 collection *C.hirundinis* was positively correlated with *C.farreni* accounting for 42% of the variation ($R=0.6469; P<0.001$)(Table 4:20). No other significant correlations were obtained.

The regressions were re-run using each species of flea as the dependent variable with the abiotic variables included with the other two species. The regressions with the weight of lining material combined gave correlations for *C.hirundinis* as the dependent variable with *C.rusticus* only in the October data as before. Similarly in the January data *C.farreni* was the only correlate and no correlations were obtained in the April data.

Using *C.farreni* as the dependent variable gave no correlations for the October data, a positive correlation with only *C.hirundinis* in the January collection and no correlations in the April data.

Re-running the program with lining materials separated gave no further correlations for any species. The results are presented in Tables 4:21.

Without fleas as independent variables.

Removing the fleas as independent variables and re-running the program with only abiotic independent variables against each species of flea in turn as the dependent variable on the three collections treated as a whole extracted the same abiotic correlates as when the fleas had been included for all three species.

4.4.2 Analysis of the other variables.

The flea populations associated with the other variables in this collection as in the previous

Table 4:19. Leicestershire 1984/1985 collection.

Results from multiple regression analysis for each species against the abiotic varaibles and the other two species of flea for 38 martin occupied nests. Only the significant correlations (P<0.005) are shown. The variables used are Weight of nestlining material (WTL), Feathers(NF), Grass(NG), and Straw(NS), Volume of mud(VM), *C.hirundinis* (C.h), *C.farreni* (C.f) and *C.rusticus* (C.r).

With fleas only as independent variables.

Dependent variable	Intercept	B_1	Var_1	B_2	B_3	Var_3	DF	R^2
C.hirundinis	1.99413	0.21056	C.r				1,36	0.20088
C.rusticus	-1.28634	0.95401	C.h				1,36	0.20088

With nest lining components combined.

C.hirundinis	1.99413	0.21056	C.r				1,36	0.20088
C.farreni	2.33650	-1.9470E-03	VM				1,36	0.12260
C.rusticus	3.08244	-5.7920E-03	VM				1,36	0.26175
	1.14880	-4.7263E-03	VM	0.69946	C.h		2,35	0.36088
Total fleas	8.1834	-9.2626	VM				1,36	0.31071

With lining components separated.

C.hirundinis	1.99413	0.21056	C.r				1,36	0.20088
C.farreni	2.33650	-1.9470E-03	VM				1,36	0.12260
C.rusticus	3.08244	-5.7920E-03	VM				1,36	0.26175
	1.14880	4.7263E-03	VM	0.69946	C.h		2,35	0.36088
Total fleas	8.1834	-9.2626E-03	VM				1,36	0.31071

Table 4:20.

Results of the multiple regression analysis for each collection from Leicestershire 1984 and 1985 for *C.hirundinis*, *C.farreni* and *C.rusticus* as the only variables.

Dependent variable	Intercept	B_1	Var_1	DF	R^2
October 1984					
C.hirundinis	1.91743	0.24046	C.r	1,16	0.32804
C.rusticus	-1.84559	1.36422	C.h	1,16	0.32804
January 1985					
C.hirundinis	0.76639	0.75962	C.f	1,10	0.41857
C.farreni	0.53915	0.55103	C.h	1,10	0.41857
April 1985					
No correlations					

Table 4:21.

Results from multiple regression analysis for the separate collections ie October, January and April Leicestershire 1984/1985. The abiotic variables are the same as those used on the data treated as one collection. Only correlations significant at 5% probability or better are shown. The variables used are Weight of nest lining material(WTL), Feathers(NF), Grass(NG), Straw(NS), Volume of mud(VM), *C.hirundinis* (C.h), *C.farreni* (C.f), and *C.rusticus* (C.r).

With nest lining components combined.

October 1984.

Dependent variable	Intercept	B_1	Var_1	B_2	Var_2	B_3	Var_3	DF	R^2
C.hirundinis	1.91743	0.24046	C.r					1,16	0.32804
C.rusticus	-1.84559	1.36422	C.h					1,16	0.32804
	0.70056	1.07361	C.h	-4.95086E-03	VM			2,15	0.48439

January 1985.

C.hirundinis	0.76639	0.75962	C.f					1,10	0.41857
C.farreni	0.53915	0.55103	C.h					1,10	0.41857

April 1985.

C.rusticus	-0.36194	0.6008	WTL					1,6	0.88364
	-1.05130	0.05515	WTL	0.82548	C.h			2,5	0.95537

With nest linings separated.

April 1985.

Total fleas	2.85209	0.81070	NF					1,6	0.64406

collections were examined using a number of statistical tests.

In this collection there was a sufficient number of nests facing a variety of directions to examine any relationship between the flea populations and the direction the nest faced. Nests from five generalised directions were collected, although of these only two nests came from an east facing wall. The numbers of each species and the total number of fleas for each direction were compared by a one-way analysis of variance. This test showed that there were no significant differences between directions for any species or the total number of fleas (*C.hirundinis*, F=1.5216; *C.farreni*, F=0.8502; *C.rusticus*, F=1.8358; total number of fleas, F=1.6263; P>0.05, DF 4,33 in all cases). This agrees with the results from the 1974 collection. These results therefore suggest that the degree of exposure of the nest site is not affecting the flea populations. No analysis of flea populations were attempted with this variable on the individual collections as relatively few nests were associated with each direction in each collection.

Nests were collected from three types of wall material brick (25), painted dash (14) and plaster (3). Two nests from each of the surfaces brick and painted dash were sparrow occupied and are omitted from the analysis. Also as only three nests came from a plaster surface they too were ommitted. The flea populations in nests collected from brick and painted dash surfaces were compared using t-tests. No significant difference

between the means was obtained for *C.farreni* nor for *C.rusticus* between surfaces. A significant result was obtained for *C.hirundinis* and for the total number of fleas which showed both to be more abundant in nests on brick surfaces to those on painted dash (Table 4:22). As with orientation the number of nests for each wall material were too few for any meaningful analysis on the individual collections.

The total number of fleas and individual species populations in each nest were then examined using t and Mann-Whitney U tests for the effects of nest age and whether the nest was colonial or non-colonial.

The t-test between new (10) and old (28) nests showed no significant differences between the means for any species or total number of fleas (Table 4:23). This agrees with results from all the other Leicestershire collections.

In this collection twentyseven nests were colonial and twelve non-colonial (+3 non-colonial but sparrow occupied). The greatest number of nests in one colony was eight from Walcote (SP567838). The other colonies comprised between two and four nests. Comparing the variances for the numbers of each species and total number of fleas between nests at Walcote with the variance for non-colonial nests, a significant difference was found for the total number of fleas only. The results are given below.

Table 4:22.

Results of the t-tests for *C.hirundinis*, *C.farreni*, *C.rusticus* and total flea population with surface texture for Leicestershire 1984/85.

Species	Mean ± SE		Difference ± SE	t	Probability
	Brick	Painted dash			
C.hirundinis	2.1222 ± 0.083	1.8018 ± 0.116	0.3468 ± 0.142	2.44	0.001<P<0.01
C.farreni	1.6518 ± 0.077	1.4600 ± 0.162	0.1918 ± 0.158	1.21	P>0.05
C.rusticus	0.8831 ± 0.202	0.7487 ± 0.254	0.1344 ± 0.336	0.40	P>0.05
Total fleas	2.4866 ± 0.070	2.1766 ± 0.109	0.3121 ± 0.129	2.41	0.01<P<0.05

Table 4:23.

Results of the t-tests for *C.hirundinis*, *C.farreni*, *C.rusticus* and total flea population between new and old nests for Leicestershire 1984/85.

Species	Mean ± SE		Difference ± SE	t	Probability
	New	Old			
C.hirundinis	2.2452 ± 0.123	2.1248 ± 0.085	0.1204 ± 0.1605	0.75	P>0.05
C.farreni	1.4750 ± 0.110	1.5896 ± 0.092	0.1146 ± 0.1685	0.68	P>0.05
C.rusticus	0.5481 ± 0.228	0.8506 ± 0.175	0.3025 ± 0.3398	0.89	P>0.05
Total fleas	2.3579 ± 0.122	2.3493 ± 0.073	0.0086 ± 0.1433	0.06	P>0.05
Weight of nest lining material					
	8.7300 ± 2.251	7.2321 ± 1.125	1.4979 ± 2.4965	0.60	P>0.05

Species	Walcote	s^2	s^2 for the twelve non-colonial nests
C.hirundinis	--	0.24113	0.13556
C.farreni	--	0.21882	0.12768
C.rusticus	--	0.37806	0.80095
Total fleas	--	0.16305	0.64628

The total number of fleas between colonial and non-colonial nests were examined further using a Mann-Whitney U test (Table 4:24). No significant differences were found for any of the flea species or the total number of fleas which confirms the results from the previous collections.

Species between collections.

A comparison was made between the three collections for each species and the total flea population using a Kruskal-Wallace one-way analysis of variance. No significant differences were found for any comparison, although the chi-square value for *C.rusticus* was very nearly significant Chi-square= 5.7638(P>0.05). This is in agreement with the Leicestershire 1977/78 results between collections. These results together imply that there is no significant reduction in the overwintering flea population.

Table 4:24.

Results of the Mann-Whitney U tests for *C.hirundinis*, *C.farreni*, *C.rusticus* and total flea population between colonial and non-colonial nests in Leicestershire 1984/85.

Species	Mean Rank		z	Probability
	Colonial	Non-colonial		
C.hirundinis	18.25	22.21	1.0209	P>0.05
C.farreni	17.85	23.08	1.3508	P>0.05
C.rusticus	20.62	17.08	0.9853	P>0.05
Total fleas	18.50	12.67	0.8165	P>0.05

Nest lining material.

The nest lining material in this collection as in the other Leicestershire collections mainly comprised feathers and grass. In eight nests straw was also present along with these materials. As these components were in combination it was not possible to examine the flea populations with individual lining materials on a presence absence basis.

The combined weights of lining materials in each nest were compared for new and old nests using a t-test. No significant differences were found implying that in this collection there had been no significant addition of lining material in second year nests ($t=0.58$ $P>0.05$).

Other Arthropods

A range of arthropods other than fleas were collected from these nests. In comparison with the other collections a similar range of taxa was encountered and are listed in appendix 1.

Sparrow occupied nests.

Although nests that were occupied by sparrows in this collection were not intentionally collected three nests in the April collection and one in January had been used or were being used by sparrows. Two of these contained a few martin fleas and the two with no

martin fleas contained only *C.gallinae* or *C.fringillae*.

The very marked reduction in the numbers of martin fleas and the presence of *C.gallinae* and *C.fringillae* is in agreement with the other collections, again indicating the deleterious effect of the sparrows on the martin flea populations.

The composition of nest lining material in these nests was the same as martin occupied nests, but as with sparrow occupied nests in the previous collections appeared in greater quantity. On comparing the weight of lining material between the sparrow and martin occupied nests using a one tailed t-test a significant t value was obtained. The higher mean in the sparrow occupied nests confirmed this impression (Martin nests mean= 7.6263$\pm$1.086, Sparrow nests mean=16.00$\pm$3.583 t=2.24 0.001<P<0.01).

4.4.3 Discussion

The results of this collection agree in part with those obtained for the other Leicestershire and the Cornwall collections, but differ on a number of points. *C.hirundinis* was again the most abundant flea with *C.farreni* the next. In the regression analyses on the whole collection *C.hirundinis* and *C.rusticus* were positively correlated although only 20% of the variation was accounted for. *C.rusticus* was found in fewer nests than *C.farreni* and at a lower density. In fact *C.rusticus* was absent in 20 of the 38 martin occupied nests. Re-running the regression taking out

nests with no *C.rusticus* resulted in the loss of the correlation between it and *C.hirundinis* (R=0.3869; P>0.05). Calculating a Kendall tau rank correlation on ranked data yielded a in agreement with the regression analysis (nests with zero *C.rusticus* included z=2.73; 0.001<P<0.01 and excluding nests without *C.rusticus* z=1.67;P>0.05). These results indicate that nests with no *C.rusticus* tend to have lower numbers of *C.hirundinis*.

Amongst the abiotic factors, the texture of the surface to which the nest was attached appears to be important for *C.hirundinis* and the total number of fleas. Both were more abundant in nests attached to brick surfaces than those on painted dash. As suggested in the earlier sections the rougher texture of the brick surface may increase the living area, but if this is the case it is not clear why the populations of the other two species are not similarly affected. Both *C.farreni* and *C.rusticus* occur in very much lower numbers than *C.hirundinis* in this collection which may be why no significant results between surface texture was obtained for them.

In the regression analyses *C.farreni*, *C.rusticus* and the total number of fleas were negatively correlated with the volume of mud in the nest wall. This is the first collection in which this variable has had any effect. The implication is that fewer fleas are found in larger nests. This result therefore does not support the hypothesis that if the living area is

increased the number of fleas will increase to fill it, as suggested for wall materials with rough sufaces. The comparison of this and other abiotic variables between collections will be considered later.

The nest lining material both as the total weight and as separate weights of the components were extracted in the April collection only. The total number of fleas was positively correlated with the lining material feathers. A response to this lining material was noted in the 1974 collection. Its presence may influence the conditions in the nest, and since it accounted for 88% of variation in the April collection, may influence survival through the winter.

The greater amount of lining material in new nests in this collection cannot be explained. In the previous collections in Leicestershire the older nests contained significantly more lining material, which might be expected if the nests were relined in their second season. However, the amount of nest lining material does not seem to be affecting the flea populations and there was no difference between the flea populations in nests older than one season and nests built in the season of collection.

The variables orientation and coloniality showed no significant differences for any species or total flea numbers, which is in agreement with the previous collections. This further supports the view that the position of the nest is not important to the flea populations and that there is no significant

interchange between nests in colonies.

The age of the nest again showed there to be no significant difference between new and old nests. As already discussed for the Leicestershire 1977/78 collection if all the fleas that overwinter breed in the next season larger autumn populations might be expected in older nests, which is not the case. But, as already suggested if the life cycle is short it may be possible for the populations to achieve a maximum for any one nest within one season.

The results for the sparrow occupied nests follow the same trends as the previous collections with a significant reduction in the numbers of martin flea and the appearance of both *C.gallinae* and *C.fringillae.* A significant increase in the total weight of lining material was found, but since the quantity of lining material does not seem to be affecting the populations of martin fleas to any great extent the presence of sparrows as previously discussed is having a more direct effect.

The conclusions from this collection then are very much the same as for the other collections. That is that the large amount of variation unaccounted for in the analyses is due in part to the chance transportation of the fleas by the martins. Thereafter, their populations are affected by a few abiotic factors, although these change in there importance from one collecting occasion to another. In Leicestershire *C.hirundinis* remains the most abundant species and

because of this is more likely to be transported to new nests thereby remaining the dominant species over a period of time. The populations of the other two species are more variable and fluctuate between collections in their dominance. These aspects will be considered further in the section on the comparisons between collections.

4.5 Nests on cliffs.

The data for the nests collected from cliffs at Cheedale in Derbyshire, 1979 and 1980 and Pistol Cove in Cornwall 1979 are set out in Table 4:25 which also shows all the parameters recorded. Only a few of the abiotic variables used in the analyses of the flea populations in nests collected from house eaves could be used on these data; those used were the weight of the various lining materials and the relative humidity of the nest on collection. Other abiotic variables that could be applied to nests on cliffs such as orientation, volume of mud, colonial or non-colonial and nest age were not used for the following reasons. All the nests at Cheedale were on a north facing cliff and at Pistol Cove all nests faced southwest. Nests on cliffs are often inaccessible for hand-collecting and therefore have to be knocked down with much loss of the mud wall, making a meaningful measure of the mud wall of the nest impossible. It is possible that, because of this loss some of the fleas were also lost, but, since the vast

Table 4:25.

Data from nests collected from cliff nests at Cheedale, Derbyshire and Pistol Cove, Cornwall. C.h= *C.hirundinis*, C.f= *C.farreni*, C.r= *C.rusticus*, F= Feathers, G= Grass (g).

Nest	C.h♂	*C.h*♀	*C.f*♂	*C.f*♀	*C.r*♂	*C.r*♀	F	G
Cheedale 1979								
1	4	20	72	166	0	0	1	6
2	8	16	0	6	1	0	1	6
3	0	1	0	7	0	0	2	5
4	0	1	0	1	0	0	1	4
5	4	9	5	17	1	3	1	3
6	0	0	19	24	0	0	2	1
7	0	0	9	13	22	13	0	4
8	0	0	7	19	14	3	2	4
9	4	3	6	4	2	3	0	8
10	6	9	12	16	3	4	0	9
11	23	29	27	31	2	4	1	8
Cheedale 1980								
12	3	5	61	157	2	13	0	6
13	14	20	26	60	0	0	1	6
14	0	0	23	36	7	26	0	8
15	4	6	27	41	0	4	0	4
Pistol Cove 1979								
1	18	0	138	168	186	152	1	2
2	0	0	0	0	2	5	1	5
3	12	60	48	61	378	396	2	3
4	0	0	40	80	115	130	0	6
5	0	0	124	262	423	436	2	3

bulk of the fleas in nests from eaves were in the nest lining material the loss on collection from cliff nests was considered negligible. It should be noted, however, that in nests from eaves because they were collected by hand the fleas had time to emerge from their cocoons which may have made a difference to where, on examination, they were in the nests. All the nests collected from these cliffs were close together, and thus were all classed as being in a colony. Lastly the ages of the nests could not be determined as, unlike nests on houses, there was no 'householder' to ask how long the nest had been there or when it was last used by martins.

The most abundant species at Cheedale was *C.farreni* which occured in all fifteen nests (range 1-238). *C.hirundinis* was the next most abundant occurring in eleven nests (range 1-52) with lastly *C.rusticus* occuring in ten nests (range 1-35). None of the nests collected appeared to have been used by sparrows (enlargement of the entrance hole, extra lining material) but in one nest 2♂1♀ *C.gallinae* occurred.

The nests from Pistol Cove in Cornwall are clearly dominated by *C.rusticus* which occured in all five nests (range 7-859). *C.farreni* was found in four nests (range 109-386) with *C.hirundinis* occurring in only two nests (range 18-72). As only a few nests were collected at Pistol cove no regression analysis was attempted.

4.5.1 Cheedale multiple regression analysis.

The variables used in these regressions were *C.hirundinis*, *C.farreni*, *C.rusticus* and the weights of the lining materials, feathers and grass, both combined (total lining) and separated. As the separate years collections were small the regressions were performed on the two combined.

Total fleas.

Using the total number of fleas as the dependent variable with the lining materials combined and taken separately the analyses gave no-significant correlations.

Individual flea species.

When each flea species was used in turn as the dependent variable with the other two as the independent variables no significant correlation was obtained. Re-running the regressions adding the nest lining materials both as combined and as separate components also produced non-significant regressions for the two collections separated or combined.

4.5.2 Species between collections.

The collections at Cheedale 1980 and Pistol Cove 1979 were both small, with four and five nests respectively. It, however, seemed worthwhile to compare

the abundances of each species between the three collections. The population densities of each species were compared between collections using a Kruskal-Wallis one-way analysis of variance. Where this was significant each collection was compared with each of the other collections separately using a Mann-Whitney U test (Table 4:26).

The analyses show that the numbers of *C.hirundinis* were not significantly different between collections. *C.farreni* was more abundant at Cheedale in 1980 than in 1979, ($P<0.001$) but neither collection was significantly different from Pistol Cove nests. *C.rusticus* was significantly more abundant at Pistol Cove than in either collection from Cheedale which were not significantly different from each other (Table 4: 26).

Nest lining material between collections.

The lining materials at both sites comprised mainly feathers and grass. Other lining components occurred namely sheep's wool at Cheedale and seaweed at Pistol Cove. However, as they occurred in very small amounts in only a few nests they were not used in any analyses. A comparison of the weights of individual lining materials between the three collections using a Kruskal-Wallis analysis of variance revealed no significant differences between individual components or total weight of lining material (Chi-square=1.42 & 0.84 $P>0.05$ respectively). This indicates that the differences between the populations of *C.farreni* and

Table 4:26.

Results of the Kruskal-Wallis one-way analysis of variance and Mann-Whitney U tests for each species between Cheedale 1979, 1980 and Pistol Cove 1979.

Species	Mean Rank			Chi-square	Probabilty
	Cheedale 1979	Cheedale 1980	Pistol Cove		
C.hirundinis	10.73	11.25	9.40	0.2649	P>0.05
C.farreni	7.55	14.00	14.20	6.1038	0.01<P<0.05
C.rusticus	7.82	9.63	17.10	8.7149	0.001<P<0.01

Mann-Whitney

Species	Mean Rank		z	Probability
	Cheedale 1979	Cheedale 1980		
C.farreni	6.36	12.50	2.3521	0.001<P<0.01
	Cheedale 1979	Pistol Cove		
C.farreni	7.18	11.40	1.6439	P>0.05
	Cheedale 1980	Pistol Cove		
C.farreni	4.00	5.80	0.9798	P>0.05
	Cheedale 1979	Cheedale 1980		
C.rusticus	7.59	9.13	0.5988	P>0.05
	Cheedale 1979	Pistol Cove		
C.rusticus	6.23	13.50	2.8554	0.001<P<0.01
	Cheedale 1980	Pistol Cove		
C.rusticus	3.00	6.60	1.9596	0.01<P<0.05

C.rusticus between collections is not influenced by the type or quantity of nest lining material.

Other Arthropods.

Very few arthropods other than fleas were found in these nests. At Cheedale in both years, adult staphylinid beetles of the species *Tachyporus chrysomelinus* (Linn) were present in a few nests but no other arthropods were found. At Pistol Cove one nest contained the Isopod *Ligia oceanica* (Linn) and two nests adult Calliphoridae. All were too few for any comparison with the fleas.

4.5.3 Discussion

The results of these collections show that the populations of *C.rusticus* were significantly higher in nests at Pistol Cove compared to those at Cheedale. A number of other workers have commented on the abundance of this species in nests on sea cliffs (eg Dunnet & Allan (1955), Claassons (1965) and Roberts (1975)). As stated in the introduction sea cliffs are thought to be the wetter habitat. The humidities recorded in nests at Cheedale and Pistol Cove are compared along with those recorded from buildings in the next section.(p 96).

C.farreni was significantly more abundant in 1980 than in the 1979 collections at Cheedale but overall was found in the majority of nests on both occasions at Cheedale and at both sites. The numbers of *C.hirundinis* were not significantly different between

any of the collections but this species was generally at a low density compared to the other two species. In both Dunnet *et al.* (*op. cit.*) in Scotland and Roberts (1975) in the Isle of Man collections, *C.hirundinis* occurred in very low numbers in nests from sea cliffs. The results of the Pistol Cove collection confirms that this species does occur in nests on sea cliffs but clearly is not nearly as abundant as it is in nests on buildings.

Nests on cliffs are generally destroyed in winter, mainly by the effects of wind and rain (*pers. obs.*), therefore virtually all nests are newly built in the next season and their populations started with fleas transported on the martins. As discussed earlier it is possible, given a surface with sufficient cracks that a proportion of the flea population may pupate or shelter within them. If this is the case then these would be available in the next year and some sort of stability in the species composition could be maintained in successive years. There is a hint of this in the Cheedale data. Unfortunately the numbers of nests available for collection varied from year to year and the second year's sample from this site was small.

In conclusion it would seem that as all three species were present at both sites the conditions for fleas overall are similar to those found in nests on buildings. Having made this generlisation, however, there does seem to be a gradient of conditions with *C.hirundinis* most abundant in nests on buildings at one end and *C.rusticus* in nests on sea cliffs (based on

these and other workers data) at the other whilst *C.farreni* is equally at home in both. Nests on inland cliffs seem to be somewhere in the middle with fairly low populations of both *C.hirundinis* and *C.rusticus* but with *C.farreni* again quite abundant.

4.6 Relative humidity in nests at the time of collection.

As mentioned earlier in this chapter the relative humidity was measured in all cliff nests and all nests from the two buildings at Coverack in 1979 and 1980, as well as in seventeen of the nests collected in Leicestershire in 1977/78.

Relative humidities were recorded in nests from Leicestershire 1977/78, Coverack Lifeboat station 1979 and 1980, Coverack stone cottage 1980, Cheedale, 1979 and Pistol Cove, 1979. The number of nests with the means and ranges for relative humidity are given in Table 4:27.

To see if the moisture content in the nests differed significantly between collections the relative humidities recorded were compared using a Kruskal-Wallis one-way analysis of variance and Mann-Whitney U tests. The nests from buildings were separated into different wall textures to see if this had any bearing on the humidities recorded.

The analysis (Table 4:28) shows that there were significant differences between some of the

Table 4:27.

Mean relative humidities recorded from nests collected from buildings in Leicestershire 1977 and 1978, Coverack 1979 and 1980 and cliffs at Cheedale Derbyshire and Pistol Cove, Cornwall.

Number of nests shown in brackets.

Locality		Mean±SE relative humidity%	Range
Leicestershire 1977/78			
Brick(5)		66.66±3.22	50-80
Painted dash(12)		59.37±3.59	45-70
Cornwall			
Coverack Life boat Stn.	1979(7)	78.00±4.08	70-85
-- -- -- --	1980(7)	77.14±3.84	55-85
Coverack stone cottage	1979(5)	77.00±6.04	60-90
-- -- --	1980(4)	65.00±5.40	55-80
Pistol Cove	1979(5)	85.00±1.58	80-90
Derbyshire, Cheedale	1979(11)	69.00±3.16	45-85

Table 4:28.

Results of the Kruskal-Wallis one-way analysis of variance and Mann-Whitney U tests for relative humidity between collections from Leicestershire 1977/78, Cornwall 1978/79/80 and Pistol Cove, and Cheedale Derbyshire 1979/80.

1= Leicestershire 1977/78 brick

2= Leicestershire 1977/78 painted dash

3= Coverack stone cottage 1980

4= Coverack Lifeboat Station 1980

5= Cheedale, Derbyshire 1979/80

6= Coverack Lifeboat Station 1979

7= Coverack stone cottage 1979

8= Pistol Cove 1979

Kruskal-Wallis

		Mean Ranks							
Chi-square	Probability	1	2	3	4	5	6	7	8
23.41	0.001<P<0.01	23.00	14.13	48.88	38.57	27.17	27.64	37.90	50.80

Mann-Whitney

1	2	3	4	5	6	7	8	Z	
10.61	7.19							1.41	NS
5.39		10.63						2.25	*
6.17			11.50					2.27	*
11.50				13.10				0.54	NS
7.89					9.29			0.58	NS
6.39						9.50		1.35	NS
5.06							11.90	2.96	**

Table 4:28 continued.

1	2	3	4	5	6	7	8	Z	
	4.69	10.13						2.51	*
	4.69		11.79					3.11	**
	8.50			13.87				1.82	NS
	6.19				10.07			1.70	NS
	5.38					9.60		1.92	NS
	4.50						11.00	2.90	**
		7.75	5.00					0.17	NS
		15.25		8.60				2.12	*
		8.50			4.57			1.89	NS
		6.13				4.10		1.12	NS
		5.50					4.60	0.15	NS
			14.71	10.00				1.62	NS
			8.93		6.07			1.30	NS
			6.14			7.00		0.41	NS
			4.50				9.30	2.34	*
				11.43	11.64			0.07	NS
				9.67		13.00		1.11	NS
				8.50			16.50	2.67	**
					5.57	7.70		1.06	NS
					4.43		9.40	2.40	*
						4.90	6.10	0.67	NS

N.S= not significant

* = 0.01<P<0.05

**= 0.001<P<0.01

collections. The humidities recorded at Pistol Cove were significantly higher than nests in all the other collections except for the Coverack 1980 stone cottage collection. The nests from Cheedale were not significantly different from any of the nests from buildings. In the nests from buildings both the collections from brick and painted dash surfaces in Leicestershire 1977/78 had significantly lower humidities than those recorded on both buildings at Coverack in 1980 but not from those recorded for these sites in 1979. The two Leicestershire samples were not significantly different from each other.

The number of nests for which humidity was recorded was small and represents the moisture content of the nests at the time of collection. What may be important from the fleas point of view is how the moisture content changes throughout the year. Fleas, particularly at the pupal stage, are vulnerable to dessication (Humphries 1967) therefore some minimal moisture content is required for further development. Presumably too high a humidity would also be detrimental encouraging fungal and bacterial growth. The humidities recorded at the time the nests were collected would be affected by the ambient conditions, particularly if some nests were collected in months with a high rainfall.

In the data for relative humidity collected at Thurnby, Leicestershire (see chapter 2) the relative humidity in unoccupied nests was close to ambient. As weather conditions varied from one locality to the next

and from one year to another the climate preceding the collection of the nests may be relevant. The weather conditions for the month and preceding month in which the nests were collected was obtained from Bracknell meteorological station for Leicestershire 1977, Derbyshire 1979 and Cornwall 1978,1979 and 1980. The climate for these localities during the martin breeding season has not been considered as the data from Thurnby indicate that the micro-climate in occupied martin nests is independent of the ambient. The data for the September and October in each locality are summarized in Table 4:29.

Comparing these data for each locality shows that the wettest conditions occurred for the collections for Cornwall 1979 and 1980 and Derbyshire 1979 with the lowest in Leicestershire. Comparing these data with the humidities obtained from the nests suggests that they were indeed affected by the ambient conditions in so far as Leicestershire had the lowest rainfall and lowest nest humidities. Clearly however, within a locality differences can occur between sites even though they are subject to very similar weather conditions. Although the data from Thurnby shows that the micro-climate in the nest is independent of the ambient conditions this may not be true for nests in more exposed places such as cliffs, which may truly be wetter throughout the martin breeding season.

Comparing the data for each species of flea in the collections where humidity was measured

Table 4:29.

Weather conditions prevailing in the preceding month and month of collection of nests where relative humidity was recorded.

Locality	Month/Year	Temperature		Rainfall	Mean Wind Speed
		Mean Max	Mean Min	(mm)	(Km h-1)
Leic.	Sept 1977	16.7	8.9	18	10.74
--	Oct 1977	14.5	7.1	27	10.00
Cornwall	Sept 1979	16.4	12.5	37	16.66
--	Oct 1979	15.0	10.8	106	18.89
Cornwall	Sept 1980	17.1	12.4	67	20.00
--	Oct 1980	13.2	8.7	117	21.85
Derby	Sept 1979	16.1	10.9	53	10.74
--	Oct 1979	14.8	9.8	102	11.66

C.rusticus is very obviously more abundant in nests from Pistol Cove than in any other collection. The population densities of each species were compared between these collections using a one way analysis of variance and SNK range test. The results (Table 4:30) show that *C.hirundinis* was significantly more abundant in the two Leicestershire 1977 samples than those from Cheedale or Pistol Cove but were not significantly different from any other collection or from each other. *C.farreni* was significantly more abundant in nests from Pistol Cove, Cheedale and Coverack stone cottage 1980, than in the two Leicestershire collections; no other difference was significant. *C.rusticus* was significantly more abundant in nests from Pistol Cove than in any other collection. This species was also more abundant in the nests from Cheedale than in all the nests from buildings although not significantly so. In the data for brick and painted dash for Leicestershire 1978/79 and Coverack painted dash 1980 there was insufficient numbers of *C.rusticus* for inclusion in the analysis.

Relating these results to those for humidity supports the view that sea cliff sites are wetter habitats and seem to provide more favourable conditions for the development of *C.rusticus*. However, the humidity results for Pistol Cove were not significantly different from those recorded from nests on the stone cottage, Coverack in 1979 where only one nest contained any *C.rusticus* and then only three individuals. Further the populations of this species were not significantly

Table 4:30.

Results of the one-way analysis of variance and SNK test for *C.hirundinis*, *C.farreni* and *C.rusticus* between collections where relative humidity was measured.

1= Leicestershire 1978/79 brick

2= Leicestershire 1978/79 painted dash

3= Coverack stone cottage 1980

4= Coverack lifeboat stn 1980

5= Cheedale

6= Coverack lifeboat stn 1979

7= Coverack stone cottage 1979

8= Pistol Cove

Species	F	DF	Probability
C.hirundinis	6.0227	7,48	P<0.001

	5	8	4	6	7	3	1	2
Mean	0.62	0.78	1.31	1.42	1.44	1.57	2.04	2.19
SNK								

Species	F	DF	Probability
C.farreni	4.09	7,48	0.001<P<0.01

	2	1	6	4	7	5	3	8
Mean	0.55	0.61	1.08	1.23	1.34	1.48	1.70	1.87
SNK								

Table 4:30 continued.

Species	F	DF	Probability
C.rusticus	20.6360	4,31	P<0.001

	7	6	3	5	8
Mean	0.12	0.14	0.60	0.65	2.32
SNK	_____				

different between the combined collections from Cheedale and Pistol Cove but Cheedale had a significantly lower moisture content than Pistol Cove. These results taken in conjunction with the determinations of relative humidity (page 96) would suggest that the amount of moisture in the nest is influencing the flea populations.

4.6.1 Nest lining material and relative humidity.

It is possible that the amount of each type of nest lining material in a nest could influence the relative humidity or moisture level. The basic types of lining material was the same in all nests (feathers and grass). To see if the amounts of these materials correlated with the relative humidity their weights were compared with the measured relative humidities in each nest using a Kendall tau rank correlation. As feathers occured rather spasmodically in the nests only the weights of grass and the total weight of lining material were used in the test.

The results, given below show that there is no correlation between the amount of grass or total weight of lining material and the relative humidity.

Results of the Kendell tau rank correlation between lining materials and relative humidity.

Grass z= 1.21452, total weight of lining material z= 1.78858.

4.6.2 Discussion

The results show that nests from Pistol Cove had the highest relative humidity of the three sites at the time at which the nests were collected. This, tends to support the hypothesis that sea cliffs are the wettest of the three major habitats which in turn seems to favour *C.rusticus*.

Amongst nests on buildings it is clear that the amount of moisture can vary from year to year as was the case at the Coverack stone cottage between 1979 and 1980. The low numbers of *C.rusticus* at this site in both 1979 and 1980 indicates that relative humidity is not the only factor influencing this species.

The populations of *C.hirundinis* were significantly higher in the Leicestershire collections compared to all the other collections. The relative humidity in the Leicestershire collections were significantly lower than those recorded on both buildings at Coverack in 1980 but not to those recorded from the same buildings in 1979 or from Cheedale. Some *C.hirundinis* occurred in nests from Pistol Cove, the wettest locality, therefore any variation in the numbers of this species is unlikely to be related to the moisture content of the nest.

The populations of *C.farreni* were most abundant in nests from the two cliff sites and from the stone cottage at Coverack in 1980. The humidities recorded for the two Cornish sites were significantly

higher than those recorded at the other sites, but those at Cheedale were no different from any of the buildings. This would again indicate that the amount of moisture within the ranges recorded are not directly affecting the flea populations of this species.

In conclusion the analyses of these data suggest that humidity is controlled by the specific conditions prevailing at any site. This in turn suggests that sea cliffs are exposed to wetter conditions than buildings even if they are quite close to the sea. This may be because the sea at high tide comes up to the base of the cliff and the nests above are subjected to spray carried on updraughts. At Coverack the nests were on the side of the buildings facing the sea which at high tide would only be 30 metres away. At times of gales they may be drenched with spray which may have been responsible for the higher humidity readings recorded at the stone cottage in 1980. Salt is hygroscopic, therefore, salty sea spray on nests may also operate to increase the moisture content of the nest. The nests on the lifeboat station although also facing the sea were afforded some protection by a substantial weatherboard.

While the moist conditions are not deleterious to *C.hirundinis* or *C.farreni* the moister conditions appear to favour *C.rusticus*.

4.7.1 Comparison between collections.

Leicestershire (martin fleas).

Taking the whole of Leicestershire as one geographic locality the individual populations and total species densities were compared between the collections made in 1974, 1977/78 and 1984/85 using a Kruskal-Wallis one-way analysis of variance . Significant differences were obtained for each species and the total number of fleas. To discover which of the collections differed significantly from one another the flea populations in each collection were compared with each of the other collections in turn using a Mann-Whitney U test (see Table 4:31).

The numbers of *C.hirundinis* were significantly smaller in 1974 than both 1977 and 1984 but were not significantly different between 1977 and 1984.

The numbers of *C.farreni* were significantly smaller in the 1984 collection than in the other two collections which did not differ significantly.

Significantly fewer *C.rusticus* occurred in the 1977 collection than in the other two collections which did not differ significantly.

In the analysis with total flea densities significantly fewer were found in 1974 than in either 1977 or 1984 but these two did not differ significantly.

The above comparisons were made taking Leicestershire as one entity, but of course each year's

Table 4:31.

Results of the comparisons for each species and total flea populations between the three major collections in Leicestershire, 1974, 1978/79 and 1984/85 using Kruskal-Wallis one-way analysis of variance and Mann-Whitney U tests.

	Mean Rank			Chi square	Probability
Year	1974	1977/78	1984/85		
Species					
C.hirundinis	79.73	121.76	119.47	23.8021	P<0.001
C.farreni	81.20	69.44	149.14	53.2104	P<0.001
C.rusticus	97.00	62.06	102.87	12.4333	0.001<P<0.01
Total fleas	79.36	113.62	126.04	25.8657	P<0.001

Mann-Whitney

Species	Mean Rank		z	Probability
	1974	1977/78		
C.hirundinis	69.04	101.34	3.4375	0.001<P<0.01
C.farreni	76.26	65.82	1.1348	P>0.05
C.rusticus	79.37	50.56	3.4026	0.001<P<0.01
Total fleas	70.02	96.52	2.8179	0.01<P<0.05

Table 4:31 continued.

Species	Mean Rank		z	Probability
	1974	1984/85		
C.hirundinis	72.69	107.91	4.0737	P<0.001
C.farreni	66.93	126.53	6.9434	P<0.001
C.rusticus	79.63	85.45	0.7221	P>0.05
Total fleas	71.33	112.29	4.7340	P<0.001

Species	Mean Rank		z	Probability
	1977/78	1984/85		
C.hirundinis	33.42	31.07	0.4988	P>0.05
C.farreni	16.62	42.12	5.4270	P<0.001
C.rusticus	24.50	36.93	3.1400	0.001<P<0.01
Total fleas	30.10	33.10	0.6674	P>0.05

collection is represented by a number of localities. In only one of these were sufficient numbers of nests collected to allow any comparison between years. This was the Parish of Oadby where the number of martin occupied nests collected was 12 in 1974, 9 in 1977/78 and 7 in 1984/85. A Kruskal-Wallis one-way analysis of variance for each species and total number of fleas between these collections gave significant results for each species but not for the total number of fleas (Table 4:32).

As before Mann-Whitney U tests were performed between pairs of collections to see which were differing significantly. This test was performed on the data for *C.hirundinis* and *C.farreni* only. *C.rusticus* was found in 10 of the nests in the 1974 collection but was present in only one nest in each of the 1977/78 and 1984/85 collections. There was therefore no point in testing these data further.

The results of the Mann-Whitney U test for *C.hirundinis* showed that it was significantly more abundant in the 1977/78 collection than either the 1974 or the 1984/85 collections; these two were not significantly different from one another. *C.farreni* was significantly more abundant in the 1984/85 than in 1974 collection but neither collection was significantly different from that of 1977/78.

4.7.2 Weight of lining material between Leicestershire collections.

The components of the lining materials in martin occupied nests were the same in each collection and comprised grass, feathers and straw. In the 1974 data a significant difference was found in the weight of lining material between nests one season old and those older than one season (Table 3:9). In the 1977/78 and 1984/85 collections, however, no significant differences were found between the two age groups although in the 1978/79 data there was 37% more lining in the more than one season old nests. To see if the amount of lining material differed significantly between collections they were compared using a Kruskal-Wallis one-way analysis of variance. A significant result was obtained from this test and the data were further analysed using Mann-Whitney U tests to compare each collection with each of the other collections in turn. The results (Table 4:33) show that there was significantly more lining material in the 1977/8 nests than in nests collected in 1974 or 1984/5. The amount of lining material in these two collections did not differ significantly.

The weights of lining material in nests from the Oadby collection were also compared between years. A significant difference was obtained from a Kruskal-Wallis one-way analysis of variance. The

Mann-Whitney U tests showed that there was significantly more lining material in the 1984 collection than in the 1974 or 1977/78 collections which were not significantly different (see Table 4:34).

The amount of nest lining material used in nests may be influenced by the prevailing weather conditions at the time of both nest building and during the martin breeding season. Jurick (1974) in Czechoslovakia noted that martins' nests taken from high elevations (*sic*) contained more lining material than those from lower elevations. If higher elevation is taken as altitude it is possible that the cooler conditions prevailing at greater altitudes are influencing the amount of lining material used. However, comparing the climate during the breeding season for Leicestershire in 1974, 1977 and 1984 (Table 4:35) both temperature and rainfall are very similar in all three years and are unlikely to account for the greater amount of lining material used in the 1977 collection. However, it should be noted that at Oadby the amount of lining material was greatest in 1984/85. Therefore, it appears that climatic conditions alone do not influence the amount of nest lining used by the martins.

The size of the nest may also influence the amount of lining material used, larger nests requiring more lining material to them than smaller ones. A t-test on log transformed data comparing the volumes of mud from nests between Leicestershire 1977/78 and 1984/85 was, however, not significant ($t=1.13$, $P>0.05$).

Table 4:32.

Results of the comparison of the populations of *C.hirundinis*, *C.farreni*, *C.rusticus* and total flea population between collections in Oadby Leicestershire 1974, 1977/78 and 1984/85 using Kruskal-Wallis one-way analysis of variance and Mann-Whitney U tests.

Kruskal-Wallis

Species	Mean Rank			Chi-square	Probability
	1974	1977/78	1984/85		
C.hirundinis	10.75	20.63	11.06	6.3552	0.01<P<0.05
C.farreni	8.58	12.75	18.25	9.4882	0.001<P<0.01
C.rusticus	16.92	8.13	8.06	10.6932	0.001<P<0.01
Total fleas	12.00	13.50	12.75	0.1500	P>0.05

Mann-Whitney

Species	Mean Rank		z	Probability
	1974	1977/78		
C.hirundinis	6.96	13.13	2.2468	0.001<P<0.01
C.farreni	7.71	10.88	1.2347	P>0.05

Species	Mean Rank		z	
	1977/78	1984/85		
C.hirundinis	10.00	4.75	2.3778	0.001<P<0.01
C.farreni	4.38	7.56	1.4462	P>0.05

Species	Mean Rank		z	
	1974	1984/85		
C.hirundinis	10.29	10.81	0.1930	P>0.05
C.farreni	7.38	15.19	2.9939	0.001<P<0.01

Table 4:33.

Results of the Kruskal-Wallice one-way analysis of variance and Mann-Whitney U tests for the weight of lining material between the Leicestershire of 1974, 1977/78 and 1984/85.

Kruskal-Wallice

Mean Rank			Chi-square	Probability
1974	1977/78	1984/85		
83.98	135.26	96.84	19.5702	0.001<P<0.01

Mann-Whitney

Mean Rank		z	
1974	1977/78		
68.26	105.18	4.0364	0.001<P<0.01

Mean Rank		z	
1977/78	1984/85		
43.08	24.71	3.8920	0.001<P<0.01

Mean Rank		z	
1974	1984/85		
77.72	91.63	1.6434	P>0.05

Table 4:34.

Results of the comparisons of nest lining weights between collections at Oadby Leicestershire, 1974, 1977/78 and 1984/85 using a Kruskal-Wallice one-way analysis of variance and Mann-Whitney U test:

Kruskal-Wallice

Chi-square	Probability
7.0021	0.01<P<0.05

Mean rank		
1974	1977/78	1984/85
10.58	7.88	17.69

Mann-Whitney

Mean Rank			z	Probability
1974	1977/78	1984/85		
9.00	7.00	---	0.7385	P>0.05
---	3.38	8.06	2.1380	0.01<P<0.05
8.08	---	14.13	2.2510	0.01<P<0.05

Table 4:35.

Temperature and rainfall data for Leicestershire May-September 1974, 1977 and 1984.

	1974			1977			1984		
	Temperature		Rainfall (mm)	Temperature		Rainfall (mm)	Temperature		Rainfall (mm)
Mean Month	max	min		max	min		max	min	
May	14.9	7.1	33	14.9	5.0	45	14.2	5.0	64
June	17.6	9.9	42	16.4	7.2	90	19.0	9.2	42
July	18.7	11.7	60	20.1	10.5	15	22.2	9.9	20
August	19.2	11.3	90	19.0	10.0	81	23.3	11.8	51
September	15.0	8.7	93	16.7	8.9	18	17.1	9.7	92

Therefore the differences in the quantity of lining material is not reflected in nest size.

4.7.3 Discussion

The results from these collections suggest that a large part of the variation in the data is due to the chance colonisation of the martin nests by the three species of flea, presumably by being carried on the martins. Having become established in a nest their populations appear to be affected by a number of factors amongst which the important ones seem to be the surface texture to which the nest is attached and the nest lining material. The effects of these, however, vary from one location to another.

The main effect that these abiotic variables have is presumably on the micro-climate. This, as demonstrated in Chapter 2, appears to be largely influenced by the martins themselves at a time when the fleas are at their most active. The quantity and type of nest lining material may also be important as a sheltering place for larvae, pupae and adults, eg. different materials may vary in the amount of protection they afford them from the activities of the martins.

The control of the nest environment by the martins may, however, only be true for nests in the comparative shelter of house eaves, as was the case with the nest environment data in Chapter 2. On the more exposed cliff sites the ambient weather conditions may be more influential, and for nests built on sea cliffs in particular the maritime environment may be exerting

an even greater influence.

Outside the martin breeding season the fleas are exposed to a much greater extent to the ambient weather conditions. Within the prevailing weather conditions in the midlands of England this does not appear to have a major reducing effect on the flea populations.

Other invertebrates in the nest which may act as predators on the fleas, as already stated, appear to be unimportant in controlling the flea populations. The presence of house sparrows using the nests as roosts leads to at least reduced martin flea populations and in many of the sparrow occupied nests sampled there was a complete absence of these fleas. The data to some extent suggest that an increase in the quantity of nest lining material in sparrow occupied nests may be exerting some influence, perhaps on the micro-climate in these nests, although disturbance by the sparrows at a time when the fleas are in a resting state may be detrimental to them. It is worth noting that Jurick (1974) in Czechoslovakia found engorged *C.hirundinis* females with mature oocytes in April before the martins had returned. The nests containing these fleas had been used by sparrows; it seems likely therefore that this species had taken a blood meal from the sparrows and was then able to maturate its oocytes. Darskaya (1964) in USSR found no reduction in the numbers of *C.hirundinis* in sparrow occupied martin nests in the autumn, but none of the fleas she examined had taken a blood meal or contained

mature oocytes. It seems therefore that the time at which the nest is taken over by sparrows is the important factor determining the fate of the 'martin fleas'. However, the evidence from these data suggests that martin fleas in nests taken over by sparrows in the autumn do not survive for any great period of time.

4.8 Ability of wall materials to retain/lose heat.

The results of the individual collections showed that the direction the nest faced was having no significant effect on the flea populations. Differences in their response to wall material, however, was noted. The likely effect of wall material and, although not significant, direction would be on nest temperatures with the wall material's ability to retain/lose heat, which to some extent may be affected by the degree of exposure (direction).

To investigate this, Grant temperature thermister probes were attached to the walls of a brick building just below the eaves out of direct sunlight. These walls faced north, south, east and west. The probes were connected to a Grant multichannel recorder and the temperature recorded every hour over a 24 hour period. This was done firstly on a day in February when cold conditions prevailed and again in June when conditions were quite warm. As flea populations were less abundant in nests attached to stone surfaces this experiment was run simaltaneously under the eaves of a stone building whose walls more or less faced in the

same directions as the brick building. Days when sunny conditions prevailed were selected in both months to see to what extent exposure of the sides of the buildings in direct sun had on the temperature under the eaves, and also to see how quickly the two different wall materials took to warm up and cool down.

The results (Table 4:36) show that in February the brick building had higher temperatures. This in part may be due to the brick building being centrally heated and the stone building not during the winter months. These differences, although small (circa $3^{o}C$), may be significant from the flea's point of view. The results for June also show small differences, but overall the means are identical, suggesting that the values in February (a difference of $3.6^{o}C$) is almost certainly due to effect of internal heating.

There was a difference between different directions in so far as south and east were warmer in the early part of the day with north and west taking longer to warm up. This is almost certainly due to the south and east facing walls being exposed to the rays of the sun in the early part of the day. Overall the north facing walls on both buildings had lower temperatures than the other directions. The upper temperatures were below those recorded for the other directions but the lowest temperatures on the north facing walls were no lower than those recorded for the other directions in February.

A comparison was made between the part of the

Table 4:36.

Means and ranges of the temperature ^{o}C with direction from brick and stone buildings.

Brick Building in February.			Brick building in June.	
Direction	Mean	Range	Mean	Range
South	7.1	3-13	16.9	12-21
North	5.8	3-10	14.1	10-20
East	6.6	3-11	16.8	11-22
West	6.7	3-12	15.0	11-20
Mean	6.5		15.7	

Stone building in February.			Stone building in June.	
Direction	Mean	Range	Mean	Range
South	3.7	0-9	16.8	12-21
North	2.5	0-7	14.2	10-19
East	3.1	0-11	16.5	11-22
West	2.5	0-6	15.1	11-22
Mean	2.95		15.6	
Ambient	3.7	-1-10	16.2	9-23

wall exposed to the sun, the temperature under the eaves and the ambient temperature on both buildings to see if one wall material transmitted heat more efficiently than the other. This was done as a spot check using a direct read Grant temperature recorder and thermister probe. The results (see below) indicate that in this situation the brick wall was slightly more efficient at transmitting heat.

Differences in temperature between brick and stone surfaces in two different situations.

	In the Sun
Brick	30^{o}_{C}
Stone	29^{o}_{C}
	Under Eaves
Brick	24^{o}_{C}
Stone	21^{o}_{C}

Air Temperature 20^{o}_{C} in both cases.

The precise way in which the flea populations are affected by the wall material is difficult to define. There would seem to be little difference between the brick and stone in their ability to absorb and retain heat at least in warmer conditions. The differences recorded between the two buildings in February, as already suggested, is probably due to the heating within the building warming the walls. Within

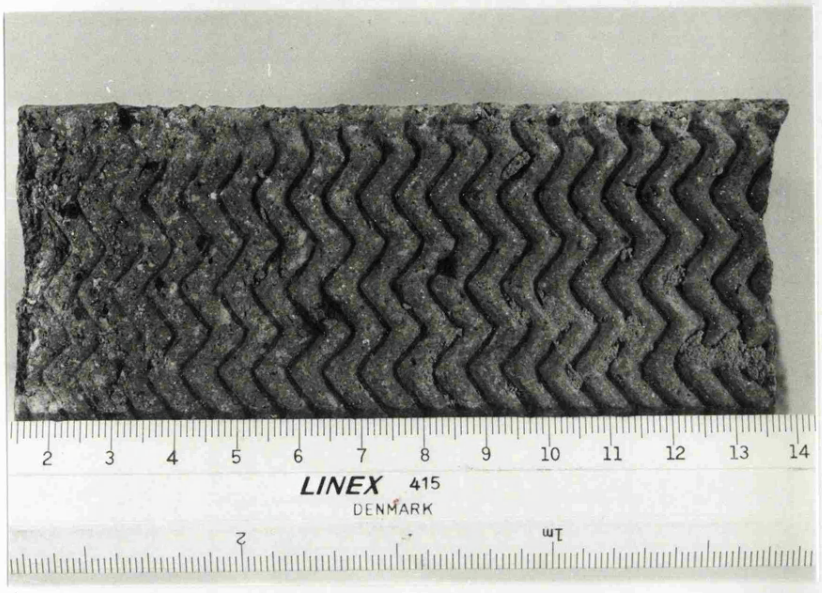
the terms 'brick' and 'stone', however, many different types occur all of which may differ to varying degrees in their ability to retain heat/moisture and also in the degree of roughness in texture. In Plate 8 the two examples of brick faces show that the degree of roughness is considerably different between the two. Therefore variation in flea numbers found in nests from one type of wall surface may be due to the variation in surface texture within the wall type. Unfortunately no records were made of the different types of brick and stone surfaces from which nests were collected, which might have permitted a more detailed analyses with the flea populations.

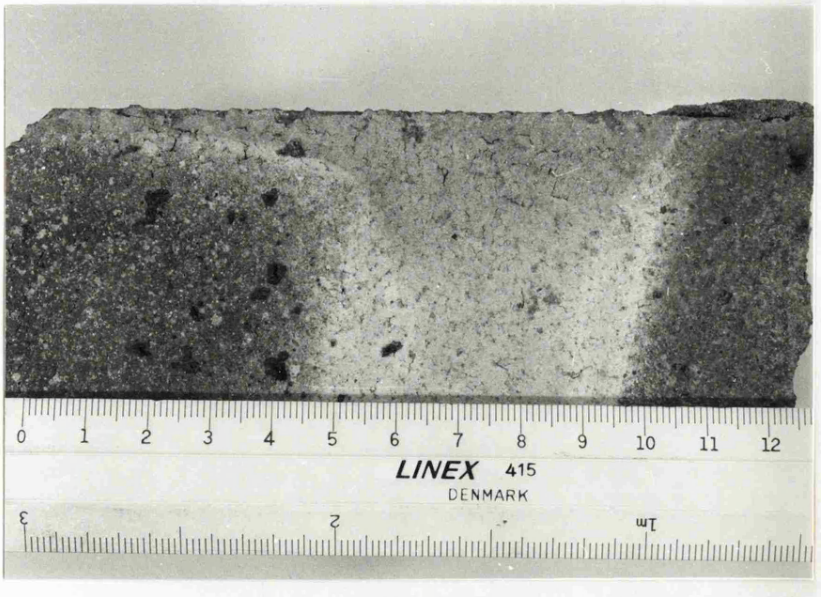
The thermal conductivity of building materials can be calculated if the density and moisture content is known (U-values)(Building Society Digest No.108, 1967). Since the moisture content is likely to vary with weather conditions and degree of exposure it is presumed that the thermal conductivity will also vary. This lends some support to the hypothesis that the micro-climate in the nest will vary with different wall materials.

Nest lining material.

The major components of the lining material regardless of where the nests were collected comprised feathers, grass, and straw, either singly or in combination. The few other materials encountered, eg., seaweed in Cornish nests and sheep's wool in Derbyshire, were in comparatively small quantities and in only the

Plate 8.





Examples of two types of brick with varying degrees of roughness.

occasional nest. As discussed earlier, the major lining components varied between years at Coverack in Cornwall as did the total weight of lining material. In Leicestershire the type of lining material was more consistent between collections but the total weight of lining differed between years.

Comparing the quantity of lining material between new and old nests produced a significant result for Leicestershire 1974 collection only with greater quantities in the older nests. As suggested earlier the most likely explanation is that in nests used a second or third time by the martins, addition of new lining material on each occasion would lead to an overall increase in the older nests. However, this result was not repeated in the Leicestershire 1977 or 1984 collections. In Cornwall the 1978 nests which were considered old contained significantly more lining material than the 1980 but not the 1979 collection.

The amount of lining material seems overall to have little effect on the fleas, for example the Leicestershire 1977 and 1984 collections had significantly larger flea populations than Leicestershire 1974 but only the 1977 collection had significantly more lining material. As discussed previously the amount of lining material used by the martins does not appear to be influenced by the climatic conditions prevailing at the time of nest building.

The volume of mud in the nest wall is an indication of the size of the lumen of the nest which

was thought may influence the size of the flea populations. This was not, however, the case in the individual collections although a weak negative correlation was obtained in the 1984/85 data, despite the range of sizes of these nests being no greater than in the other collections. Comparing the volume of mud in the nest wall between the collections, where data were available using a Kruskal-Wallis one-way analysis of variance showed no significant differences between them (Table 4:37). Therefore there are no significant differences in nest size geographically or temporally. In only one colection was any species correlated with the volume of mud in the nest wall; this was for *C.farreni* in Leicestershire 1984/85 collection as a negative correlate accounting for 12% of variation (See Table 4:19). As this was the only case overall it seems that the size of the nest is not playing a significant part in determining the size of each species' populations. The quantity of lining material in each collection did not vary significantly with the size of the nest and therefore is not influencing to any significant extent the amount of lining material selected by the martins.

In conclusion the positive correlation between *C.hirundinis* and the other two species implies that they are not competing inter-specifically at the densities recorded. Further, conditions suiting *C.hirundinis* are also suitable, at least in part for *C.farreni* and *C.rusticus*. Since *C.farreni* and *C.rusticus* are not correlated, some environmental variable may favour one

species in some nests, the other species in other nests. It therefore appears that all species are maintained below the level at which intra-specific or inter-specific competition are a major problem.

As discussed earlier the large amount of variation in the flea data is possibly caused first by the variability in the numbers transported on the martins themselves and secondly the number of broods the martins rear in one season which might determine the size of the population in the autumn. Neither of these biotic factors was known for these collections.

The indication from the data collected in autumn, winter and spring suggest that there is no significant decline in the flea populations over winter. It is not known how many of these individuals, although alive in the spring, are capable of reproduction. It is possible that the lack of difference between the autumn populations of nests that were newly built in that year and those that were more than one season old is due to similar starting populations. This could either be through very large numbers of fleas being transported to new nests by the martins or a proportion of the overwintering population not being able to reproduce, or both. Clearly these aspects require closer examination.

Table 4:37.

Results of the Kruskal-Wallis one-way analysis of variance with Log Volume of mud in the nest wall between all collections from house eaves in Leicestershire 1977, 1984 and Cornwall 1978, 1979 and 1980.

Location	Mean Rank	Chi-Square	Probability
Leicester 1977	52.54	7.6579	P>0.05
Leicester 1984	56.95		
Cornwall 1978	42.08		
Cornwall 1979	37.21		
Cornwall 1980	38.36		

Chapter 5

Emigration and overwintering in adult fleas.

5.1 Introduction

The results from the field data showed that there was no significant difference in autumn densities of fleas between nests used by martins for breeding in only one season and those used by martins for breeding in more than one season. As autumn flea populations are large it might be expected that nests used for breeding by martins in more than one season would have larger starting populations in spring in the second and subsequent years than newly built nests; this should give rise to still larger autumn populations. That this is not the case is susceptible of various explanation. These include:

1. stability being reached during or at the end of the first season.
2. the variation within the data being sufficiently great that any difference is masked.
3. large numbers of fleas being brought to new nests by the martins or that there is considerable emigration away from old nests either on the martins themselves or by some other means.
4. mortality in the overwintering populations being sufficient to give both nest categories a similar starting population in the next spring.
5. predation by either the martins or nest dwelling

arthropods being sufficiently great that the flea population does not exceed a certain maximum.

It is difficult to analyse further the first two points. The non-homogeneous nature of the data demonstrates that there is considerable variation. Also from the field data there is no evidence that predation significantly affects the flea populations, and since flea populations from nests in colonies and nests found singly do not differ significantly it also suggests that migration is not a controlling factor. The evidence from nests collected in spring indicates that mortality in the overwintering populations is low and therefore the starting population is large unless large numbers of fleas leave the nest in spring on the martins or by some other means. The results of the field data suggests that the rate of colonisation, nest lining material, microclimate and survival overwinter are all important in determining flea numbers and therefore these factors were investigated further.

5.2 Emigration.

Many species of bird fleas emigrate from old nests in order to find a new host. For example, Humphries (1963) studied migration patterns in *C.gallinae* and found that after emergence from their cocoons in the spring there is a period of time when they are negatively phototactic and positively geotactic. This keeps them together in the nest and

enables mating to occur before dispersal. After this period, which lasts from a few hours to a few days, the fleas become positively phototactic and negatively geotactic, leave the nest and move away to a vantage point where any bird activity in close proximity stimulates the fleas to jump. The main stimuli considered to initiate jumping was a change in light intensity, which would happen when a bird flies over, or an increase in temperature or vibration when the bird comes into close proximity. This type of strategy makes good sense for a species of flea whose host (eg blackbirds, starlings) builds new nests in different localities in each breeding season.

Emigration, however, has been shown for species of flea whose host returns to the same nest or nest site each year. Bates (1962) studying the sand martin flea *Ceratophyllus styx styx* Rothschild found that, before the sand martins (*Riparia riparia*) returned to the nest site in the spring from wintering in Africa, *C.s.styx* could be found at the entrances to burrows and over the face of the sand cliff face into which the burrows had been dug, even up to 33 metres away from the colony. Bates concluded that, because at least some of the returning martins dig new nests and sometimes an old colony is not recolonised but a new one dug some distance from the old nests, migration is still important for the colonisation of nests. Humphries (1969) also studied migration in *C.s.styx* and demonstrated that this species also displayed negative phototaxis after emergence from the cocoon but became

positively phototactic after 24hr and then moved towards the light at the entrance to the burrow. At the burrow entrance they then waited for a suitable stimulus, the major one for jumping being a change in light intensity and not air currents or vibration (Bates *op. cit.*, Benton & Lee 1965).

Recent studies by Hopla & Loye (1983) on *Ceratophyllus celsus celsus* in the nests of the swallow *Hirundo pyrrhonota* have shown that this species of flea moves unaided from one nest to another although the same nest may be used for breeding by *H.pyrrhonota* in successive seasons. *H.pyrrhonota* has similar habits to those of the house martin, building similarly shaped mud nests in colonies either on cliffs or on buildings. *H.pyrrhonota* like the house martin and sand martin is a migratory species; it breeds in North America and winters in South America. It is unclear why *C.c.celsus* should need to expose itself to the uncertainties of moving unaided from one nest to another. That much dispersal is not necessary in all cases is demonstrated by the study of Foster & Olkowski (1968) in California; they investigated the natural invasion of artificial swallow nests by *Ceratophyllus petrochelidoni* placed near natural nests. No fleas were caught by sticky tape traps around the artificial nests although fleas were found in the artificial nests. They concluded that these fleas had been transported to the artificial nests on the bodies of swallows visiting the nests and postulated that this is the usual method by which *C.petrochelidoni*

colonises new nests.

Little information exists on the movement of house martin fleas between nests. Darskaya (1964) found that in spring *C.hirundinis* and *C.farreni* as well as *C.delichoni* (a species not recorded in Britain) were active around the entrance holes of the nests and on the walls to which the nests were attached. Rothschild (1952) removed fleas from the bodies of martins and found that very few fleas were transported on the martins themselves. To investigate migration of house martin fleas between nests the following aspects were examined.

1.Fleas carried on the martins.
2.Fleas moving between nests by walking.
3.Fleas leaving the nests by jumping.

Fleas on martins.

To investigate this aspect bird ringing groups were contacted around Britain and asked to remove fleas prior to ringing martins routinely caught. Fleas were removed using a modified Fair Isle apparatus supplied by me. This modified apparatus consisted of a perspex cylinder 6cm in diameter and 10cm high. The open end of the cylinder was covered with a piece of oiled silk with a hole cut in its centre large enough for a martin's head to be pushed through and retained (Williamson 1954). Chloroform was pumped into the cylinder via a

tube inserted through the side near the bottom with a rubber hand pump.

From 1979 a greatly simplified design was used (Fowler *pers. comm.*). This design is based on a coffee jar, with various sizes of jar being used depending on the size of the bird. A hole is cut in the lid of the jar so as to leave a 5mm lip. A rubber diaphragm, made from a car tyre inner tube, is glued over the lid. A cross is cut into the centre of the diaphragm sufficient to allow a martin's head to pass through. The jar is lined with a tube of white filter paper and the bottom covered with a disc of the same material. The bird's head is pushed through the cross in the diaphragm and its body is suspended in the jar. The bottom of the jar is moistened with ethyl acetate and the assembly left for about 30 minutes. After this time the bird is released and the filter paper examined for fleas. The method was later described in Fowler & Cohen (1983) and is shown in Plate 9.

House martins are difficult birds to catch and are usually caught by 'Flip-netting'. Partly because of these difficulties only a very few ringing groups co-operated in my requests. The results are set out in Table 5:1 and are compared with Rothschild (1952).

5.2.1 Fleas moving between nests by walking.

To measure movement between nests by walking, sticky traps were used to surround nests on eaves. These

Table 5:1.

Fleas from the bodies of house martins.

Leicester 1977 2♀*C.hirundinis* on one juvenile house martin.

Dronefield Sewage Farm, Hertfordshire 1979. Ten house martins examined of which three had fleas.
1♀*C.hirundinis*, 1♀*C.farreni*, 1♀*C.rusticus*.

Budds Sewage Farm, Bedhampton, Hampshire, 1979. Six house martins examined of which two had fleas.
1♂*C.hirundinis*, 2♂3♀*C.hirundinis*.

Rothschild 1952 Wiltshire 1946. Seven house martins examined of which three had fleas.
5♂5♀*C.hirundinis*, 13♂12♀*C.rusticus*, 1♀*C.rusticus*.

traps comprised strips of sticky tape 2cm. wide which were stuck to the eaves to form two continuous barriers surrounding the nests (Plate 10). These tapes were then smeared with vaseline to trap any fleas going to or from the nest.

This method was thoroughly tested in the laboratory using treated tape stuck to the sides of a large enamel tray 86cm.x50cm. This tray was placed inside a larger tray containing water to catch any fleas that managed to move over the barrier. Fifty *C.hirundinis* were liberated in the inner tray which was left for one week in a constant temperature room at 26^{o}c. In fact after about two hours all but one of the fleas had become stuck to the tape and although left for one week all these fleas remained stuck to the tape.

This type of trap was placed around eight martin nests that had just been built (May 1978) on house eaves at Thurnby, Leicestershire, and left until May 1979. The traps were examined once or twice a month for fleas or any other arthropods and the tapes smeared with fresh vaseline as required. The results are given in Table 5:2.

5.2.2 Fleas jumping from the nest.

To trap fleas jumping from the outside of the nest a piece of black card measuring 10cm X 10cm smeared with vaseline and passed within 10cm to 20cm over the entrance hole to the nest. Black card was

Plate 9.

Apparatus for removing fleas and other ectoparasites.

Plate 10.

Sticky traps around nests.

Plate 11.

Sticky card being passed over a martins nest.

chosen because it had been demonstrated by Humphries (1969), that this elicited the greatest jumping response in *C.s.styx*. To test the efficiency of this trap it was passed over the entrance hole of a nest box that had been used for breeding by blue tits (*Parus caeruleus*). *C.gallinae* could be seen congregating around the entrance hole to the box. Passing the card over the hole caused *C.gallinae* to jump and many were caught in the vaseline. This then was considered a fair method for collecting fleas in similar situations ie on the outside of martins' nests. This was done on each visit to the nests at Thurnby and also to a number of nests before collection for field population data (Plate 11, it should be noted that in this plate the piece of card used was black on one side and white on the reverse side, the black side is facing the nest). In no test was any flea caught.

5.2.3 Results and discussion.

The results from the bird ringing groups, although meagre, are in agreement with the results for house martins given by Rothschild (1952).It is also worth noting that similar results have been obtained for other species of bird fleas; for example Hopla *et al.* (*op. cit.*) found very few adults of *C.c.celsus* on *H.pyrrhonota* and Fowler, Cohen & Greenwood (1983) found the same to be true for *C.gallinae* and *Dasypsyllus gallinulae gallinulae* (Dale) on *Turdus merula*. Gordeyeva (1969) working in the USSR on *C.farreni*

examined 18 mature and 36 fledglings of *Hirundo daurica* and found no adult *C.farreni* or any other flea species, although the 114 nests examined yielded 8265 adult *C.farreni*.

Very few fleas were caught on the sticky tape traps around the nests (Table 5:2), and the few that were caught were all taken in April with large numbers of the acarine *Dermanyssus hirundinis* (Plate 12).

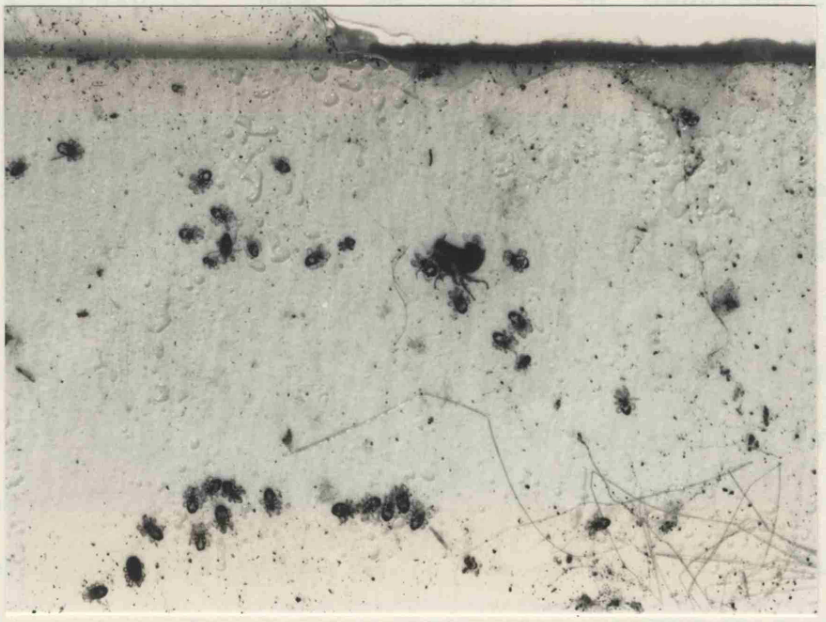
During the period that the traps were around the nests two were taken over by house sparrows after the martins had bred in the summer and had then departed in the autumn. Nests taken over in this way contained few martin fleas, although *C.gallinae* and *C.fringillae* are present. In the field data (Chapters 3 & 4) the decline of martin fleas is thought to be because sparrows introduce large amounts of coarse lining material; as a result the nest environment becomes unsuitable for martin fleas and they leave. If this were the case, then some fleas should have been caught on the tapes around sparrow occupied nests. Assuming martin fleas were present in the nest, it must be inferred that the more efficient preening of the sparrows killed the fleas unless they select nests with low flea densities. That these nests contained populations of martin fleas in the first place can only be assumed, but since all the nests had been used by martins for breeding and since substantial populations of martin fleas were found in all the other nests it seems reasonable to presume that these two also had good populations of fleas.

Table 5:2.

Results from sticky traps at Thurnby 1979.

Flea community on collection May 1979.	On the inside tape		On the outside tape
Nest 1. 36♂42♀*C.hirundinis*	0		0
25♂22♀*C.farreni*	0		0
Nest 2. 41♂49♀*C.hirundinis*	1♂2♀*C.hirundinis*		0
3♂ 8♀*C.farreni*	0		0
Nest 3. 67♂76♀*C.hirundinis*	0		0
1♂12♀*C.farreni*	0		0
Nest 4. 45♂54♀*C.hirundinis*	0		0
Nest 5. 18♂24♀*C.hirundinis*	0		0
Nest 6. 4♂ 3♀*C.gallinae*	0	Taken over by sparrows	0
Nest 7. 85♂93♀*C.hirundinis*	0		0
Nest 8. 12♂16♀*C.gallinae*	0	Taken over by sparrows	0
2♂ 4♀*C.fringillae*	0		0

Plate 12.



One *C.hirundinis* and *Dermanyssus hirundinis* caught on sticky traps.

The results of the sticky traps conflict with the observations of Darskaya (1964). On none of the many visits to martin nests throughout the year was any flea seen outside the nest. The contrast between these and Darskaya's results may be due to geographical differences affecting behaviour. Darskaya's observations were made in the USSR which does not have a maritime climate and therefore climatic conditions may affect behaviour patterns within a species. As has been pointed out by Wellington (1957, 1959 & 1960) from his work on the western tent caterpillar, *Malacosoma pluviale*, behaviour of individuals within a population can differ quite markedly and this variability inherent in populations is the raw material upon which selective pressures act. It is possible therefore that if behaviour of individuals varies within a population then the behaviour of geographically widely separated populations of the same species, given different climatic conditions might also differ.

Emigration from the nest may also be related to density or species composition or both. In the nests examined by Darskya in addition to *C.hirundinis* and *C.farreni*, the flea *C.delichoni* was present and all three were found on the outside of the nest. It is possible that the density of this species was affecting the behaviour of the other two species. The numbers of fleas in the nests surrounded by sticky traps are average compared with the rest of the field data (see Table 5:2). The only fleas caught on sticky traps at

Thurnby were around a nest containing both *C.hirundinis* and *C.farreni* in average numbers. Some of the other nests at Thurnby contained both of these species in about the same numbers which suggests that if density and species composition stimulate emigration a greater population density than those recorded is required.

No fleas were caught on the vaseline covered cards that were passed over the nest entrances. This contrasts with the activity of *C.c.celsus*. Hopla *et al. (op. cit.)* used pieces of black card of similar size to the ones used in this study, except theirs were smeared with honey. They found that when their cards were passed over the nests of *H.pyrrhonota* many *C.c.celsus* were caught on the honey. This apparently happened throughout their hosts breeding season indicating that at least part of the nest population of *C.c.celsus* are actively emigrating even under what must be considered favourable nest conditions. Similar results were obtained for *C.s.styx* by Humphries (1969) who passed bird shaped sticky cards over the entrance holes to sand martin burrows. By this method he collected many *C.s.styx* and concluded that there was considerable interchange between nests.

It is worth commenting here that Humphries (*op. cit.*) observed that in *C.s.styx* rapid head movement preceded orientation and jumping. He wondered how, with only two ocelli, the flea could distinguish the position of objects. Adult fleas, of course, do not have simple ocelli but, as shown for *C.gallinae* by Wachman (1972)

have a simplified compound eye.

The results of these studies indicate that house martin fleas, at least in the midlands of England emigrate only on the martins themselves and then only relatively few fleas are carried at one time. The starting population therefore in newly built nests is probably quite small. The need for unaided emigration in these species therefore has either been lost or never developed.

Further evidence for house martin fleas evolving to a completely nidicolous life is found in the reduction of the pleural arch, particularly in *C.rusticus*, making all three species comparatively poor jumpers. House martins frequently use old nests to roost in while on migration and often return to breed in the same nest as the previous season. The fleas therefore have no need to do anything more than sit tight in the nest. If the martins fail to return to the same nest in the next breeding season there would not be much point in emigrating from an isolated nest with no martins in the vicinity. Nests in colonies might be expected to be favourable for unaided flea movement, but even in this situation returning martins will often go into every nest in the colony and after the occupancy of each nest is established martins will visit and enter nests they are not breeding in (*pers. obs.*). House martins when they do come to their own or another nest rarely hover in front of it but alight on the outside and invariably go straight in (*pers. obs.*). This is in contrast to the

behaviour of the sand martin and cliff swallow which both tend to hover in front of the entrance to their nests and burrows, and it is at this time that *C.s.styx* and *C.c.celsus* waiting at the entrance are stimulated to jump thereby gaining the bird (Humphries 1969, Hopla & Loye 1983). These basic differences in host behaviour would seem to be reflected in the behaviour of their respective species of flea.

5.3 Overwintering and survival under various conditions.

Previous investigations into overwintering in a number of flea species indicate that survival over winter is high even when exposed to temperatures as low as $-25^{o}C$. Millar & Benton (1970) in North America investigated cold tolerance in *Orchopeas leucopus (Baker)* and *O.sexdentatus (Baker)* from small mammals and found they could survive for up to three months at temperatures of $-10^{o}C$ to $-15^{o}C$. These same authors reported that *Ceratophyllus idius* (Jordan & Rothschild), a common parasite of the purple martin (*Progne subis* (L)) in North America, could tolerate severe freezing winter temperatures and found viable adults after three weeks exposure of $-10^{o}C$ to $-20^{o}C$. Larson (1973) also examined the overwintering ability of *C.idius* in North Dakota, where *P.subis* is away from the nest for up to eight months of the year. He found after a series of experiments at two temperatures ($-8^{o}C$ & $+5^{o}C$) that this species had double the survival rate at the lower

temperature than the higher (84.4% at -8°C and 42.2% at +5°C).

More recently Schelhaas & Larson (1986) measured glycerol and glycogen levels in *C.idius* after exposure to low temperatures. They found that at temperatures as low as -6°C glycerol levels increased and glycogen levels dropped, with a reversal of the process when the fleas were warmed up. This indicated that glycogen is the major carbon source for glycerol synthesis, and that the system is reversible. Only quiescent insects have so far been found to possess glycerol. Higher levels of glycerol may reduce the risk of damage at sub-zero temperatures as higher solute concentrations have been shown to reduce the risk of damage at low temperatures (Salt 1961).

Nest temperatures in house martin nests when not occupied by martins stay within a degree or two of the ambient (see chapter 2), and freezing (sub-zero) temperatures usually last for only short periods of time in midland England.

Relative humidity has been shown to be as important as temperature for the survival of some flea species. Humphries (1967) reported that *C.gallinae* is capable of active uptake of atmospheric moisture and that successful emergence from the cocoon depends on high abdominal turgidity. Partially dessicated fleas were unable to break through the cocoon. Buxton (1948) noted similar failures at low humidity with the plague flea (*Xenopsylla cheopis* Roths.). More recently Silverman

(1982), working with *Ctenocephalides felis* (Bouche), found that adult longevity increased with increasing relative humidity and decreasing temperature within the limits of 13°C to 32°C and 50% to 92% RH.

The results from the nest collections made in the autumn and spring (chapter 4) showed that there was no significant drop in population density over winter.

5.3.1 Field studies.

To investigate the effect of different conditions on successful overwintering and survival in the absence of the host, the survival of fleas was assessed at different temperatures and humidities in several nest linings. In the ethyl acetate treated nests collected in winter and spring (see chapter 4) the vast majority of the fleas were contained in cocoons or in the process of breaking through the wall of the cocoon, (see Plate 7). This implied that the fleas stay in the cocoons as adults until stimulated to emerge. This stimulus seems to be vibration, an increase in temperature or both, and it is assumed that those fleas that died whilst breaking through the wall of the cocoon had been stimulated by the disturbance caused by the introduction of the ethyl acetate soaked cotton wool. It has been shown that other species of bird fleas overwinter in this way. For example Bates (1962), using the same ethyl acetate method, found that *C.s.styx*, *C.gallinae* and *D.gallinulae* in winter and spring were contained in the cocoon as adults.

As the fleas emerged from their cocoons when the nests were collected in the autumn all of the survival trials in the field and in laboratory trials at different temperatures and humidities had to be done on fleas not contained in cocoons. However, to compare survival between fleas contained in cocoons and those that were not, larvae collected in the autumn were maintained and pupated in similar treatments as the fleas without cocoons and were kept with the adult fleas under field conditions. The larvae of the three species of martin flea could not be distinguished, therefore they were identified as adults at the end of the trial.

5.3.2 Materials and methods.

Adult fleas collected in the autumn from vacated martin nests were anaethsetised with CO_2 and their sex and identity determined using the methods described in chapter 2.

To examine survival under natural conditions with different nest lining materials in different quantities ten replicates of twenty individuals of each sex and each species were set up separately in plastic containers covered with a fine mesh with each of the following treatments (1) 2g feathers and 10g cut grass, (2) 10g feathers and 2g cut grass, (3) 10g straw, (4) 40g straw and (5) no nest lining.

Another field trial was run with larvae to see what the survival rate was for fleas in coccons. Twenty larvae were placed into each of five replicates of each

of the same treatments as the adults and allowed to pupate. Both trials were set up in November and were left undisturbed in an outbuilding until the next May. The ambient temperature was monitored throughout the period with a Grant temperature recorder and thermistor probe (see Table 5:3). Fleas still surviving at the end of the trial were offered a blood meal on the ear of a rabbit to see how many fleas were capable of feeding after the overwintering period. The feeding of these species of flea on unusual hosts is discussed later.

5.3.3 Results.

The survival under natural conditions with different treatments of nest lining material were compared using a three-way analysis of variance on the log losses of each species and each sex in each treatment. These gave significant F values for both lining and sex in the main effects and for lining/sex in the first order interaction (Table 5:4). No significant differences were found between species.

Multiple range tests were performed on the data for lining and lining/sex. The range test for lining material showed that there was significantly greater mortality in the no lining treatment than with lining which were not significantly different from each other. The comparison between sexes showed that there was a significantly higher mortality in males than in the females. The results for the first order interaction

Table 5:3.

Mean maximum and minimum temperatures(^{o}C) and rainfall (mm) for each month during the overwintering trials with different nest lining materials (1983/1984).

Month	Mean Daily Maximum	Mean Daily Minimum	Rainfall
November	9.8	4.8	36
December	7.4	2.6	33
January	5.8	0.6	72
February	5.4	0.3	46
March	7.4	1.5	46
April	12.8	1.7	11
May	13.6	4.7	81
June	19.0	9.6	44

Table 5:4.

Results of the three-way analysis of variance on log losses for each species and sex in different nest lining treatments over winter under natural conditions.

	F	DF	P
Lining	7.004	4,299	P<0.001
Species	0.420	2,299	P>0.05
Sex	12.337	1,299	0.001<P<0.01
First order interaction			
Lining/Sex	2.463	4,299	0.01<P<0.05
Species/Lining	0.556	8,299	P>0.05
Species/Sex	1.460	2,299	P>0.05

Lining

Treatment	Mean	Range
No lining	0.68	
2gr feathers/10g grass	0.52	|
10gr feathers/2g grass	0.51	|
Straw 10g	0.47	|
Straw 40g	0.46	|

Sex

	♂	♀
Mean	0.58	0.48

Table 5:4 continued.

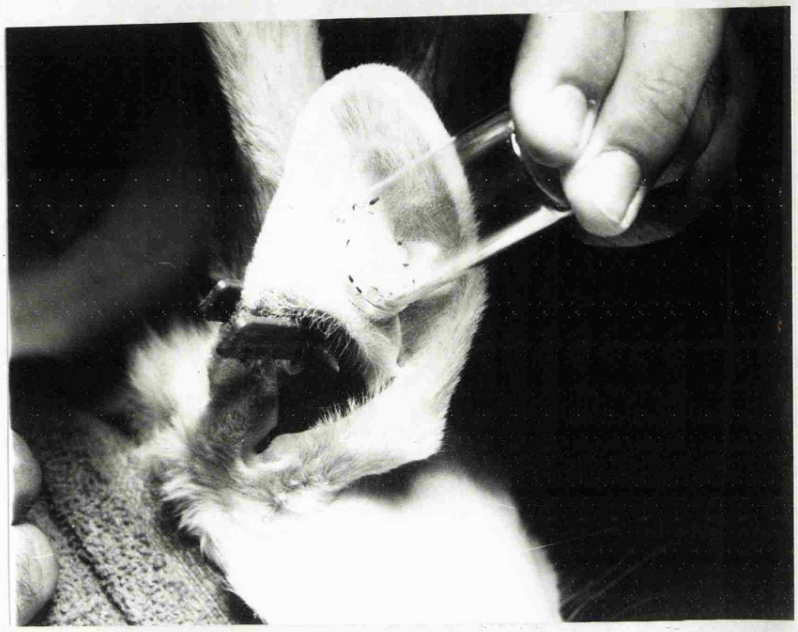
Lining/sex Treatment	Mean	Range
No lining ♂	0.72	
No lining ♀	0.65	
10g feathers/2g grass ♂	0.62	
2g feathers/10g grass ♂	0.57	
Straw 40g♂	0.55	
Straw 10g♂	0.53	
2g feathers/10g grass♀	0.45	
10g feathers/2g grass♀	0.42	
Straw 10g♀	0.40	
Straw 40g♀	0.38	

lining/sex showed that there was greater survival in the females when nest lining was present, regardless of type, than in the no lining situation. Males did less well than the females when lining was present and were not significantly different from the no lining treatment.

5.4 Feeding in adult fleas after overwintering.

It was clear from the survivors that had overwintered under natural conditions that some were more active (fitter)? than others. The number of fleas still alive in the spring therefore may not all be capable of feeding and hence of reproducing. It seemed reasonable to suppose that a measure of fitness would be given by the number of fleas that were capable of taking a blood meal. The fleas surviving from the overwintering trials were offered a blood meal on the ear of a rabbit. The rabbit was immobilised by wrapping a towel around its body and legs. The fleas were contained on the ear in an inverted glass tube held firmly in place by hand (see Plate 13), and were allowed to feed for thirty minutes. In fact all the fleas that fed did so within ten to fifteen minutes (the feeding rates of these species are discussed in chapter 8). Although adapted to living on house martins all three species will readily feed on rabbits, man and a variety of other unusual hosts. Rabbits were chosen because of the ease with which the fleas could be introduced onto the ear, contained and removed.

Plate 13.



Feeding fleas on the ear of a rabbit.

The number of fleas that had fed from each of the lining treatments was recorded and initially analysed using an analysis of covariance using the number of survivors as the covariate. This, however, was found to be no more useful than an analysis of variance on arcsin transformed data performed on the proportion fed of those that had survived.

Significant F values were obtained for species, lining and sex in the main effects and for species/lining and lining/sex but not for species/sex in the first order interaction. No second order interactions were significant.

Multiple range tests showed that significantly fewer *C.rusticus* fed than either *C.hirundinis* or *C.farreni* which were not significantly different from each other. For the lining material, the results show that significantly more fleas fed regardless of the lining material compared with the no lining treatment, and overall significantly more females fed than males. In fact 85% of females fed as against 75% males (ie. the vast majority of females took a blood meal).

In the two-way interaction of sex with lining significantly more females fed regardless of the type of lining material than males or females with no lining material, except that males in 10g of straw were not significantly different from the females. Comparison of the means for the interaction between species and lining reveals that significantly fewer *C.farreni* exposed to the no lining treatment took a blood meal than *C.farreni*

in any other treatment. The only other difference which attained significance (P=0.05) was that more *C.hirundinis* maintained in straw fed than did *C.farreni* from the 'no lining' treatment.These results are given in Table 5:5.

The results of the analysis of variance for both the losses and number of individuals fed for each species and sex suggests that the type of lining material has an effect on them. However, examining the percentage surviving and the percentage of survivors feeding in each treatment (Tables 5:6 & 5:7) shows that even in the treatments which had significantly low counts, in both cases the numbers were above 50% of the starting number, therefore nest lining appears to be having only a marginal effect. Also the effects of the lining material is variable in so far as males of one species show poorer survival in a particular material than females. For example significantly more females survived in the feathers greater than grass treatment than did males.

5.5 Mating of fleas after feeding.

The number of survivors taking a blood meal was considered to be an indication of fitness. A further test of fitness, however, was to see how many of the male fleas were capable of mating and successfully transfering sperm and of the females to receive it.

Bird fleas generally mate before taking a blood meal (Bates 1962), although they will also mate

Table 5:5.

Results of the three-way analysis of variance on the proportion fed of those that had overwintered under natural conditions in different nest lining treatments using arcsin transformed data.

	F	DF	P
Species	3.499	2,269	0.01<P<0.05
Lining	7.570	4,269	P<0.001
Sex	33.472	1,269	P<0.001
First order interaction			
Species/Sex	1.018	2,269	P>0.05
Lining/Sex	3.977	4,269	0.001<P<0.01
Species/Lining	2.124	8,269	0.01<P<0.05

Species	Mean	Range
C.farreni	64.53	|
C.hirundinis	63.82	|
C.rusticus	60.77	

Sex

	♂	♀
Mean	59.48	66.59

Table 5:5 continued.

Lining

Treatment	Mean	Range
2g feathers/10g grass	66.10	
10g feathers/2g grass	65.31	
Straw 10g	63.88	
Straw 40g	63.26	
No lining	56.64	

Sex/Lining

Treatment	Mean	Range
Straw 40g ♀	69.96	
10g feathers/2g grass ♀	69.53	
Straw 10g ♀	69.36	
2gr feathers/10g grass ♀	68.34	
Straw 10g ♂	62.84	
Straw 40g ♂	60.66	
10g feathers/2g grass ♂	58.22	
2g feathers/10g grass ♂	58.19	
No lining ♂	57.49	
No lining ♀	56.78	

Table 5:5 continued.

Species/lining Treatment	Mean	Range
C.hirundinis Straw 40g	69.37	
C.farreni 2g feathers/10g grass	68.15	
C.farreni Straw 10g	67.72	
C.hirundinis Straw 10g	67.43	
C.farreni Straw 40g	67.15	
C.farreni 10g feathers/2g grass	66.05	
C.hirundinis 10g feathers/2g grass	65.02	
C.rusticus Straw 10g	63.15	
C.hirundinis 2g feathers/10g grass	60.85	
C.rusticus 2g feathers/10g grass	60.79	
C.rusticus 10g feathers/2g grass	60.55	
C.rusticus No lining	59.94	
C.rusticus Straw 40g	59.42	
C.hirundinis No lining	56.41	
C.farreni No lining	53.55	

Table 5:6.

Percentage survival and the percentage of the survivors that fed after overwintering in natural conditions in different lining materials.

Species	Treatment	% Survivors	% survivors fed
C.hirundinis			
♂	2g feathers/10g grass	82	78
♀	2g feathers/10g grass	93	88
♂	10g feathers/ 2g grass	81	75
♀	10g feathers/ 2g grass	91	86
♂	Straw 10g	83	80
♀	Straw 10g	89	85
♂	Straw 40g	82	76
♀	Straw 40g	90	88
♂	No lining	78	68
♀	No lining	76	59
C.farreni			
♂	2g feathers/10g grass	83	66
♀	2g feathers/10g grass	90	81
♂	10g feathers/ 2g grass	83	75
♀	10g feathers/ 2g grass	89	84
♂	Straw 10g	90	77
♀	Straw 10g	91	88
♂	Straw 40g	84	82

Table 5:6 continued.

Species	Treatment	% survivors	% suvivors fed
♀	Straw 40g	91	87
♂	No lining	76	66
♀	No lining	73	66
C.rusticus			
♂	2g feathers/10g grass	84	64
♀	2g feathers/10g grass	77	79
♂	10g feathers/2g grass	83	59
♀	10g feathers/2g grass	88	85
♂	Straw 10g	83	71
♀	Straw 10g	90	82
♂	Straw 40g	85	61
♀	Straw 40g	90	82
♂	No lining	79	72
♀	No lining	74	73

Table 5:7.

Percentage survival and the percentage of the survivors that fed after overwintering under natural conditions in cocoons with different nest linings.

Treatment	% Survived	% Survivors Fed
2g feathers/10g grass	82	85
10g feathers/ 2g grass	86	82
Straw 10g	81	92
Straw 40g	87	82
No lining	87	86

Table 5:8.

Percentage males mating after overwintering and feeding under natural conditions with various lining materials.

Species	Treatment	% Mated
C.hirundinis		
♂	2g feathers/10g grass	81
♂	10g feathers/ 2g grass	79
♂	Straw 10g	86
♂	Straw 40g	76
♂	No lining	80
C.farreni		
♂	2g feathers/10g grass	78
♂	2g feathers/10g grass	87
♂	Straw 10g	81
♂	Straw 40g	82
♂	No lining	82
C.rusticus		
♂	2g feathers/10g grass	82
♂	10g feathers/2g grass	82
♂	Straw 10g	86
♂	Straw 40g	84
♂	No lining	84

quite readily when fully fed (*pers. obs.*). In these experiments it was not possible, due to the limitations of the number of fleas available for experiments, to test mating efficiency before feeding.

To test the numbers capable of copulation the males of each species in each nest lining treatment were added to the females of the same treatment. Each species from a given treatment was tested one replicate at a time in a constant temperature room at 25^{o}C under red light and observed until copulation was complete. This temperature was chosen as it was around the temperature found in the lining material in occupied martin nests. Red lighting was chosen as there is some evidence that white light has a disturbing effect on these species (see later chapter).

Within 5 min. many of the fleas had paired. As the numbers of females were always in excess of the males those that were not copulating within 10 min. were removed and placed in another container. Copulation usually lasted from between 10 and 20 min. and was the same for each species. When copulation was complete the female was removed and the males were put with the unmated females. After one hour all the females had mated. The females were then killed with ethyl acetate and the spermatheca removed, opened and examined in Insect Ringer under, X40 phase contrast, for active sperm. In all cases active sperm was present.

The males that had not mated were given another opportunity with some unfed females of the same species

from stock. None of these males had mated after several hours with the females, therefore they were judged as unfit, and would therefore not contribute to future generations. Microscopical examination of the testes of these males revealed that they all possessed active spermatozoa. Examination of the copulatory apparatus prior to dissection revealed no obvious abnormalities therefore it is unclear why these individuals did not mate.

The combined numbers of males in each treatment that had fed and copulated are given in Table 5:9. The proportions of males that mated out of those that had fed were compared between treatments using a three-way analysis of variance on arcsin transformed data. The results show that there was no significant difference between any species or lining treatment (Table 5:10) with around 50% of males of each species successfully copulating.

5.6 Overwintering of fleas in cocoons.

The fleas left undisturbed in cocoons were examined in the spring at the same time as the fleas that had overwintered without cocoons. As suspected when the larvae were set up in each treatment the adults emerging at the end of the period comprised at least two and sometimes all three species in varying numbers of species and sex. As this was the case no direct comparison could be made between these trials and those with fleas that had emerged. However, a comparison could

Table 5:9.

Number of males mating after feeding in each treatment with all ten replicates combined.

Species	Treatment	Fed	Mated
C.hirundinis	2g feathers/10g grass	129	105
- -	10g feathers/ 2g grass	123	98
- -	Straw 10g	133	115
- -	Straw 40g	126	97
- -	No lining	107	86
C.farreni	2g feathers/10g grass	111	87
- -	10g feathers/2g grass	125	109
- -	Straw 10g	140	114
- -	Straw 40g	140	116
- -	No lining	102	84
C.rusticus	2g feathers/10g grass	109	90
- -	10g feathers/ 2g grass	99	81
- -	Straw 10g	108	91
- -	Straw 40g	106	90
- -	No lining	115	97

be made between the number of fleas surviving in cocoons and those without in each treatment. As there was no significant difference between species in the trials with known numbers of each species or with sex these data were combined and compared using t-tests with the number of fleas surviving contained in cocoons. The fleas contained in cocoons were offered a blood meal in the same way as those not in cocoons, but as there were mixed sexes in these trials no measure of mating ability could be made. The species, total number surviving and number taking a blood meal in each treatment are given in Table 5:11.

The results of the t-tests (Tables 5:12 & 5:13) show that there was no significant difference between the two for any of the different lining types for either survival or feeding. There was, however, a significant difference between the two in the no nest lining treatment with significantly higher numbers surviving and feeding when contained in cocoons. It is worth noting that although not significantly different fleas in cocoons gave a greater mean number fed than those without in each treatment (see Table 5:13). It seems therefore that both the lining materials and the cocoon are providing more favourable conditions. The most likely way that they do this is by providing sufficient insulation to buffer the changes in ambient temperature or humidity or both.

Silverman (1982) working on the cat flea (*Ctenocephalides felis*) showed that there was a

Table 5:10.

Results of the two-way analysis of variance with the proportion of males mated out of those that had fed after overwintering in various treatments of nest lining material.

Main effects

	F	DF	P
Treatment			
Species	2.22561	2,132	P>0.05
Lining	0.3367	4,132	P>0.05

	F	DF	
Species/lining	0.5311	8,132	P>0.05

Table 5:11.

Species of flea emerging from cocoons kept overwinter under natural conditions in different nest lining materials and the number taking a blood meal.

Treatment 2g feathers/10g grass

Species	Fed	Total Suviving	Number fed
C.h 4 ♂4♀	4 ♂4♀		
C.f 2 ♂6♀	1 ♂5♀	16	14
C.h 2♂ 3♀	2, 2♀		
C.f 1♂ 3♀	1♂ 3♀		
C.r 2♂ 1♀	1♂ 1♀	12	10
C.h 8♂ 7♀	8♂ 6♀		
C.f 2♂ 2♀	2♂ 1♀	19	17
C.h 5♂ 5♀	5♂ 5♀		
C.f 1♂ 6♀	1♂ 6♀	17	17
C.h 0♂ 4♀	0♂ 3♀		
C.f 3♂ 7♀	1♂ 4♀		
C.r 1♂ 3♀	0♂ 3♀	18	11

Table 5:11 continued.

Treatment	10g feathers/2g grass		Total surviving	Number fed
C.h	9♂10♀	8♂ 7♀	19	15
C.f	3♂ 5♀	3♂ 5♀		
C.r	3♂ 6♀	3♂ 6♀	17	17
C.h	4♂ 9♀	3♂ 4♀		
C.r	0♂ 2♀	0♂ 2♀	15	9
C.h	6♂11♀	6♂10♀		
C.r	1♂ 0♀	0♂ 0♀	18	16
C.f	8♂ 9♀	7♂ 7♀	17	14

Table 5:11 continued.

Treatment Straw 10g		Total surviving	Number fed
C.f 4♂ 9♀	4♂ 9♀		
C.r 1♂ 3♀	0♂ 2♀	17	15
C.h 1♂ 7♀	0♂ 6♀		
C.f 3♂ 6♀	2♂ 6♀	17	14
C.h 5♂ 3♀	4♂ 2♀		
C.f 3♂ 2♀	3♂ 2♀		
C.r 3♂ 0♀	3♂ 0♀	16	14
C.h 3♂ 3♀	3♂ 3♀		
C.f 2♂ 6♀	2♂ 6♀		
C.r 4♀ 0♀	4♂ 0♀	18	18
C.f 3♂ 2♀	3♂ 2♀		
C.r 2♂ 7♀	2♂ 7♀	14	14

Table 5:11 continued.

Treatment	Straw 40g	Total surviving	Number fed
C.h 5♂10♀	3♂ 8♀	15	11
C.h 3♂11♀	2♂10♀		
C.f 1♂ 5♀	0♂ 4♀	20	16
C.h 1♂ 7♀	1♂ 5♀		
C.f 5♂ 5♀	5♂ 5♀	18	16
C.h 8♂ 9♀	7♂ 9♀		
C.r 1♂ 0♀	0♂ 0♀	18	16
C.h 5♂ 4♀	5♂ 4♀		
C.f 2♂ 5♀	1♂ 3♀	16	13

Table 5:11 continued.

		Total surviving	Number fed
Treatment no lining			
C.h 4♂15♀	4♂14♀	19	18
C.h 3♂ 3♀	3♂ 2♀		
C.f 4♂ 8♀	1♂ 5♀	18	11
C.h 4♂10♀	4♂10♀		
C.r 3♂ 1♀	3♂ 1♀	18	18
C.h 2♂ 3♀	2♂ 3♀		
C.f 1♂ 5♀	1♂ 5♀		
C.r 1♂ 3♀	1♂ 2♀	15	14
C.h 2♂ 6♀	1♂ 6♀		
C.f 3♂ 5♀	1♂ 5♀		
C.r 0♂ 1♀	0♂ 1♀	17	14

Table 5:12.

Results of the t-tests between total fleas contained in cocoons and those without in different nest lining conditions under natural conditions over winter.

Treatment 2g feathers/10g grass

Mean±SE Without cocoon	Mean±SE With cocoon	Difference±SE	t	P
17.01±0.325	16.40±1.208	0.61±1.244	0.49	P>0.05

Treatment F>G

17.23±0.237	17.20±0.663	0.03±0.600	0.05	P>0.05

Treatment Straw 10g

17.58±0.239	16.20±0.735	1.38±0.770	1.79	P>0.05

Treatment Straw 40g

17.48± 0.267	17.40±0.872	0.08±0.888	0.09	P>0.05

Treatment no lining material

15.23±0.408	17.40±0.678	2.17±0.791	2.74	P<0.01

Table 5:13.

Results of the t-tests between the number of fleas fed from those that had suvived in cocoons and total number of fleas surviving without cocoons in different nest linings under natural conditions overwinter.

Mean±SE without cocoons	Mean±SE with Cocoons	Difference±SE	t	P
Treatment 10g feathers/2g grass				
13.08±0.406	14.00±1.483	0.92±1.533	0.60	P>0.05
Treatment F>G				
13.46±0.417	14.20±1.393	0.74±1.480	0.50	P>0.05
Treatment Straw 10g				
14.25±0.356	15.00±0.775	0.75±0.852	0.88	P>0.05
Treatment Straw 40g				
14.00±0.419	14.40±1.1030	0.40±1.111	0.36	P>0.05
Treatment no lining				
10.33±0.436	15.00±1.342	4.67±1.410	3.31	P<0.01

consistently higher water loss in pupae outside cocoons compared with those inside cocoons, although this was not significant. Mellanby (1933), however, showed that although the cocoon of *X.cheopis* offered no protection from dessication, pupae were still capable of developing at 0% relative humidity and therefore must be capable of conserving their water. It seems therefore that the ability of the cocoon to reduce water loss varies with species. As far as the cocoon's ability to buffer temperature changes goes no reference could be found, but it is assumed that, with the small size of fleas and the permeability of the cocoon to water vapour, temperature changes would be rapid.

5.7 Ability of the cocoon to reduce water loss.

To see to what extent the cocoon was permeable to water vapour in the genus *Ceratophyllus* similar experiments to those carried out by Silverman (1982) were performed. In Silverman's experiments larvae were allowed to pupate in gelatine capsules. The pupae were then removed by making a small incision in the wall of the capsule. A small piece of cobalt thiocyanate paper, 2mm X 1mm, was inserted into the empty cocoon and the incision sealed with a silicon sealant. A number of replicates of these were placed in two containers with controlled humidities of 2% and 100% RH for one hour after which they were removed and the colour change noted.

In this study cocoons were removed from a martin nest in the autumn. The occupants of these cocoons had emerged as the nest lining was being sorted, therefore the cocoons could not be assigned to any species, but as the fleas collected from the nest were *C.hirundinis* and *C.farreni* the cocoons almost certainly belonged to these species. Forty cocoons were removed and a piece of cobalt thiocyanate paper inserted into each. The end of the cocoon was sealed with a small drop of low melting point histology wax. Twenty cocoons were placed in open petri dishes in each of two dessicators with the humidity maintained at 100% relative humidity in one and 10% RH in the other. Twenty pieces of cobalt thiocyanate paper measuring 2mm X 1mm were also placed in the same dishes for comparison with those contained in the cocoons. Every hour for four hours 5 cocoons and 5 pieces of cobalt thiocyanate paper were removed from each dessicator, placed in liquid paraffin and examined in a comparator.

The results showed that at both the low and high humidies the RH inside of the cocoons had equilibrated with that outside within one hour. The trials therefore were re-run. This time five cocoons were removed every 10 min., the cobalt thiocyanate paper was removed and examined as before along with five pieces of paper from those placed separately from the cocoons in the petri dish.

The results this time (Table 5:14) show that at both humidities the relative humidity within the

Table 5:14.

Results of the measurement at two different relative humidities inside cocoons.

	10% RH	100% RH
Time 10 minutes		
cocoon number.	% RH	% RH
1	40	80
2	60	85
3	55	95
4	30	90
5	25	70
Time 20 minutes		
cocoons		
1	10	95
2	15	100
3	10	100
4	20	100
5	10	90

Time 30 minutes. All cocoons at 10% and 100% respectively.

cocoons took between 10 and 30 min. to reach ambient, although the majority had reached ambient by 20 min. These results agree with those reported by Silverman (*op. cit.*) for the *C.felis* and Mellanby (1933) for *X.cheopis* that the cocoon is not vapour tight. However, under conditions where currents of air are passing over the cocoon the still air around the adult flea or pupa would reduce evaporation and would presumably reduce dehydration in dry conditions. However, it is unlikely in an enclosed nest, such as the house martin has, that currents of air often occur.

5.8 Laboratory Studies, survival at three different temperatures, humidities and nest linings.

To study the effects of various nest conditions for overwintering, a number of trials were performed at different temperatures and humidities within the range normally found in nests. The factors examined were three temperatures (5^{o}C, 15^{o}C and 25^{o}C), two humidities (40-45% and 90-95%) and three lining materials (2g feathers or grass or straw). Because of the low numbers of fleas available for these trials feathers and grass were used in combination. In the laboratory twenty fleas were placed in 5cm X 2.5cm glass tubes.Each combination of treatments was tested on each sex of the three species, and each was replicated three times. The tubes were covered with gauze to prevent fleas escaping and placed in dessicators over saturated

solutions of $MgCl_2.6H_2O$ (40-45% RH) or NaCl (90-95% RH) (*cf* Winston & Bates 1960). The humidity within each dessicator was checked using a Vaisala humidity recorder and probe. Each treatment was kept in the dark at the required temperature in controlled constant temperature rooms. Only enough *C.rusticus* were available for trials at 5^oc and 15^oc at both humidities. Also there were insufficient numbers of all three species to do the experiments without lining material. The tubes were examined once a month between November and May and any dead fleas removed and counted.

Results

The results of survival of fleas at different temperatures, humidities and nest linings are presented in Figures 14,15 & 16. These show that the greatest survival for each sex and each species occurred with high humidity (95%) at 15^oC with only marginal differences between the feathers/grass combination and straw. In the results for *C.hirundinis* the males survived for a little longer at the higher humidity in straw than in the feathers/grass combination, but realistically at a constant temperature and humidity it is difficult to see how precisely nest lining would influence longevity. At the low temperatures (5^oC) there was little difference between the two humidities for any species. The similarity in the results between the lowest and highest temperatures at both humidities is a little puzzling. At the highest temperature it might be expected that

Fig 14

SURVIVAL OF ADULT CERATOPHYLLUS HIRUNDINIS AT DIFFERENT TEMPERATURES AND HUMIDITIES

TREATMENT FEATHERS AND GRASS

TREATMENT STRAW

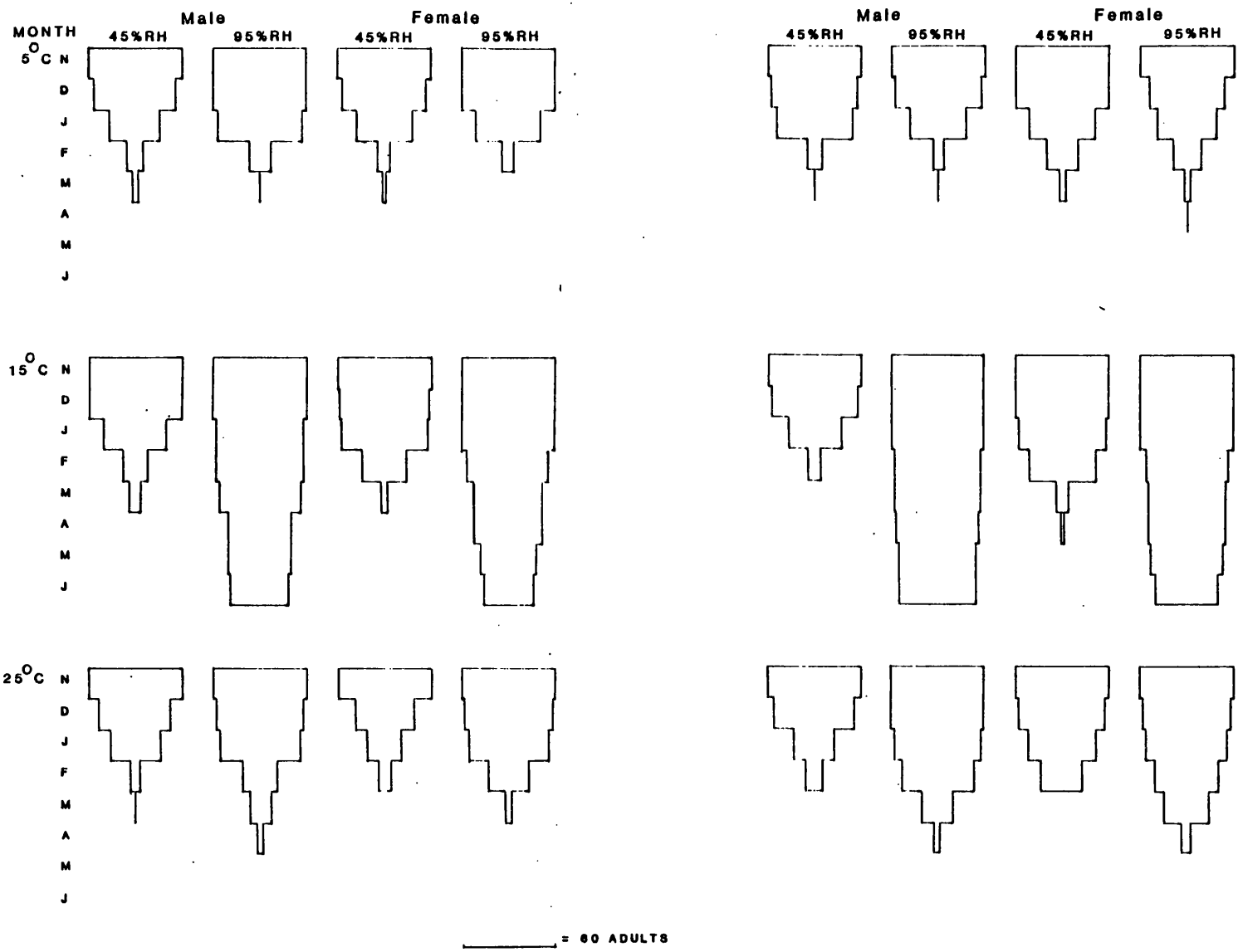


Fig 15

SURVIVAL OF ADULT CERATOPHYLLUS FARRENI AT DIFFERENT TEMPERATURES AND HUMIDITIES

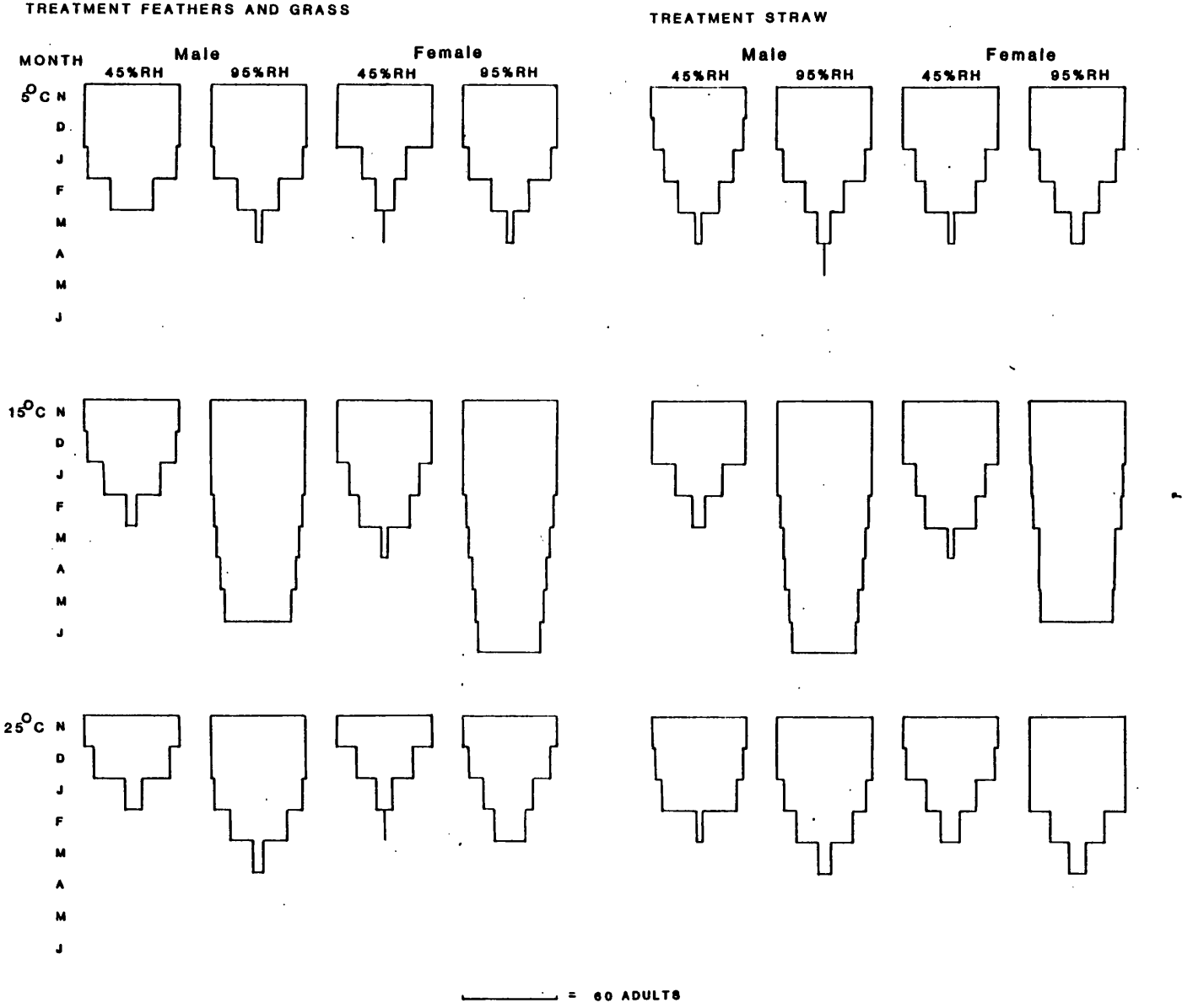
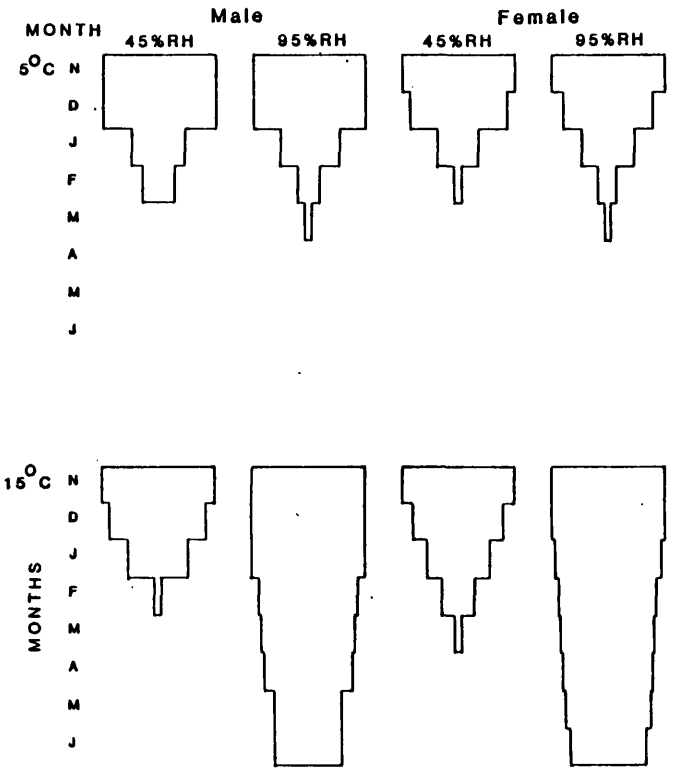


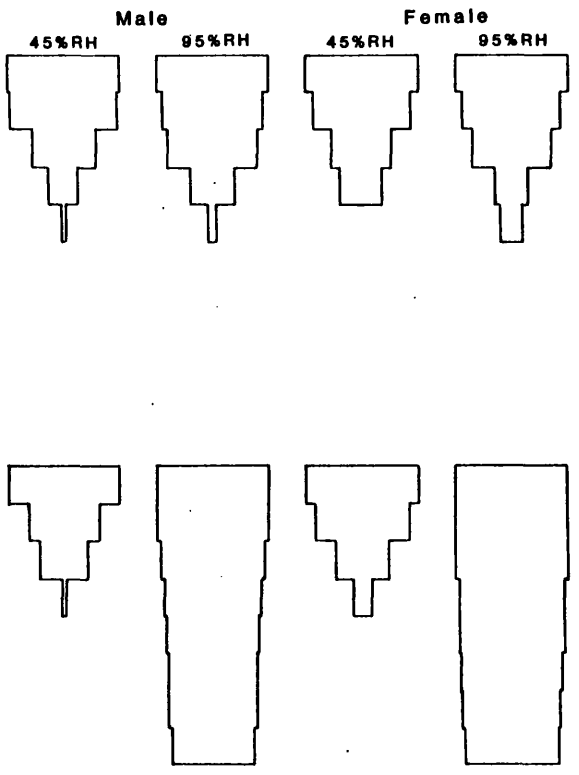
Fig 16

SURVIVAL OF ADULT CERATOPHYLLUS RUSTICUS AT DIFFERENT TEMPERATURES AND HUMIDITIES

TREATMENT FEATHERS AND GRASS



TREATMENT STRAW



60 ADULTS

metabolic activity would be considerably greater than the lowest thereby reducing longevity at the higher temperature without the intake of food. Also, if there is a significant increase in metabolic activity at the higher temperature, the increase in respiration rate would presumably lead to a greater loss of water at the lower humidity. This in turn could lead to a decrease in longevity, which was not the case in these trials.

The temperatures $5^{o}C$ and $15^{o}C$ and humidities selected for these trials were within those recorded in nests over winter although 45%RH is a little lower than the lowest humidity recorded. As demonstrated by the field data and the overwintering trials with different nest lining materials, a very large proportion of the overwintering fleas survive until the spring. Therefore a good level of survival might be expected for $5^{o}C$ and $15^{o}C$, although there are clearly limits to how long fleas could withstand chilling at the lower temperature, and also being kept at a constant temperature and constant humidity is a very atypical situation. Further, it is unknown to what extent disturbance by the experimenter affected the fleas.

The highest temperature was considerably higher than the highest recorded in a martin nest over winter, except when taken over by house sparrows. Under these circumstances the martin fleas disappear from the nest. This was thought to be due to general disturbance at a time when they are normally quiescent. Part of this disturbance would be an increase in temperature and

perhaps humidity. These results suggest that they are capable of surviving for up to three months at a high temperature when normally they would be in a quiescent state. Therefore increased temperature and humidity would not seem to be the major cause of their dissapearance from sparrow occupied nests.

The interaction of temperature and humidity is normally expressed in terms of mm Hg water vapour pressure or saturation deficit (SD)(Ferro & Chapman 1979). Saturation deficit represents the absolute amount of water vapour present in a system. Because water vapour pressure at any RH varies with temperature, many workers have found it useful to describe a biological response relative to the saturation deficiency rather than temperature or RH (see for example Ferro *et.al.* (*op.cit.*)).

Silverman (1982) working with *C.felis* found no relationship between SD and survival at any stage of its life cycle. These results show that the same is true for the adults of at least *C.hirundinis* and *C.farreni*. At 95% RH at all three temperatures the Saturation Deficit is 1mm Hg. At 45% RH the SD at each temperature is 5mm Hg($5^{o}C$) 9mm Hg($15^{o}C$) and 14mm Hg($25^{o}C$). The similarity between the results for *C.hirundinis* and *C.farreni* between $5^{o}C$ and $25^{o}C$ at 45% RH suggests that the Saturation Deficit is not affecting survival significantly. Unfortunately no data was available for *C.rusticus* at $25^{o}C$ for comparison. The saturation deficits in these trials were taken from a prepared

graph (see Buxton 1931).

The results overall indicate that all three species of flea are capable of tolerating a wide range of conditions over several months.

5.9 Insulation ability of different lining materials.

The indication from the trials with different nest lining materials and no lining material is that each species is not greatly affected by any variation in the quantities or type of lining material present. However, it seemed worth testing for any differences in the insulation capabilities of these materials. This was done with feathers, grass and straw with 20g of each material placed in separate glass dishes 100mm X 50mm the bottom of which was covered with mud. A Grant multichannel thermistor probe was placed into each material. Two further probes were connected to the recorder, one was placed inside a 5mm hole in a block of mud measuring 50mm X 25mm and the other probe was left in air to measure the ambient temperature. Each lining material was compressed around the probe to try and simulate the state of the lining material inside a nest. The probe inside the mud block would, it was hoped simulate an unlined nest. The whole assembly was placed in a constant temperature room which was initially set at $25^{o}C$. The temperature of the room was then lowered to $15^{o}C$ and the rate at which the temperature fell was recorded every 5 minutes. When the temperature in the

lining materials was the same as the ambient the temperature was lowered to 10°C. The same procedure was followed as before and when ambient was reached the temperature was lowered to 5°C. When this temperature had been reached in all materials the temperature of the room was raised back to 25°C and the rate at which the materials warmed up was recorded.

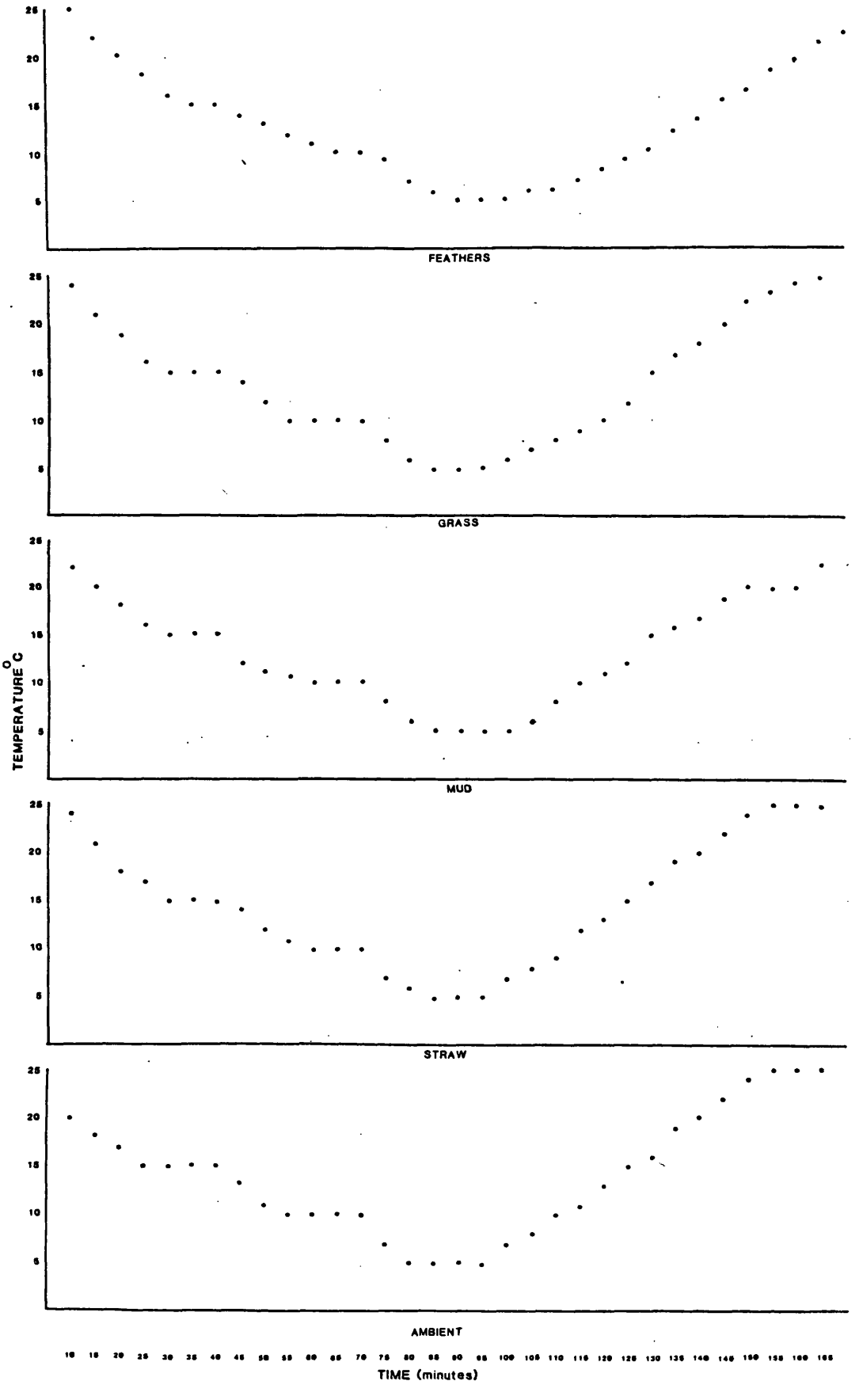
Results

The results are presented in Figure 17. It is clear that the most rapid change occurred in the mud block. Straw did not appear to possess very good insulation qualities as the changes were more rapid in this than the other two, but this material does not compress as well as the others. The temperature changes in grass were faster than in feathers which took longest to cool down and to warm up. It seems therefore that where lining material is present any change in ambient temperature is slowed down. When no lining material is present the changes are more rapid. However the differences between each treatment are small and, as shown in the temperature measurements in a nest containing lining material during the winter (chapter 2), the nest temperature was very close to ambient, although always lagging behind.

The presence of lining material thus seem to have a buffering effect on the ambient changes which over a period of several months may be less stressful to

Fig 17

TEMPERATURE CHANGES IN DIFFERENT NEST LINING MATERIALS WITH CHANGING AMBIENT TEMPERATURE.



the fleas.

Concluding remarks.

The results given in this chapter indicate that each species rarely undertakes unaided emigration and that colonisation of newly built nests is by fleas transported by the martins at one time and are generally few in number.

Mortality in overwintering fleas is generally low, regardless of the type or quantity of lining material or whether fleas are contained in cocoons. However, not all fleas that overwinter are capable of feeding or reproducing. Also a proportion of the flea community is likely to be transported to other nests by martins roosting in the nest, and then moving on to either build new nests or re-occupy other old nests. This would also introduce new fleas to existing flea populations in these nests. Therefore the number of reproducing individuals in a nest going into its second season may not be much higher than the starting populations in newly built nests. This would therefore account for similar numbers of fleas in autumn populations of one season and older than one season nests.

Chapter 6.

Metabolic activity in adult House Martin fleas over winter.

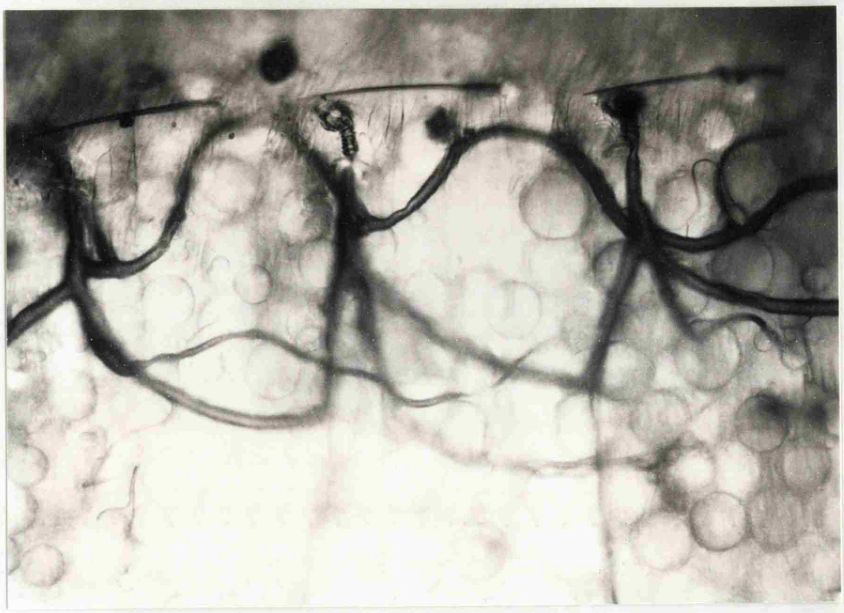
6:1 Introduction

The reserve fat body of insects is usually in the form of triglycerides (Gilby 1965). Individuals of all three species of martin flea examined in the autumn prior to overwintering had a considerable fat body reserve (Plate 14), which was greatly depleted by the spring (Plate 15). The amount of fat body left after overwintering will presumably dictate the fitness of the flea to gain a host, feed and reproduce in the spring. Therefore overwintering success in fleas, like other arthropods, will depend to some extent on the ambient temperatures which will determine the rate of metabolic processes.

Darskaya (1964) studied the size, number and distribution of fat bodies in a number of species of *Ceratophyllus*. She concluded that species living in nests above ground, such as the three species considered here, have more numerous and larger fat bodies than those species inhabiting nests on or near the ground, eg. *Ceratophyllus gallinae*. It must be said ,however, that the diagrams she gave in support of her statement are not altogether convincing, since the species with small fat bodies look just like those with large fat bodies after fat body depletion. She does not say how many individuals of each species were examined or how old each individual was.

The similarities in the survival of all three

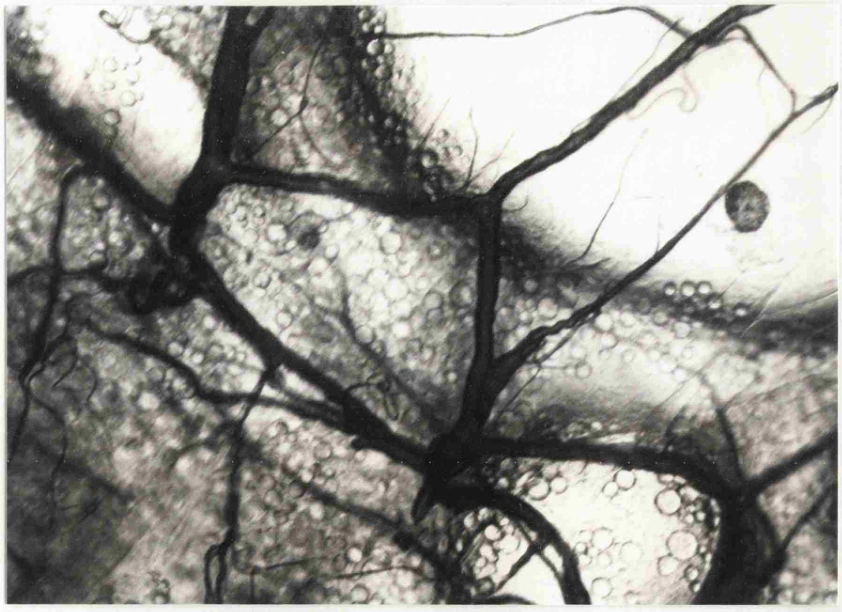
Plate 14.



100µm

Fat body of *C.hirundinis* in autumn veiwed under phase contrast.

Plate 15



100µm

Fat body in *C.hirundinis* in spring veiwed under phase contrast.

species between the lowest temperature (5°C) and the highest (25°C) regardless of RH indicated a wide temperature tolerance (see Chapter 5). However, one would reasonably expect a higher metabolic activity at the higher temperature, and therefore presumably reduced metabolic reserves. It seemed appropriate therefore to examine metabolic activity at the three temperatures used in the overwintering laboratory experiments.

Respiration is a chemical oxidation of assimilated material resulting in the release of energy and therefore provides a convenient measure of metabolic activity and hence energy utilization. Respiration can be measured in terms of the heat liberated during oxidation or the chemical exchange involving O_2 uptake and the subsequent liberation of CO_2 from the animal. The chemical exchange is quantitatively related to the heat liberated for each particular metabolite. With carbohydrates the volume of O_2 consumed and carbon dioxide evolved is equal (RQ=1)(Petrusewicz & Macfadyen 1970) while with fat and protein metabolism the quotient is 0.71 and 0.8 respectively. In this study, oxygen consumption was preferred for the measurement of metabolic activity, since no convenient method was available for the determination of heat liberated in such small animals.

Little work on the respiration of fleas is reported in the literature, and the only references found are for studies by Russian workers. For example Kondrashkina and Dudinkova (1964) studied oxygen

consumption in seven species of mammal flea using fed and individuals. Unfortunately the paper neither describes nor even indicates the method used to determine the rate of respiration. These workers concluded that "oxygen requirements depend on the environment to which a particular species is adapted".

Two methods are available for measuring O_2 consumption, analytical and manometric. The analytical methods of oxygen assay are not highly sensitive (Petrusewicz *et al., op. cit*) and are therefore unsuitable for very small animals.

In the manometric methods the carbon dioxide evolved by the animals is absorbed chemically so that as the O_2 is removed from the system, the total volume of gas in the system is reduced. Changes in the quantity of O_2 is then measured through the reduction in either the volume or the pressure of air in the chamber, or a combination of both. A review of the types of manometric systems available for respirometry is given by Umbreit, Burris & Stauffer (1972).

Probably the most widely used manometeric method is the Warburg apparatus. This consists of a detachable reaction flask attached to the manometer containing a liquid of known density. The volume of the flask and part of the adjacent manometer limb is kept constant by varying the pressure of the system. The changes of pressure needed to keep the volume constant can be related to oxygen uptake by standard calculation. This apparatus, however, is sensitive to external

pressure changes which must therefore be included in all calculations.

Gilson (1963) designed a differential respirometer in which the volume of O_2 used by the animal is determined by adjustment of a micrometer syringe to return the manometer to equilibrium by reducing the gas volume. The syringe is calibrated in µl and provides a direct volume reading. Changes in atmospheric pressure are compensated by the connections between the reference arms of all manometers to a common compensation vessel through a manifold. The advantage in this system is that all the experimental flasks are directly comparable, since they all have the same reference flask, which leads to a several fold increase in accuracy and reproducibility over the non-differential Warburg flasks.

6.1.1 Description of the Gilson Respirometer.

The main body of the respirometer consists of 20 reaction flasks which are connected by tygon capillary tubing to the manometers. These manometers are arranged above a temperature controlled water bath and the reference arms of all the manometers are connected to a common compensation vessel (reference flask) through a manifold. This arrangement permits the simultaneous evacuation and gassing of all vessels and of the reference flask which eliminates the need for corrections for barometric changes. The micrometer gives a digital reading for the volume changes which accompany

Fig 18

Diagram of Gilson differential respirometer

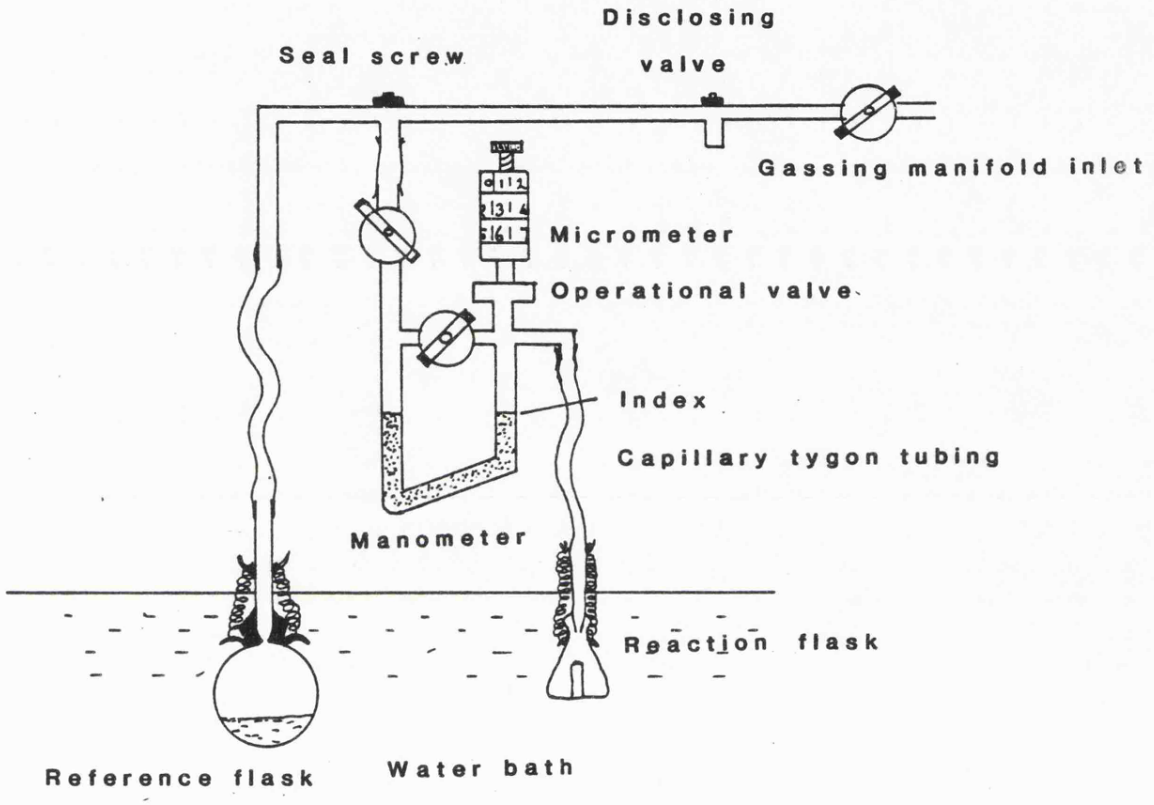
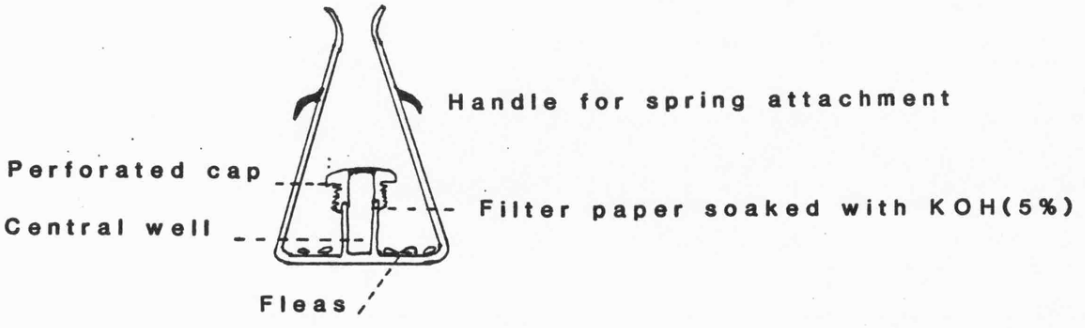


Diagram of reaction flask



the inward and outward movement of the plastic plunger required to maintain the system at a constant pressure. The micrometers and manometers are in fixed positions to which the reaction flasks are connected by flexible tygon tubing. The reaction flasks and reference flask are submerged in the water bath which is maintained at a constant temperature ($\pm 0.02^{o}C$) by means of heating and refrigeration units.

The whole apparatus was operated in a constant temperature room kept at the same temperature as that at which the water bath was being operated to reduce the effect of ambient temperature oscillations on the unsubmerged parts of the apparatus (Carver & Glyone 1971). Aluminium foil baffles were fitted to reduce the effect of the heat produced by the stirrer motor and refrigeration unit on the exposed tygon tubing of the respiration vessels, (see figure 18 for a diagram of the Gilson respirometer).

More sensitive methods for measuring O_2 consumption in very small animals exist, for example the Cartesian Diver (Linderstrom-Lang 1943), where one animal at a time can be respired, but no such apparatus was available.

6.1.2 Collection of fleas used in respirometry and the conduct of experiments.

The fleas used in respirometry were obtained

from house martin nests collected in the autumn. Those fleas used for respirometry in the spring were left in the nest lining material contained in a sealed cloth bag in an unheated outbuilding to allow them to overwinter in as near natural conditions as possible. All the fleas were anaethestised with CO_2 and identified under a compound microscope. They were then allowed to recover and equilibrate at the experimental temperature for a minimum of twentyfour hours before the experiment was run.

The major problem encountered in using the Gilson respirometer was that, although it is a sensitive instrument ($\pm$0.2µl), a minimum of 20 animals had to be used in each reaction vessel to give a measurable change in the manometers even at the highest temperature ($25^{o}C$). At $5^{o}C$ as many as 40 animals were needed in a single reaction vessel. The limited availability of fleas available meant therefore only a few replicates (4-8) at each temperature for each species could be tested.

The Gilson respirometer was switched on and the water bath allowed to reach and settle at the working temperature. A $250cm^3$ flask containing $100cm^3$ of distilled water, thus leaving an air space of $150cm^3$ which is equivalent to that in 20 reaction flasks ($7.5cm^3$ each), was connected to the system before equilibration. 20 reactions flasks with a centre well were used. A 1.5 X 1cm piece of filter paper (Whatman No

1) moistened with 5%KOH solution was placed in the centre well of each reaction flask to absorb CO_2. Care was taken that no alkali was dropped outside the well which was covered with a perforated plastic cap to prevent fleas entering it. The reaction flasks were loaded with fleas and connected to the manometers. The ground glass attachment was first coated with silicon grease to form a gas tight joint. The assembly was held together with two springs to prevent the reaction flasks falling off. Six of the flasks contained no animals and were kept as controls. Two of these controls were connected at each end of the respirometer, with two in the middle.

After a further hour for equilibration, the gassing valves were closed and the micrometers set at 100µl to allow for negative readings. A movable index was set against each meniscus so that the movement of the meniscus as the fleas respired was readily ascertained. When a reading was taken the meniscus was returned to the index line by rotating the plunger on the micrometers. Readings were taken every hour for six hours. At the end of this period the gassing valves were opened and the fleas removed and checked for mortalities; no deaths were noted. The fleas were killed with ethyl acetate, air dried in an oven at $60^{o}C$ for three hours and then placed in a vacuum oven at $60^{o}C$ and a reduced pressure (circa 400-500 mm Hg $cm^{-2-}h$) for a further twelve hours. After this time they were removed

to a dessicator where they were allowed to cool over silica gel for one hour and then weighed on a micro-balance.

Three temperatures were chosen for respiration; $5^{o}C$ and $15^{o}C$ covered the range found during overwintering and $25^{o}C$ is approximately the temperature found in the nest lining when the nest is occupied by martins. Temperatures below $5^{o}C$ were not tested, for although overwintering fleas are at times subjected to temperatures below $0^{o}C$ respiration rates at such low temperatures were likely to be below the detection capabilities of the respirometer.

6.1.3 Calculation of oxygen consumption.

Oxygen consumption with time was calculated for each reaction vessel using linear regression analysis. In all cases a significant correlation coefficient was obtained ($r=>0.05; P<0.001$) and the regression coefficient was therefore taken as the O_2 consumption per hour for the number of individuals in the reaction vessel. To calculate the relation between body weight and the O_2 consumption per mg body weight (dried) per hr further regressions were performed using the dry weight of the fleas in each reaction vessel, for a given species at a given temperature, weight being taken as the independent variable.

Because of the great variation in O_2 consumption with weight in the results the correlation

coefficients in most of these regressions were not significant and therefore the regression coefficients must be considered unreliable. In all cases therefore O_2 $mg^{-1}hr^{-1}$ was calculated by dividing the hourly O_2 consumption by the dry weight and meaning over all replicates. The results are given in Table 6:1.

These results show, as might reasonably be expected, that the oxygen consumption increases with increasing temperature. Table 6:2 shows the oxygen consumption per mg for each reaction flask with the number and sex of the fleas. To see if there was any significant difference in O_2 consumption between the species at each temperature in both autumn and spring these data were analysed further using a one-way analysis of variance with a Student-Newman-Keuls range test. The results (Tables 6:3 (Autumn) and 6:4 (Spring)) show that in autumn at 5^oC and 25^oC there was no significant difference in O_2 consumption between the three species. At 15^oC, however, *C.hirundinis* had a significantly higher consumption than the other two species ($0.01<P<0.05$) which were not significantly different from each other.

In the analysis for spring, significant differences were found at each temperature. At 25^oC *C.rusticus* had a significantly lower rate of consumption than the other two species ($0.01<P<0.05$) which were not significantly different from each other. *C.hirundinis* at both 5^oC and 15^oC had a significantly higher consumption than either of the other two species ($0.01<P<0.05$ in

Table 6:1.

Oxygen consumption µl $mg^{-1}hr^{-1}$ at 5^{o}, $15^{o}C$ and $25^{o}C$ for *C.hirundinis*, *C.farreni* and *C.rusticus* in autumn and spring.

Species	Temperature	Autumn	Spring
C.hirundinis	$5^{o}C$	0.036	0.220
C.farreni	--	0.026	0.038
C.rusticus	--	0.031	0.069
C.hirundinis	$15^{o}C$	0.337	0.405
C.farreni	--	0.105	0.252
C.rusticus	--	0.101	0.208
C.hirundinis	$25^{o}C$	3.311	2.418
C.farreni	--	3.000	1.598
C.rusticus	--	2.888	2.354

Table 6:2.

Mean readings µl $mg^{-1}hr^{-1}$ for each reaction vessel at $5^{o}C$, $15^{o}C$ and $25^{o}C$ for *C.hirundinis*, *C.farreni* and *C.rusticus*.

N= Number of individuals and sex in a reaction flask.

$5^{o}C$ Autumn

C.hirundinis	N	*C.farreni*	N	*C.rusticus*	N
0.028	40♀	0.021	40♀	0.038	40♀
0.030	40♀	0.039	40♀	0.027	40♀
0.028	40♀	0.013	40♀	0.024	40♂
0.044	40♀	0.029	40♀	0.036	40♂
0.048	40♀	0.018	40♂	-----	--
0.046	40♂	0.037	40♂	-----	--
0.028	40♂	-----	--	-----	--

$5^{o}C$ Spring

C.hirundinis	N	*C.farreni*	N	*C.rusticus*	N
0.029	40♀	0.031	40♀	0.042	40♀
0.186	40♀	0.021	40♀	0.028	40♀
0.370	40♀	0.053	40♀	0.167	40♀
0.298	40♂	0.049	40♂	0.041	40♂

Table 6:2 continued.

15°C Autumn

C.hirundinis	N	*C.farreni*	N	*C.rusticus*	N
0.209	20♀	0.222	20♀	0.049	20♀
0.232	20♀	0.092	20♀	0.090	20♀
0.282	20♀	0.102	20♀	0.156	20♀
0.423	20♀	0.071	20♂	0.104	20♀
0.158	20♂	0.041	20♂	0.091	20♂
0.403	20♂	0.125	20♂	0.125	20♂
0.653	20♂	0.088	20♂	-----	--

15°C Spring

C.hirundinis	N	*C.farreni*	N	*C.rusticus*	N
0.552	20♀	0.337	20♀	0.180	20♀
0.299	20♀	0.262	20♀	0.249	20♀
0.280	20♀	0.177	20♀	0.205	20♀
0.452	20♀	0.219	20♀	0.200	20♂
0.496	20♂	0.267	20♂	-----	--
0.355	20♂	-----	--	-----	--

25°C Autumn

C.hirundinis	N	*C.farreni*	N	*C.rusticus*	N
1.900	20♀	3.270	20♀	1.490	20♀
3.360	20♀	3.050	20♀	2.320	20♀
3.610	20♀	2.570	20♀	1.390	20♀
3.790	20♀	2.930	20♀	2.570	20♀
3.310	20♂	2.590	20♀	4.190	20♂
2.540	20♂	3.060	20♂	4.050	20♂
4.670	20♂	3.530	20♂	4.210	20♂

Table 6:2 continued.

25° Spring

C.hirundinis	N	*C.farreni*	N	*C.rusticus*	N
2.130	20♀	2.100	20♀	2.020	20♀
2.020	20♀	1.220	20♀	2.860	20♀
2.090	20♀	1.630	20♀	2.120	20♀
2.390	20♀	1.580	20♀	2.570	20♂
2.330	20♂	1.380	20♂	2.200	20♂
2.980	20♂	1.680	20♂	-----	--
2.990	20♂	-----	--	-----	--

Table 6:3.

One-way analysis of variance with oxygen consumption ($\mu l\ mg^{-1}hr^{-1}$) between *C.hirundinis*, *C.farreni* and *C.rusticus* at $5^{o}C$, $15^{o}C$ and $25^{o}C$ in the autumn.

$5^{o}C$

F	DF	Probability
0.4671	2,15	P>0.05

$15^{o}C$

F	DF	Probability
12.0033	2,17	0.01<P<0.05

Species	Mean	SNK
C.hirundinis	0.337	
C.farreni	0.105	|
C.rusticus	0.101	|

$25^{o}C$

F	DF	Probability
0.4064	2,18	P>0.05

Table 6:4.

One-way analysis of variance with oxygen consumption (µl $mg^{-1}hr^{-1}$) between *C.hirundinis*, *C.farreni* and C.rusticus at $5^{o}C$, $15^{o}C$ and $25^{o}C$ in the spring.

$5^{o}C$

F	DF	Probability
4.2772	2,9	0.01<P<0.05

Species	Mean	SNK
C.hirundinis	0.220	
C.rusticus	0.069	|
C.farreni	0.038	|

$15^{o}C$

F	DF	Probability
9.031	2,12	0.01<P<0.05

Species	Mean	SNK
C.hirundinis	0.405	
C.farreni	0.252	|
C.rusticus	0.208	|

Table 6:4 continued.

$25^{o}C$

F	DF	Probability
11.411	2,15	0.01<P<0.05

Species	Mean	SNK
C.hirundinis	2.418	|
C.farreni	2.354	|
C.rusticus	1.598	

both cases). There was no significant difference between *C.farreni* and *C.rusticus* at the two hour temperatures.

Having found significant differences in O_2 consumption between species within a season the data were analysed further for each species at each temperature between autumn and spring using t-tests. The results (Table 6:5) show that *C.hirundinis* had a significantly higher consumption in autumn compared to spring at 25°C ($0.01<P<0.05$). At 15°C no significant difference was obtained and at 5°C this species had a higher consumption in the spring than in the autumn ($0.001<P<0.01$). The results for *C.farreni* show that it had a significantly higher consumption in the autumn at 25°C ($P<0.001$) but at 15°C had a significantly higher consumption in the spring ($0.001<P<0.01$). while at 5°C, although mean consumption was greater in spring, the difference was not significant. *C.rusticus* showed a significantly higher rate in the spring at 15°C ($0.001<P,0.01$) but no significant differences were found between seasons at the other two temperatures although again the mean consumption was higher in autumn than spring at 25°C but higher in spring than autumn at 5°C. Too few males were available for any meaningful comparison between sexes, but as can be seen in Table 6:2 there was a comparatively higher O_2 consumption per unit weight in the males.

Temperature coefficient (Q_{10})

The rate of all chemical reactions, cellular

Table 6:5.

Results of t-tests for oxygen consumption ($\mu l\ mg^{-1}\ hr^{-1}$) for *C.hirundinis*, *C.farreni* and *C.rusticus* at each temperature between autumn and spring.

NS= Not significant, *=0.01<P<0.05, **=0.001<P<0.01, ***=P<0.001.

Species	Temperature	Autumn Mean±SE	Spring Mean±SE	t
C.hirundinis	25°C	3.311±0.3364	2.418±0.1554	2.44*
	15°C	0.337±0.0643	0.405±0.0452	0.84 NS
	5°C	0.036±0.0049	0.220±0.0740	3.74**
C.farreni	25°C	3.000±0.1307	1.598±0.1222	7.73***
	15°C	0.105±0.0217	0.252±0.0265	4.28**
	5°C	0.026±0.0043	0.038±0.0075	1.53 NS
C.rusticus	25°C	2.888±0.4734	2.354±0.1569	0.97 NS
	15°C	0.101±0.0147	0.2085±0.0145	4.88**
	5°C	0.031±0.0034	0.069±0.0326	1.16 NS

or otherwise, is dependent on temperature. This relationship is usually expressed simply as a temperature coefficient (Q_{10}), derived from the equation

$$Q_{10} = (k1/K2)(10/(t1-t2))$$

where K1 and K2 are velocity constants (proportional rates of reaction) found at temperatures t1 and t2.

In this study K1 and K2 were rates of respiration. The results of the Q_{10} calculations gave ridiculously high values (3.0 to 30.0). In biological reactions the Q_{10} decreases progressively as the temperature increases and normally Q_{10} values lie between 2 and 3 (Wigglesworth 1972). Fleas are essentially ectoparasites whose "normal" functioning temperature would be between 25°C and 30°C. At low temperatures there is reduced metabolic activity, therefore with such large differences in respiration rates between temperatures a comparison of temperature coefficients has little meaning.

6.1.4 Discussion

The only respirometric data available for fleas seems to be that of Kondrashkina *et al.* (*op. cit.*); their data are reproduced in Table 6:6 for comparison. As can be seen in all species a steady rise in O_2 consumption is recorded in their data with increasing temperature except at the extreme of 40°C where *N.setosa* and *C.tesquorum* show a very marked reduction. However, quite large differences are apparent

between species at the same temperature.

Relating Kondrashkina's results to those obtained for *C.hirundinis*, *C.farreni* and *C.rusticus* shows that some of the values obtained are very similar at the highest temperature($25^{o}C$), but at $15^{o}C$ only the result for *C.hirundinis* is close to their values. The results for *C.farreni* and *C.rusticus* at $15^{o}C$ and for all three species at $5^{o}C$ are considerably lower than those recorded by Kondrashkina *et al.*, at $0^{o}C$. The fleas that Kondrashkina tested were all fed, so that digestion of the blood meal may account for a higher metabolic activity. If this is the case, however, it is surprising that this was not apparent at the higher temperatures although the amount of energy required to digest a blood meal may be masked by the increase in metabolic activity at the higher temperature. All the fleas tested by Kondrashkina *et al.*,were from small mammals, the differences between these and house martin fleas at the lower temperatures therefore may reflect the difference between species where the host is present throughout the year and those where the host is absent during the winter months.

Ceratophyllus hirundinis, however, gives similar results to those for small mammal fleas at $15^{o}C$, although it apparently shares the same niche as the other two species of martin fleas. Does *C.hirundinis* therefore have different behaviour patterns where it is more active than *C.farreni* or *C.rusticus* at $15^{o}C$? The differences may be a result of differences in behaviour

Table 6:6.

Results of O_2 consumption ($\mu l\ mg^{-1} hr^{-1}$) at 7 temperatures for 6 species of small mammal flea recorded by Kondrashkina & Dudinkova (1964).

Species	Temperature						
	0°C	10°C	20°C	25°C	30°C	35°C	40°C
Neopsylla setosa	0.361	0.625	0.929	1.037	1.789	1.926	0.270
Ceratophyllus tesqorum	0.159	1.047	1.153	1.425	2.875	3.320	0.488
Ceratopyllus fasciatus	0.129	0.916	2.162	2.464	2.996	3.573	3.336
Ceratophyllus laeviceps	0.106	0.709	1.968	2.668	2.715	3.832	6.043
Xenopsylla cheopis	0.146	0.301	1.252	1.834	2.511	4.086	5.887
Xenopsylla conformis	0.105	0.511	1.590	2.663	2.866	3.277	6.955

patterns between species at a given temperature and may also be a physiological response depending on the state of the fat body.

6.2 Activity in *C.hirundinis*, *C.farreni* and *C.rusticus*.

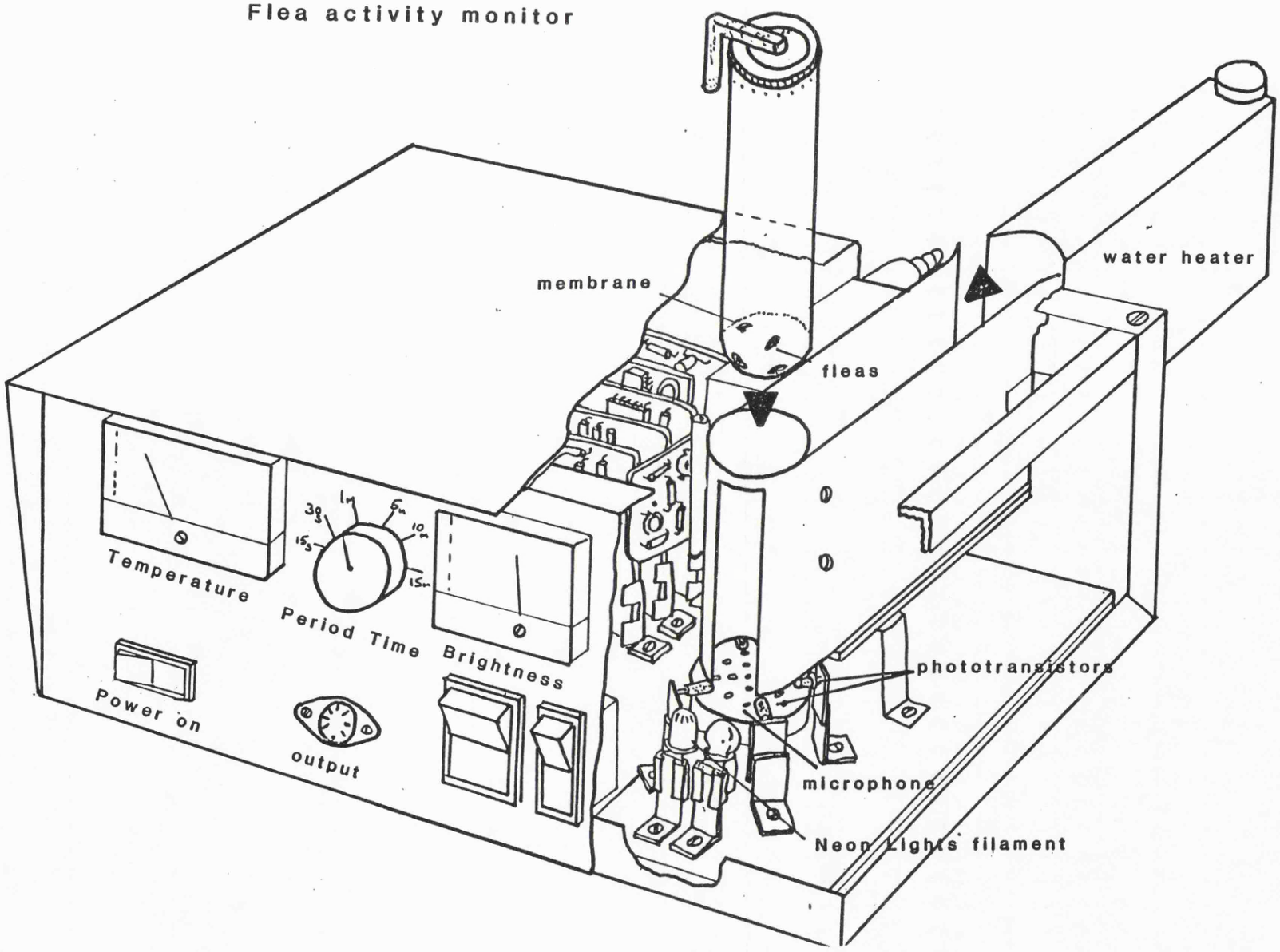
The respiration rates in fleas, as in other animals, will be affected by the degree of physical activity. This in turn will be affected by a number of other factors, eg. temperature and presence of the host. An attempt was made to measure the activity of these three species using a flea activity monitor, designed by Loughborough University of Technology, the use of which was kindly granted by Malcolm Greenwood.

6.2.1 Description of monitor.

The activity monitor is shown in Figure 19. The fleas are contained in a clear plastic cylinder measuring 8cm long by 2cm in diameter. The bottom of the cylinder is covered with a thin rubber membrane while the top is closed with a plastic cap. The cap is pierced by a tube which can be connected to various gases such as dry or humidified air. The cylinder fits into a sleeve so that the membrane is in contact with a microphone. The vibration caused by a flea jumping on the membrane is transmitted via the microphone to the computer where it is recorded as a 'jump'.

Around the outside of the cylinder are

Figure 19


Flea activity monitor
membrane
water heater
fleas
Temperature
Period Time
Brightness
Power on
output
phototransistors
microphone
Neon Lights filament

arranged two phototransistors that pick up infra-red light from two emitting diodes opposite them. Any flea breaking either infra-red beam will be recorded as having made a 'run'. The electronics of the monitor are constructed in such a way that if a flea stays in the beam it is recorded only as a single run.

The tube is kept at a constant temperature by means of a thermostatically controlled water heater. Readings of 'jumps' and 'runs' can be made from every 15 seconds to every 15 minutes. Periods of illumination can also be controlled. At the end of a trial the results in jumps and runs for each selected time period are printed out via an Apple micro-computer.

Unfortunately the activity monitor had no cooling facility and a cold room was not available, therefore of the three temperatures used in the respirometry study only 25^{o}C was possible. The closest to 15^{o}C that could be achieved was 18^{o}C. The trials were therefore run at these two temperatures. Three replicates, each of ten individuals, were tested for each sex of each species.

The fleas were identified and sexed on the day before the trials were performed. The fleas were kept in the dark at the temperature at which the trial was to be conducted. No special effort was made to control humidity but it was always between 80%-90%. As these species normally live in the nest in very subdued lighting all the trials were carried out in the dark. Each trial lasted 30 minutes with recordings of jumps

and runs made every minute.

6.2.2 Results.

The result (Figures 20-23), which give total 'jumps' and 'runs' combined for all three replicates, show that activity, regardless of species, sex and temperature, is erratic. A three-way analysis of variance using log transformed data between all components gave significant F values for sex and temperature but not for species in the main effects and for species/temperature and sex/temperature but not species/sex in the first order interaction (Table 6:7). The result for sex indicated that females were more active than males. For temperature the fleas were significantly more active at $25^{o}C$ than at $18^{o}C$.

A Student-Newman-Keuls range test was applied to the means for species/temperature and sex/temperature. The result for species/temperature showed that *C.farreni* was significantly more active at $25^{o}C$ than either of the other two species at $25^{o}C$, and then all three species at $18^{o}C$. *C.hirundinis* at $25^{o}C$ was significantly more active than *C.hirundinis* or *C.farreni* at $18^{o}C$ but not from *C.rusticus* at $18^{o}C$ or $25^{o}C$. *C.rusticus* at $18^{o}C$ and $25^{o}C$, *C.hirundinis* and *C.farreni* at $18^{o}C$ were not significantly different from each other (Table 6:7).

The result for sex/temperature showed that all females were significantly more active than males at $25^{o}C$ or males and females at $18^{o}C$. Males at $25^{o}C$ were

Figure 20

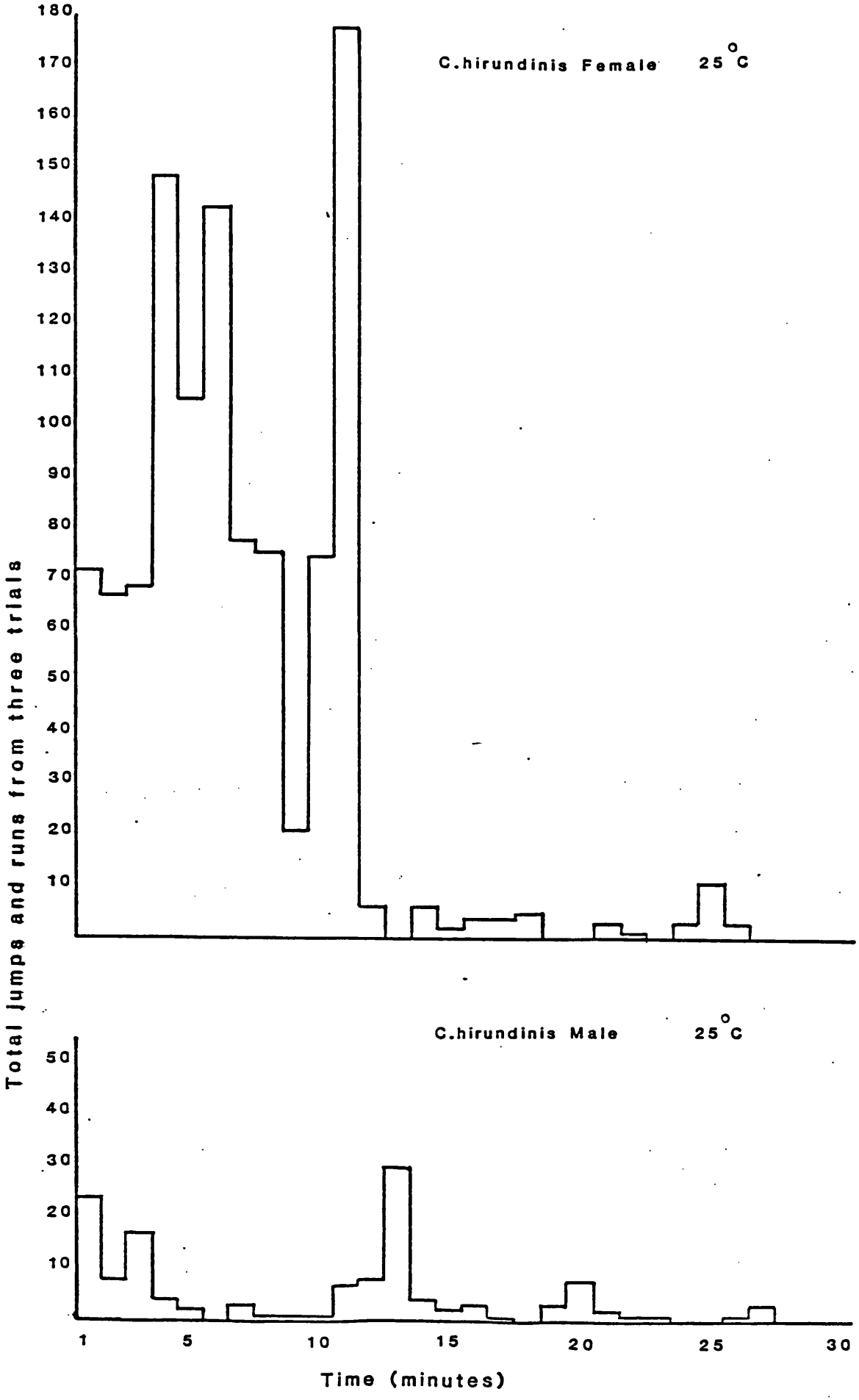

C.hirundinis Female 25°C
C.hirundinis Male 25°C
Total jumps and runs from three trials
Time (minutes)
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
50
40
30
20
10
1
5
10
15
20
25
30

Figure 21

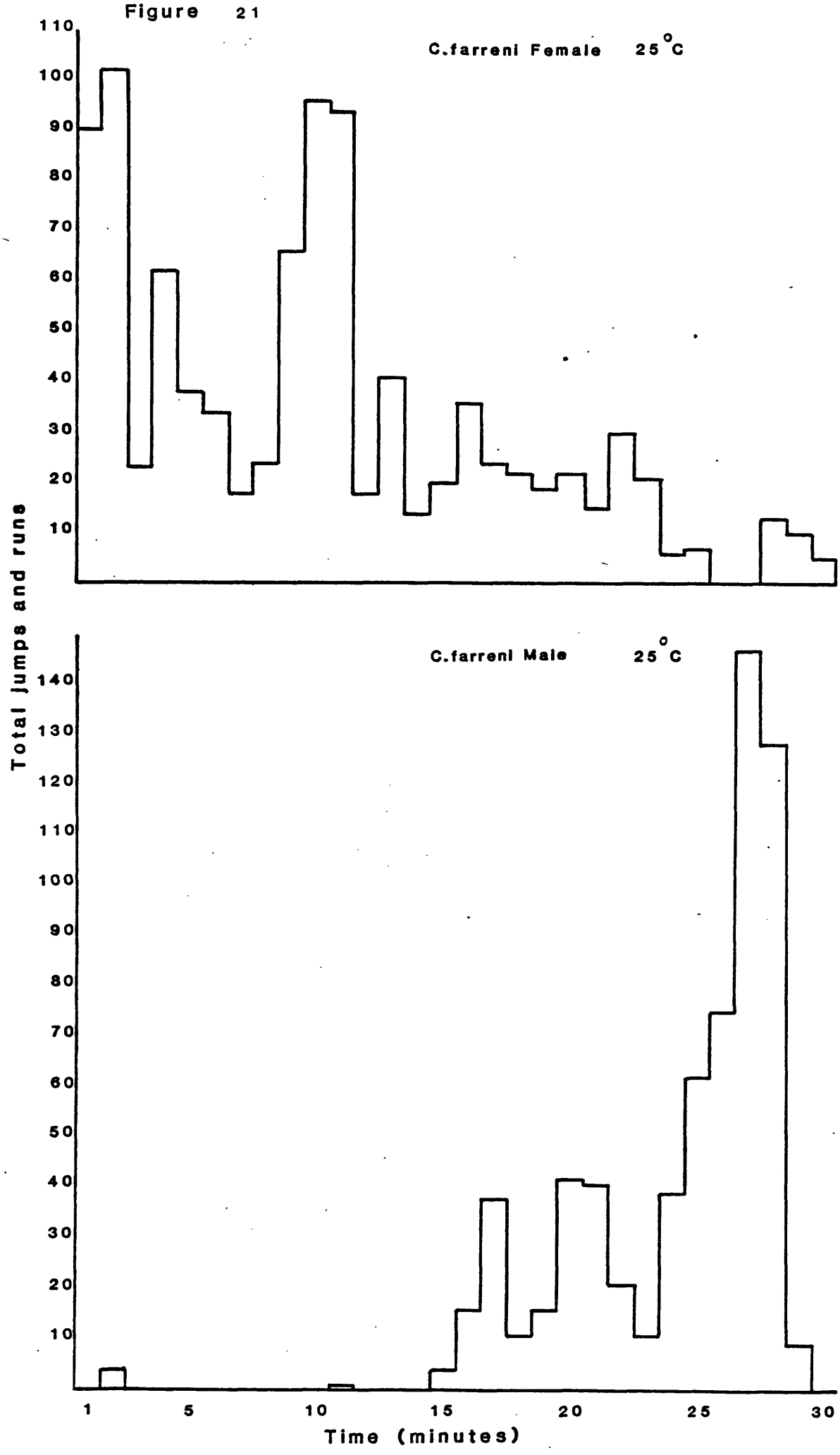

C.farreni Female 25°C
C.farreni Male 25°C
Total jumps and runs
Time (minutes)
110
100
90
80
70
60
50
40
30
20
10
140
130
120
110
100
90
80
70
60
50
40
30
20
10
1
5
10
15
20
25
30

Figure 22

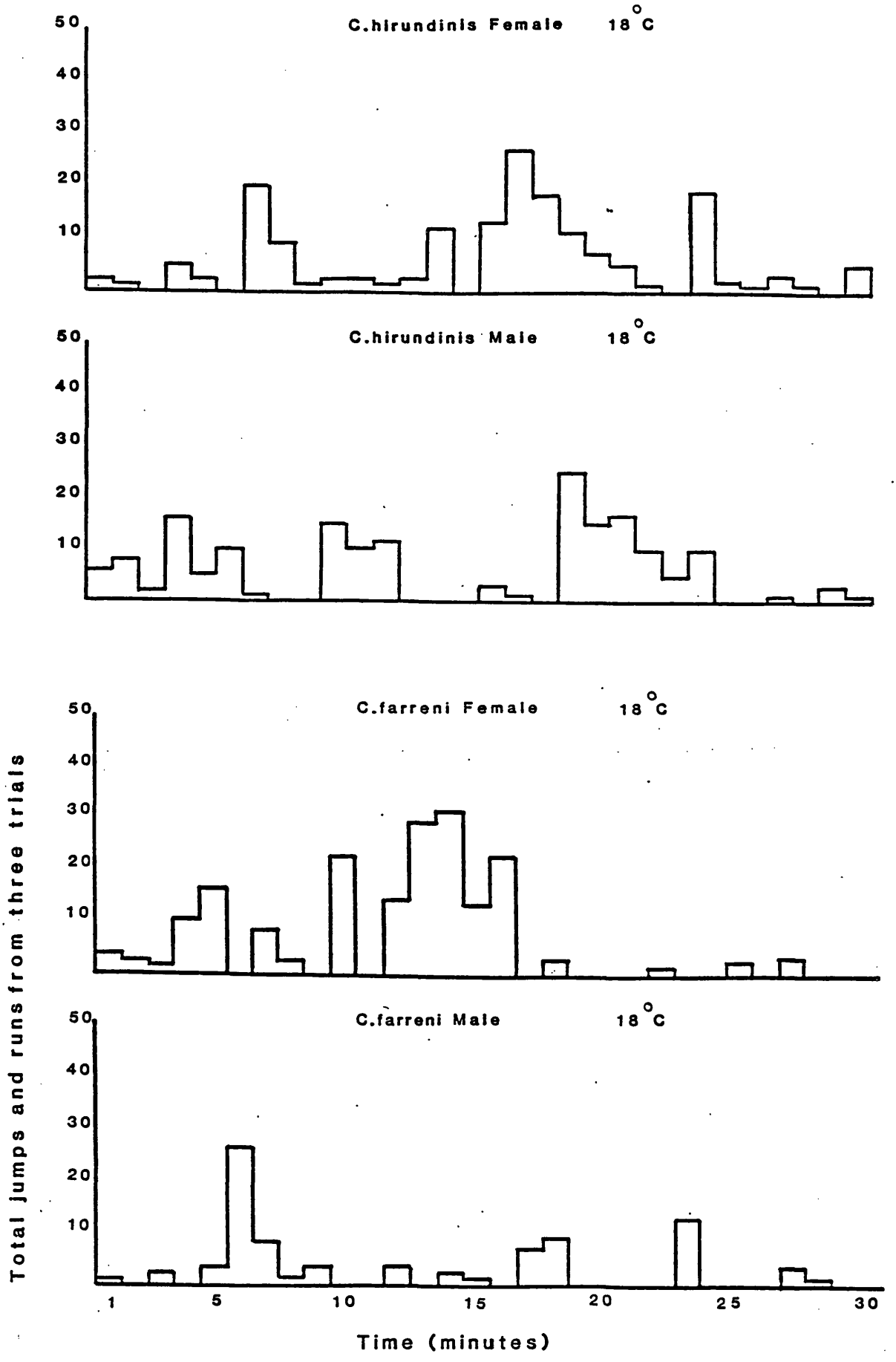
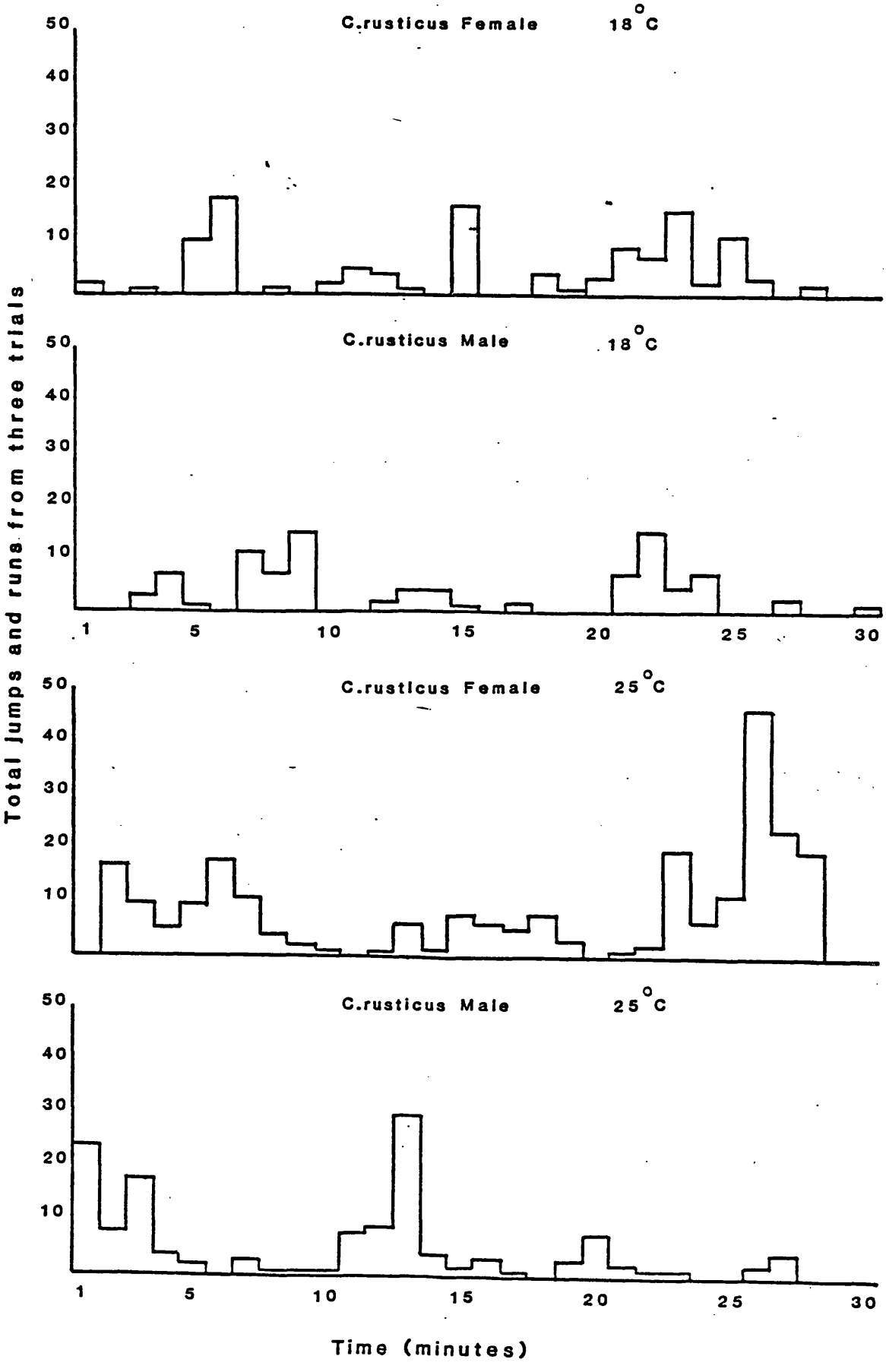

C.hirundinis Female 18°C
C.hirundinis Male 18°C
C.farreni Female 18°C
C.farreni Male 18°C
50
40
30
20
10
Total jumps and runs from three trials
1
5
10
15
20
25
30
Time (minutes)

Figure 23


C.rusticus Female 18°C
C.rusticus Male 18°C
C.rusticus Female 25°C
C.rusticus Male 25°C
Total jumps and runs from three trials
Time (minutes)
50
40
30
20
10
1
5
10
15
20
25
30

not significantly different from males or females at $18^{o}C$ (Table 6:7).

6.2.3 Discussion

Erratic behaviour as a protective device against predation has been described in a number of invertebrates (Humphries & Driver 1967). Humphries (1971) also describes erratic movements and cataleptic posture in the escape behaviour of two species of bird flea *Ceratophyllus garei* Rothschild and *C.fringillae*.

There is little doubt from these data that the three martin fleas behave in a similar erratic way. This activity was significantly less at the lower temperature although the difference in temperature was only $7^{o}C$. A number of workers, for example Humphries *et al.* (*op. cit.*), suggest that the greatest risk to fleas is the activity of the host and therefore the closer the temperature is to that of the occupied nest or the host's body the greater this type of activity needs to be.

These data when related to the results of the respirometry suggest that some of the variability in oxygen uptake between reaction vessels may be due to sudden bursts of activity which, because it is random, is different between flasks. However, although the greatest amount of activity was found at the higher temperature, variation in oxygen uptake was found at all three temperatures in the respirometry data (*cf.* Table 6:2). If these differences are due to activity it would

Table 6:7.

Results of the comparison of activity using a Three-way analysis of variance on log transformed data for temperature, species and sex.

	F	DF	Probability
Species	2.323	2,348	P>0.05
Temperature	31.211	1,348	P<0.001
Sex	18.281	1,348	P<0.001
Species/sex	1.742	2,348	P>0.05
Species/Temperature	10.117	2,348	P<0.001
Sex/Temperature	7.428	1,348	0.01<P<0.05

Sex	Mean
♂	♀
0.53	0.81

Temperature	Mean
$18^{o}C$	$25^{o}C$
0.49	0.80

Table 6:7 continued

Species/Temperature	Mean	SNK
C.farreni 25°C	1.05	
C.hirundinis 25°C	0.74	
C.rusticus 25°C	0.62	
C.rusticus 18°C	0.61	
C.hirundinis 18°C	0.44	
C.farreni 18°C	0.42	

Sex/Temperature	Mean	SNK
♀ 25°C	1.00	
♂ 25°C	0.61	
♀ 18°C	0.53	
♂ 18°C	0.45	

suggest that random erratic movement takes place at lower temperatures where fleas would normally be overwintering and the host absent.

All these activity experiments were carried out in the autumn. In the results from the respirometry carried out in the same season the only significant differences found was at 15°C where the oxygen consumption of *C.hirundinis* was higher than that of the other two species. No significant differences were found in activity between species at 18°C, the result from the respirometry therefore may not to be due to the amount of activity. In the spring respirometry, significant differences were found between species and temperatures. Unfortunately too few fleas were available to measure activity in any species in the spring.

Of the three species *C.rusticus* displayed the least activity. This species has a reduced pleural arch and is thought to have had a longer association with the nest niche than the other two species (Rothschild & Clay 1952). Both these and other workers, eg. Darskaya (1964), distinguish between "nomadic" fleas that possess well developed pleural arches and "settled" fleas such as sticktight fleas, *Echidnophaga* spp., which spend their entire lives on the body of the host and have the pleural arch greatly reduced or lost. The three species of martin fleas appear to be somewhere in the middle of this scale. No precise measure or comparison in the jump between these three species has ever been made, but these results suggest that *C.rusticus* is a less active

species.

The significantly greater activity in the females is of interest. Male fleas are generally thought to be more active than females (Marshall 1981), but it appears that at least in *C.hirundinis*, *C.farreni* and *C.rusticus* the reverse is true. Bird fleas usually mate soon after emerging from the cocoon before a blood meal is taken. This ensures that if only females reach a new nest the next generation is assured. Therefore, since the females will require a blood meal before maturation of oocytes can be achieved, it is far more important for them to gain a host and consequently a greater amount of activity might be expected.

6.3 Weight changes in *C.hirundinis*, *C.farreni* and *C.rusticus* between autumn and spring.

During the calculation of oxygen consumption it was noted that there were often quite large differences in fresh weights between the autumn and spring flea populations.

To see if there was a significant difference overall between autumn and spring fresh weights the data for each species at each temperature were combined and a three-way analysis of variance performed on sex, species and season. The results (Table 6:8) gave significant F values for the main effects, sex($0.01<P<0.05$), season($P<0.001$) and species($0.01<P<0.05$). No first or second order interactions attained significance $P=0.05$).

Table 6:8

Results of the three-way analysis of variance for fresh weight (mg) between seasons with sex, species

	F	DF	P
Sex	8.409	1,92	0.001<P<0.01

	♂	♀
Mean	$0.30_{(38)}$	$0.31_{(66)}$

	F	DF	P
Season	49.684	1,92	P<0.001

	Autumn	Spring
Mean	$0.33_{(60)}$	$0.28_{(44)}$

	F	DF	P
Species	7.761	2,92	0.01<P<0.05

	C.hirundinis	*C.farreni*	*C.rusticus*
Mean	$0.32_{(38)}$	$0.31_{(36)}$	$0.28_{(30)}$
SNK	_____		

The result for sex showed that females were significantly heavier than males and for species *C.hirundinis* and *C.farreni* were significantly heavier than *C.rusticus* but not from each other. The result for season showed that there had been a significant reduction in fresh weight in the spring.

The analysis performed on the fresh weights were repeated for dry weights. The results (Table 6:9) only gave significant F values for species in the main effects, ($0.01<P<0.05$) with *C.hirundinis* and *C.farreni* significantly heavier than *C.rusticus* but not from each other. No first or second order interactions attained significance.

The reduction in fresh weight was unexpected as fleas that have overwintered at relatively low temperatures with high relative humidity are unlikely to lose much moisture. The fleas used in the respirometry almost certainly overwintered outside the cocoon as the disturbance during the collection of the nests in the autumn would have stimulated emergence from the cocoon. However, as discussed in chapter 5, the cocoon does not act as a barrier to water vapour, therefore overwintering inside or outside the cocoon would make little difference to the flea as far as moisture is concerned. The fleas were weighed after acclimation and respirometry at the various temperatures, but as the decrease was observed at all temperatures with a high relative humidity maintained throughout, it seems reasonable to assume that the loss had taken place

during normal overwintering rather than during acclimation.

As respirometry takes place in the presence of a strong alkali some reduction in the relative humidity may occur (Petrusewicz *et al.* (*op.cit.*)). Although this would have been true for both the autumn and spring sets of fleas the spring fleas having overwintered may be more vunerable to stress and the associated drying effects of low humidity may affect their ability to balance water reserves.

To test this, 2 replicates of 12 *C.hirundinis* that had overwintered were placed in reaction flasks containing filter paper soaked in 5% KOH in the centre well after their fresh weights had been determined. Two replicates were also set up with 12 *C.hirundinis* in each but with the filter paper soaked in water. These were left in a 20^{o}C constant temperature room for 16 hours. After this time the fleas were killed with ethyl acetate and weighed. No change in their weights was recorded, therefore the loss of fresh weight in the spring fleas cannot be explained by problems in water balance due to reduced relative humidity. Errors in weighing between the two occasions were considered, but as the same balance was used and recalibrated on all occasions it is unlikely that this was the cause of the differences found. These differences therefore must be due to a loss of water at some time during overwintering.

The water balance in fleas is likely to be controlled by respiration (transpiration), evaporative

cooling and the production of metabolic water by metabolic processing of the fat body. Respiration is certainly a way in which water is lost. Edney (1977) points out that membranes that are permeable to oxygen but not water are unknown, therefore for a particular metabolic rate in terms of oxygen consumption, there is probably a minimal obligatory water loss from the respiratory surfaces.

Temperature regulation by evaporative cooling is directly relevant to water balance and it has been shown in larger insects, such as cockroaches, that short exposures to high ambient temperatures at low humidity can be tolerated (Gunn & Notley 1936). However, owing to the relatively small size and consequently high surface/volume ratio of arthropods, long term evaporative cooling is out of the question. As Scmidt-Neilson (1964) points out, for any animal to maintain a body temperature by evaporative cooling at a particular level under a given heat load, it is necessary to evaporate water at a rate which is roughly proportional to the surface area. No such ability therefore has been demonstrated in small insects. Edney (*op.cit.*) considers that arthropods, such as lice and fleas, are unlikely to show the effects of evaporative cooling for two reasons: first, they are well water proofed because the surface is large relative to their volume, and, secondly, convection is bound to keep their body temperature close to ambient.

Oxidative metabolism is a source of water in

all arthropods. It was apparent from the comparison of fat bodies between autumn and spring that a reduction in the size and distribution had occured between seasons, presumably due to metabolism overwinter. As water is produced during metabolism of the fat body a reduction in water is unlikely.

According to Edney (*op.cit.*) adult fleas do not take up water vapour although Humphries (1967) claims that *C.gallinae* is capable of water vapour uptake. The three species considered here are all closely related to *C.gallinae* but a reduction in fresh weight was observed in all three. Since all three species had been kept at high relative humidity it suggests that these species do not have the ability to take up water vapour.

A loss in fresh weight therefore cannot be explained by the processes discussed. In fleas the most likely loss of water is through respiration. But at the temperatures at which they were overwintered, respiration would be low and little moisture could therefore be expected to be lost in this way. Further, as pointed out by Wigglesworth (1935), even at high temperatures not all of the spiracles are necessarily open being controlled by spiracular valves, which reduces moisture loss. If a depleted fat body in the spring means less metabolic water is produced, water balance may pose more of a problem at this time of the year but, as the results from the experiment with KOH in the respirometer reaction flasks showed even under

drying conditions no loss of fresh weight was observed. The loss of fresh weight in the spring fleas therefore cannot be explained.

The comparison of dry weight between autumn and spring shows no significant reduction despite the fact that visual examination showed a marked decrease in the fat body (Plates 14 and 15). However, the mean dry weight in both sexes show a decline, although not significant, in the spring (Table 6:10), which indicates that some fat body has been used overwinter.

Table 6:9

Results of the three-way analysis of variance for dry weight (mg) between seasons with sex and species.

	F	DF	P
Season	2.085	1,92	P>0.05
Sex	2.425	1,92	P>0.05

	F	DF	P
	4.229	2,92	0.01<P<0.05

Species	*C.hirundinis*	*C.farreni*	*C.rusticus*
Mean	$0.107_{(38)}$	$0.105_{(36)}$	$0.093_{(30)}$
SNK	_____	_____	

Table 6:10

Dry weight means for each species and sex between seasons.

	Autumn Mean
C.hirundinis ♂	0.105
C.farreni ♂	0.102
C.rusticus ♂	0.090
C.hirundinis ♀	0.113
C.farreni ♀	0.114
C.rusticus ♀	0.102
	Spring
C.hirundinis ♂	0.103
C.farreni ♂	0.101
C.rusticus ♂	0.089
C.hirundinis ♀	0.105
C.farreni ♀	0.104
C.rusticus ♀	0.091

Chapter 7

Population dynamics, breeding cycles, larval morphology and survival of *C.hirundinis*, *C.farreni* and *C.rusticus*.

7.1 Introduction

Little has been written on the population growth of *C.hirundinis*, *C.farreni* and *C.rusticus* but Jurik (1974) in Czechoslovakia studied populations of *C.hirundinis* and *C.rusticus*. He found engorged individuals of both species over the period March-September. Females of both species were found with developing eggs between April and August. As the earliest engorged individuals were found before the return of the martins, Jurik took this as a clear indication that part of the population had fed on incidental hosts, probably intruding sparrows, before the arrival of the major host. Flea larvae of both species were recorded over the period May-September, although unfortunately he does not say how he differentiated larvae of the two species.

Newly emerged, but not yet engorged, individuals were detected over the period July-September. At the end of the martins' first brood a mixture of reproducing and non-reproducing individuals was present as well as larvae. Jurik concluded from these data that both species produce one generation annually, which increases gradually throughout the

martin breeding season.

In the USSR, Darskaya (1964) observed that *C.farreni* started laying eggs soon after the martins returned (5-10 days). After the martins left in the autumn *C.farreni* ceased to multiply and the old fleas died off during the winter, while the next generation overwintered in cocoons.

Gordeyeva (1969) also studied the development of *C.farreni* in the USSR over a period of 3 years in the nests of *Hirundo daurica*. He reported that during the winter the principal mass of *C.farreni* were in the pupal stage (November-February). In March, nests on the south side of the buildings began to warm up which stimulated emergence of the adults. The fleas mated in the nest and copulation lasted up to 2 hours, the duration seemingly dependent on temperature. He recorded development of the eggs as soon as *C.farreni* emerged from the cocoon and before a blood meal had been taken.

It is clear from these studies that reproduction in all three species of flea takes place principally when the martins are resident, although it appears that they are able to reproduce in the presence of unusual hosts. As these studies had all taken place in Eastern Europe where the tendency is for longer winters and shorter summers than England, it seemed appropriate to study the breeding cycles of these species in England.

7.2 Artificial nests.

To investigate how populations of *C.hirundinis*, *C.farreni* and *C.rusticus* increase throughout the martins' breeding season, 10 artificial nests were secured to house eaves at a house in Thurnby Leicestershire in March 1978. Such artificial nests have been used successfully in the study of house martin energetics in Scotland (Bryant *pers. comm.* and 1979), and also in a study of *Crataerina hirundinis* (Summers 1975). Both these workers made their nests from exterior "Polyfilla" and sawdust in a Plaster of Paris mould. In this study nests were purchased from a supplier (Nerine Nurseries, Welland, Worcestershire).

The nests were lined with a small quantity of cut grass and feathers and seeded with fleas, a known number of each species and sex being placed in each nest. When the martins arrived in May they initially showed interest in the artificial nests but then built their own mud nests between the artificial ones. As can be seen from Plate 16 the artificial nests were placed so that they faced along the eaves because it was much easier to attach them with screws to the protruding wooden beams than to the brick. As the natural nests often have their entrances facing outwards, it was felt that the entrances facing along the eaves were making them less attactive to the martins. In March 1979 all of the artificial nests were re-postitoned so that their entrances faced outwards (Plate 17). On re-positioning the nests the contents were examined only dead fleas

Plate 16.

Artificial nest with entrance hole facing along the eaves.

Plate 17.

Artificial nests with entrance holes facing out from the eaves.

were recovered. After the nests were re-positioned all of the natural nests were removed in the hope that the returning martins would take the easy option and use the artificial nests.

The artificial nests were lined and seeded as before. The martins showed only a passing interest again prefering to build their own mud nests. Why these nests were not attractive to the martins is not clear. The supplier of the nests assured me that the information he had received, not only in this country but elsewhere in Europe, was that these nests were a great success. It was decided to discontinue the use of artificial nests.

Rothschild (*pers. comm.*) suggested seeding occupied nests of the swallow *Hirundo rustica* with martin fleas. These species are recorded in swallows', nests from time to time although it is not clear if breeding has ever occurred. In spring 1979 4 occupied swallow nests were seeded with *C.hirundinis* (2 nests) and *C.farreni* (2 nests) at a farm in Sapcote, Leicestershire. The nests were examined shortly after the young had flown, and revealed only dead fleas which proved to be 3 *C.hirundinis* in one nest and 1 *C.farreni* in another with two nests containing no fleas. Seeding swallows nests with martin fleas was repeated in the following year but again no living fleas were recovered. It was concluded that swallows nests, at least in the midlands of England, are not suitable for either species. It is worth noting that in twentytwo swallow nests collected in Leicestershire incidental to this

study, no martin fleas were found.

Recently a study by Brown & Bomberger Brown (1986) on *Ceratophyllus celsus* in nests of the cliff swallow in America found that this bird would avoid nests with large numbers of fleas. They discovered this by fumigating some nests in the winter when they were not occupied and then watching the behaviour of the returning swallows in the spring. *C.celsus*, as already mentioned in chapter 5, gathers on the outside of the nest, particularly in spring. Returning swallows hover in front of the nest and presumably at this time the fleas jump onto them. Brown *et al.,(op. cit.)* felt that at this time the birds could see the fleas and would therefore avoid nests with large numbers on the outside. The question here is whether the artificial nests failed because the returning martins detected the fleas. Based on personal observations and the results of the sticky cards passed over occupied nests at various times during the martins' breeding season (see chapter 5) the answer is almost certainly no.

Since the artificial nests had failed it was decided to monitor the breeding cycles in natural nests. Taking samples from natural nests is virtually impossible, since the entrance hole is too small to allow any sampling device, for example a pooter, to be inserted. Any widening of the entrance hole or a hole made elsewhere in the nest wall big enough to take a sampling device would weaken the stucture and almost certainly cause the nest to fall down. Since house

martins are often two brooded it was decided to collect nests, if possible, when newly built but before any egg was laid, after the first brood had flown and finally, immediately after the second brood had flown.

The removal of nests at these different stages posed a number of problems. For example it is illegal to remove nests whilst they are still occupied; also the vast majority of people approached would not allow the removal of nests from their property while they were still in use. However, natural disasters happen to nests during the breeding season and by making an appeal in the local press and radio a few nests were obtained. Nests from the following categories were collected and comprised, 5 nests that had just been built in the spring, 1 nest from the previous season colonised in spring, 3 nests after the first brood had flown and 10 nests soon after the young martins had fledged and departed in September. All nests were sorted by hand for all stages of the life cycle (Table 7:2). Pupae were, however, difficult to find concealed in cocoons amongst the nest debris; the numbers found therefore must be considered an under estimate. In all cases the pupae were not sufficiently advanced to allow identification, therefore only the total number of pupae found is given. Similarly eggs were extremely difficult to find, their presence therefore was noted but no count was made.

In order to study the breeding cycles in these fleas it was necassary to make microscopical examination of adult female ovaries in order to assess reproductive

condition and also attempt to distinguish between the larvae of each species.

7.3 Methods used in the examination of oocytes.

Two methods were used in the examination of oocytes, histological and dissection.

7.3.1 Histology.

Two histological methods were tried, firstly the method employed by Rothschild (1976) and secondly a method usually used for the preparation of material for electron microscopy.

In the Rothschild method living fleas were aneathetised with CO_2, identified under a dissecting microscope and then placed in Duboscq-Brasil fixative for 12 hours at $30^{o}C$. After fixation the fleas were dehydrated in a series of alcohols, cleared in cedar wood oil and embedded in Paraplast high melting point wax. Sections were cut on a rotary microtome at a thickness of 6-8µm. The sections were stained with Mallory triple stain. For a full account of the method see appendix 2.

The major problem encountered in using this technique was that because flea cuticle is very tough a large number of failures occured due to inadequate penetration of the wax. This caused pieces of the body to be torn out of the block during section cutting. Removing the thorax and a small piece off the end of the

abdomen just prior to fixation improved penetration of both fixative and wax. However this did not eliminate parts of the body wall being torn away during sectioning. This was apparently caused by the wax not being sufficiently rigid to hold the cuticle as the microtome knife cut through the block. If the sectioning of a large amount of material was to be possible a more rigid material was needed for blocking.

Epoxy resins are widely used for blocking a wide range of biological materials to be sectioned for electron microscopy, and can be used for light microscopy. As resin is considerably more rigid than wax it therefore seemed worth while trying this method.

Method

Fleas were anaethetised as before. Their abdomens were separated from the thorax and a small piece cut from the posterior end of the abdomen to ensure rapid penetration of the fixative and resin. (The complete schedule for this method is set out in appendix 2).

This method produced good sections with little tearing of the cuticle. After a few sections (20-30), however, the glass knife had to be changed because its edge became damaged and would start to score the block face. Because 1µm sections were the thickest that could be cut using this method and because of the frequency the knife had to be changed, this proved a very time

consuming method, taking up to 6 hours to section one flea.

Since the main aim of this exercise was to ascertain at what times mature eggs were present in female fleas and because the examination of a large number of fleas would be involved, this method would clearly take too long for practical purposes. Dissection of various organs in the flea have been used to examine changes in other organs associated with oocyte maturation (Mead-Briggs 1964). It seemed therefore that this might be a better proposition for dealing with a large amount of material.

7.3.2 Dissection of ovaries.

Female fleas were anaethetised with CO_2 and anchored to the bottom of a petri dish which had been covered with a layer of insect wax, (*Cf* Krogh & Weis-Fogh 1951) with a pin pushed through the head/thorax region, with the flea lying on its side.

The dish was flooded with Insect Ringer which had been kept at $5^{o}C$. To keep the whole arrangement cool the petri dish was placed inside a larger petri dish containing ice. It was essential to keep everything as cool as possible as rapid breakdown of tissues occurred if temperatures rose above $10^{o}C$. The fleas were dissected under a dissecting microscope by gently tearing the sternites along the ventral line with two fine tungstan needles. When the abdomen had been opened along its length the body wall was gently peeled back and anchored with pins. At this stage all the organs

could be seen. By gentle teasing, the ovary was freed by severing the terminal filaments, at the anterior end, and by a posterior cut across the common oviduct at about the spermatheca. The whole ovary was placed on a microscope slide in a drop of Insect Ringer. A coverslip was placed over the preparation and, to prevent the ovary being squashed, was supported by a coverslip on either side of the preparation.

Routine examination was carried out with the aid of phase contrast under a compound microscope at a magnification of X100. Photographs were taken with the aid of a Nomarski interference contrast system. This had the advantage over phase contrast in that the image is not greatly affected by thick structures out of the plane of focus and is particularly valuable for studying thick refractile objects. With phase contrast haloes are usually visible when thick objects are viewed. A comparison between dissected and sectioned oocytes can be seen in plates 16-19. Of the two methods dissection and examination of the oocytes under phase contrast was found to be the more satisfactory for handling large numbers of fleas.

7.3.3 Description of flea ovary and methods of examination.

The anatomy and maturation of oocytes has been studied in a number of flea species. The internal anatomy is well described (eg. Rothschild 1976;

Rothschild, Schlein & Ito 1986), whilst the embryology has been studied in a number of species, notably the rabbit flea *Spilopsyllus cuniculi* (Dale) (Mead-Briggs 1964, Rothschild & Ford 1966, 1973).

In *C.hirundinis, C.farreni* and *C.rusticus* the ovary comprises 6 panoistic ovarioles. These lie in the dorsal half of the abdomen with 3 ovarioles on each side of the gut. Each ovariole consists of a linear array of oocytes in different stages of development which can be divided into five regions (Counce & Waddington 1972). The regions are I terminal filament, II germarium, 3 previtellogenic stages of the vitellarium, IV vitellogenic stages, V mature ovum.

In this study oocytes were considered immature if the follicular epithelium, follicle cells and nucleus were visible (Plates 18 & 19). In mature oocytes the follicular epithelium and follicle cells are stretched as the volume of the oocyte increases with yolk droplets (Plates 20 & 21). The diameters of the immature oocytes in zone IV are between 50µm and 80µm and in the mature oocytes up to 200µm. Yolk droplets in the mature oocyte reach diameters of 15µm to 20µm. The largest oocyte observed was in *C.hirundinis* and had a diameter of 300µm. The number of ovarioles containing mature eggs varied in each species from 3-5.

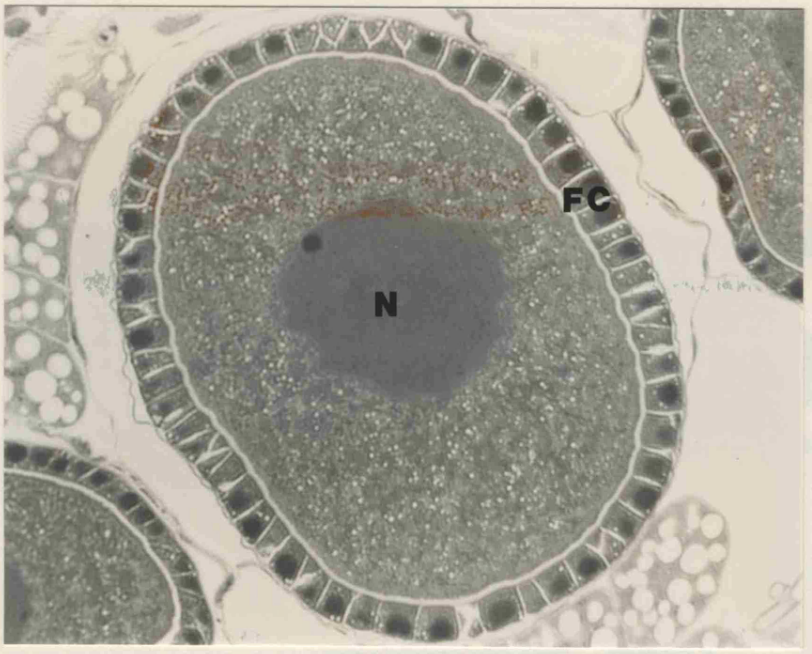
No special study of spermatogenesis in the male fleas was made as in these, and other species of bird fleas, spermatogenesis is already complete on emergence from the pupa, with mating occurring shortly

Plate 18.

50µm

Stage IV oocytes of *C.hirundinis* viewed under Nomarski Interference Contrast.

Plate 19.

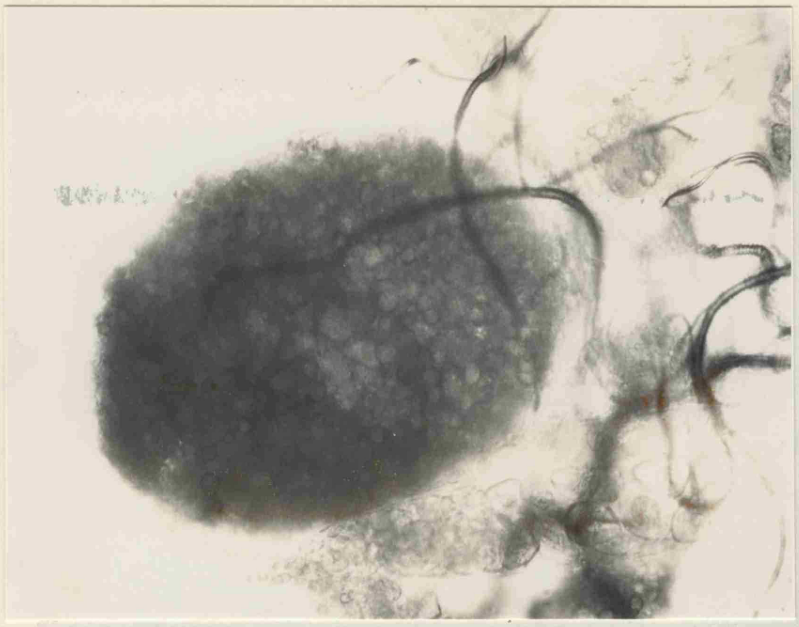


50µm

Stage IV oocyte of *C.hirundinis* in section.

N= nucleus; FC= follicle cells.

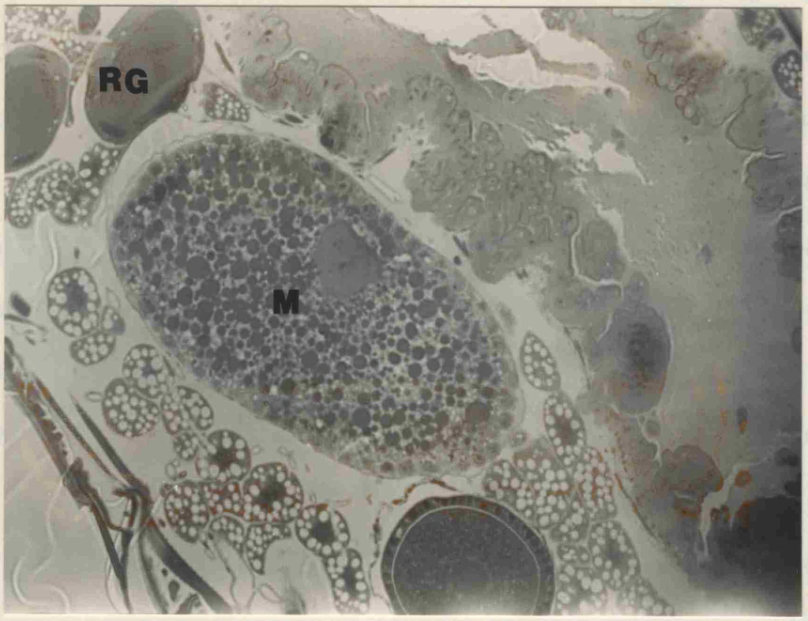
Plate 20.



100µm

Mature oocyte (stage V) of *C.hirundinis* viewed under Nomarski Interference Contrast.

Plate 21.



100µm

Mature oocyte (stage V) of *C.hirundinis* in section.

M=Mature oocyte, RG=Regressing oocyte.

after emergence from the cocoon and before a blood meal is taken (Holland 1955; Rothschild & Clay 1952).

7.4 Rearing larvae.

In an attempt to establish criteria for larval identification, larvae taken from martins nests aquired incidental to those nests used in the study were reared singly in tubes containing a 50/50 mixture of dried chickens' blood and powdered dried mud, approximately 5g of each. Chicken's blood was the nearest blood to house martin's that could be obtained and powdered dried mud was used as this covers the bottom of the nests where most larvae appear to live. The larvae were kept at a temperature of $20^{o}C$ and a relative humidity of 80%-90% until adult.

Of the 100 larvae set up 36% died before pupation. As all the larvae collected for this experiment came from nests in the autumn they were mostly third instar larvae which took around 1 week to pupate, and all larvae had pupated after 3 weeks. At $20^{o}C$ the time from pupation to emergence as an adult took between 14 and 17 days. The rather high mortality was a little surprising since all the larvae appeared healthy at the beginning. A number of workers (eg. Sikes 1931) have found that different diets, relative humidities and temperatures affect the survival of flea larvae. However, since 64% of the larvae survived, the conditions offered must have been acceptable to them, unless those that died were all of one species that was

particularly intolerant of these conditions.

To investigate larval survival under different conditions of temperature, relative humidity and varying quantities of food 5 replicates of 25 larvae were set up under each of the following treatments; 3 different food treatments, at 3 different humidities and at 3 temperatures. These were left until all of the adults had emerged. The treatments were 10g blood/10g mud, 2g blood/18g mud and 18g blood/2g mud. Each food treatment was kept at $15^{o}C$, $20^{o}C$ and $25^{o}C$ and at each temperature at relative humidities of 40%, 70% and 90%.

In the treatment with 18g blood/2g mud only 7 larvae survived out of all the treatments. This was almost certainly because the blood was hygroscopic even at the lowest humidity and coated the outside of the larvae which affected locomotion and may also have blocked their spiracles.

Larvae in the other treatments were compared between treatments using a three-way analysis of variance on arcsin transformed data on the percentage surviving in each treatment. The results (Table 7:1) gave no significant F values for the main effects or first order interaction indicating a tolerance of a range of conditions, although humidities and temperatures used were within those found in the nest when occupied by martins. Unfortunately larvae were sufficiently difficult to obtain that only a limited number of trials could be performed. No differential

Table 7:1

Results of the analysis of variance on the percentage survival (arcsin transformation) of flea larvae with two food treatments, three humidities and temperatures.

Temperature	Food	
	Mean±SE	
15^0C	10g blood/10g mud	2g blood/18g mud
	57.9305±3.1774	61.4870±2.4443
	56.1591±1.8978	57.1823±2.0825
	57.3268±2.9921	60.0768±3.3371
20^0C	56.4248±3.8044	64.5373±3.0051
	56.8125±2.9023	60.1548±3.4001
	58.2172±2.2563	61.9452±2.0524
25^0C	59.8182±2.3201	59.4649±3.0705
	57.2568±2.4658	57.1125±1.5165
	58.1442±1.6303	55.8001±2.7610

Humidity		
Mean±SE		
40%RH	70%RH	90%RH
59.9438±1.2170	57.4463±0.9433	58.5851±1.0224

	F	DF	P
Food	2.968	1,72	P>0.05
Temperature	0.689	2,72	P>0.05
Humidity	1.295	2,72	P>0.05

Table 7.1 continued.

First order interaction.

	F	DF	P
RH/Food	0.391	2,72	P>0.05
RH/Temperature	0.141	4,72	P>0.05
Food/Temperature	1.879	2,72	P>0.05

survival between species could be detected as the species of larvae were not known at the beginning of the trials. At at the end of the trials adults of both *C.hirundinis* and *C.farreni* were present regardless of treatment.

7.5 Larval morphology.

The larvae of fleas are apodous and pass through 3 larval instars before pupation. Little has been written on the morphology of the larvae of the Ceratophyllidae. Kirjakova (1965) describes the 3rd instar larva of both *C.gallinae* and *Monopsyllus sciurorum*. Smit (*pers. comm.*) considers it unlikely that the larvae of closely related species of flea can be distinguished on morphological criteria. Pilgrim (*pers. comm.*) has examined larvae from house martin nests that contained adults of *C.hirundinis*, *C.farreni* and *C.rusticus* but has so far been unable to find any consistent differences in chaetotaxy or any other characters that have been used in larval flea taxonomy eg. number of teeth on the mandibles, (Cotton 1970).

In the nests taken at different times of the martin breeding season each nest contained more than one species, and consequently the larvae were always likely to be of mixed species populations. From the attempt to maintain monocultures of each species in the laboratory (described inChapter 8) four 3rd stage larvae of *C.hirundinis* were reared. To see if larvae of *C.hirundinis* could be separated from larvae of other

species in mixed populations a detailed examination of the external morphology of known *C.hirundinis* larvae was made. Of the four larvae reared three were prepared for scanning electron microscopy and the other mounted on a slide in polyvinl lactophenol. Also mounted on slides in polyvinl lactophenol was the moulted 3rd stage larval skins from which adults had been reared.

7.5.1 Description of *C.hirundinis* larvae.

The larva of *C.hirundinis* shows a typical flea larva habitus having an apodous, cylindrical body with a sclerotized head at the anterior end. There are 13 body segments, the last is produced into a pair of anal struts. The body-length when mounted of third instar *C.hirundinis* larvae was between 4mm and 4.4mm.

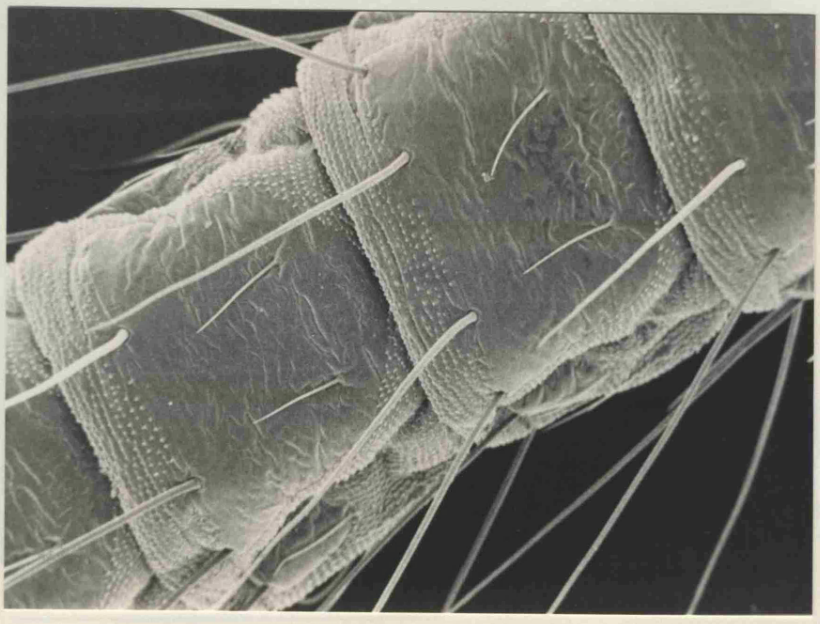
The dorsal surface of each body segment has a plate of thickened chitin which is somewhat saddle-shaped. Each "saddle" possesses 2 short anterior setae and 4 long posterior setae (Plate 22).

The lateral surface of each segment possesses a single chitinous plate from which a single seta arises with a single short seta at the anterior edge of the plate (Plate 23).

On each segment of the ventral surface are two chitinous plates from each of which arises a single long outer and shorter inner seta. Towards the anterior edge of each segment are 4 small chitinous plates with a single seta arising from each (Plate 24).

Between these plates over the whole body are

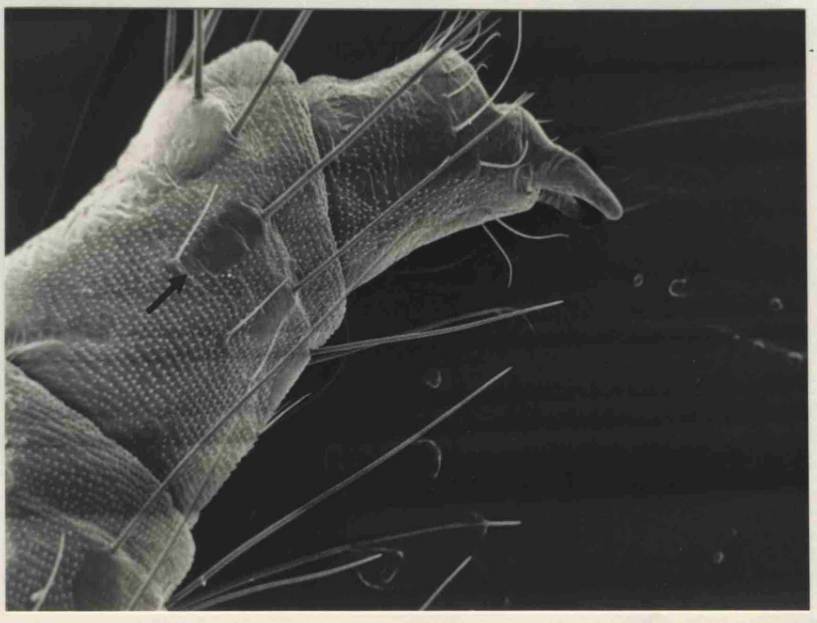
Plate 22.



0.25mm

C.hirundinis larva, dorsal view of body segments 7 and 8.

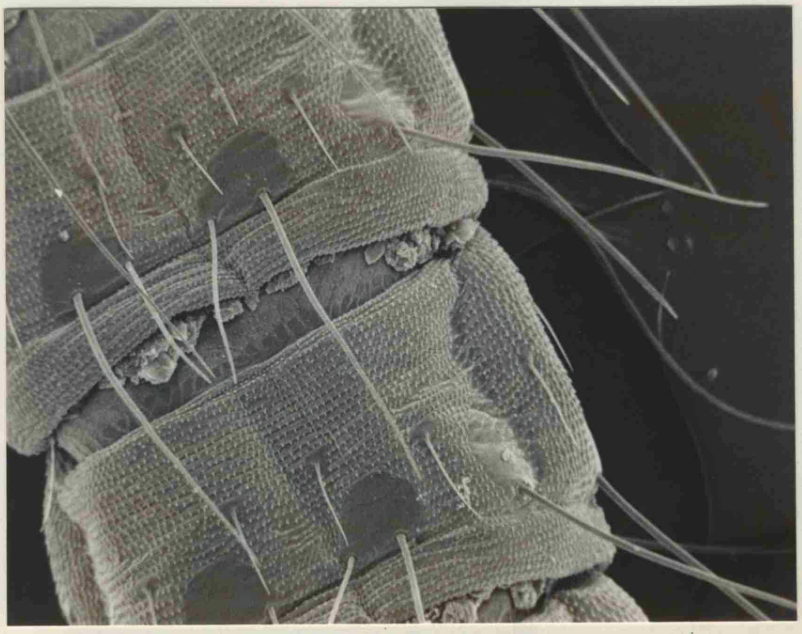
Plate 23.



0.25mm

C.hirundinis, lateral view of posterior body segments showing plate (arrowed).

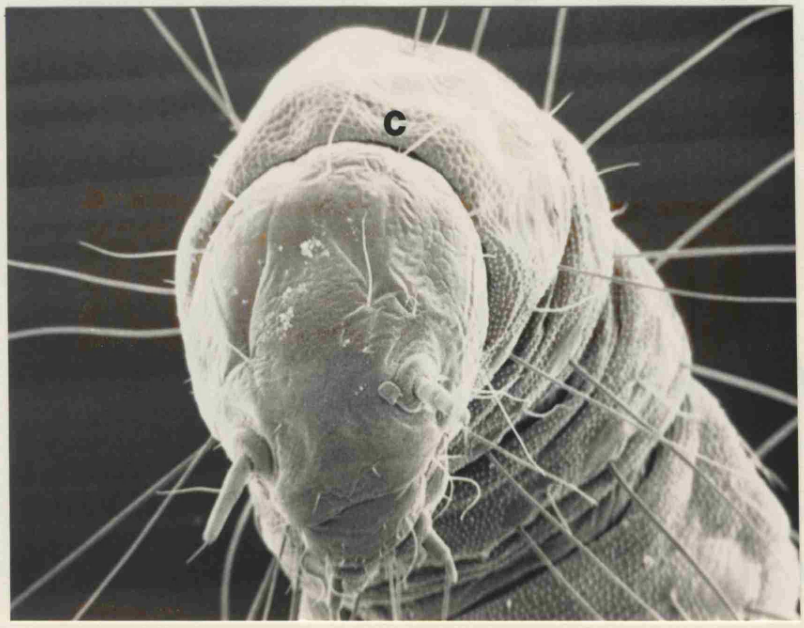
Plate 24.



0.25mm

C.hirundinis, ventral view of body segments 7 and 8.

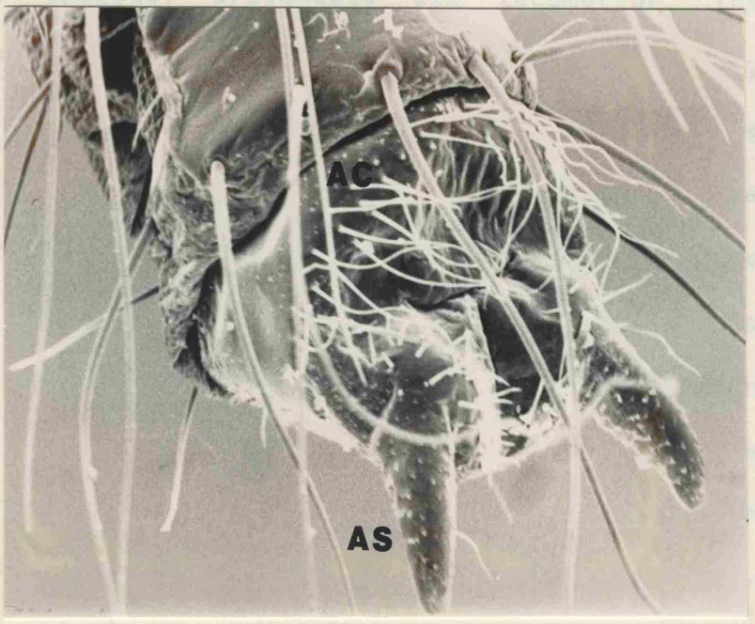
Plate 25.



0.25mm

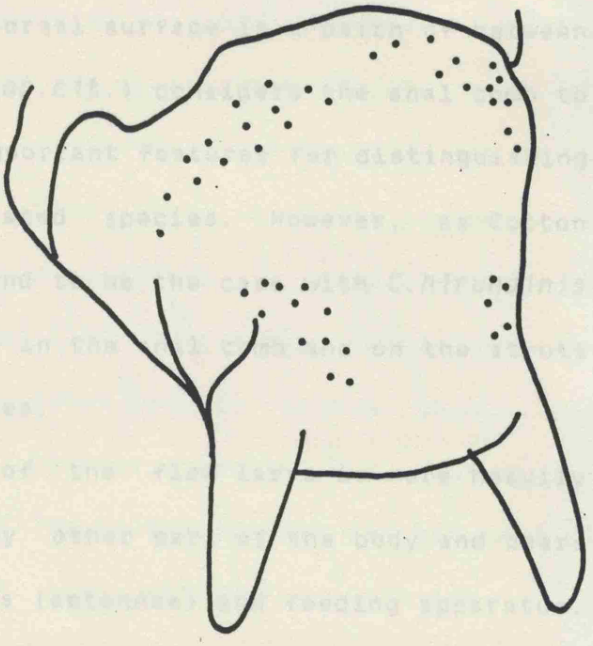
C.hirundinis larva, head and collar (C) on first thoracic segment.

Plate 26.



0.25mm

C.hirundinis larva last body segments showing anal struts (AS) and anal combs (AC).



0.25mm

C.hirundinis larvae showing last body segments and the positions of setae in the anal comb and on the anal struts.

small backwardly pointing denticles, which, as these larvae are apodous, presumably aid locomotion. The pattern of setae appears the same on 11 of the body segments. The 1st thoracic segment differs from the others in that it has a collar of what appear to be small chitinous plates along its anterior margin (Plate 25). The 13th segment is produced into two anal struts which are, as in other species of flea larvae, the main locomotory appendages (Bacot & Ridewood 1914). On the dorsal surface of this segment are the anal combs. In descriptions of other ceratophyllid larvae eg. *Megabothris turbidus, M.walkeri and M.penicilliger* (Cotton *op.cit.*) and *C.gallinae* (Kirjakova *op.cit.*) the anal comb comprises 2 rows of setae. In *C.hirundinis* 2 rows are also present (see Plate 26). At the base of each strut on the dorsal surface is a patch of between 8-12 setae. Cotton (*op.cit.*) considers the anal comb to be one of the most important features for distinguishing between closely related species. However, as Cotton found and as was found to be the case with *C.hirundinis* the number of setae in the anal comb and on the struts varies within a species.

The head of the flea larva is more heavily sclerotized than any other part of the body and bears the main sense organs (antennae) and feeding apparatus. Setae are arranged on the dorsal surface of the head to form anterior and posterior rows. Klein (1964) and Kirjakova (*op.cit.*) considered that the ventral seta belonged to the posterior row but Elbel (*op.cit.*),

Stark, Campos & Elbel (1976) consider it to belong to the anterior row which in larve of *C.hirundinis* it clearly does (see Figure 24). Elbel (*op.cit*) considers the position of these setae may be important in distinguishing between related species.

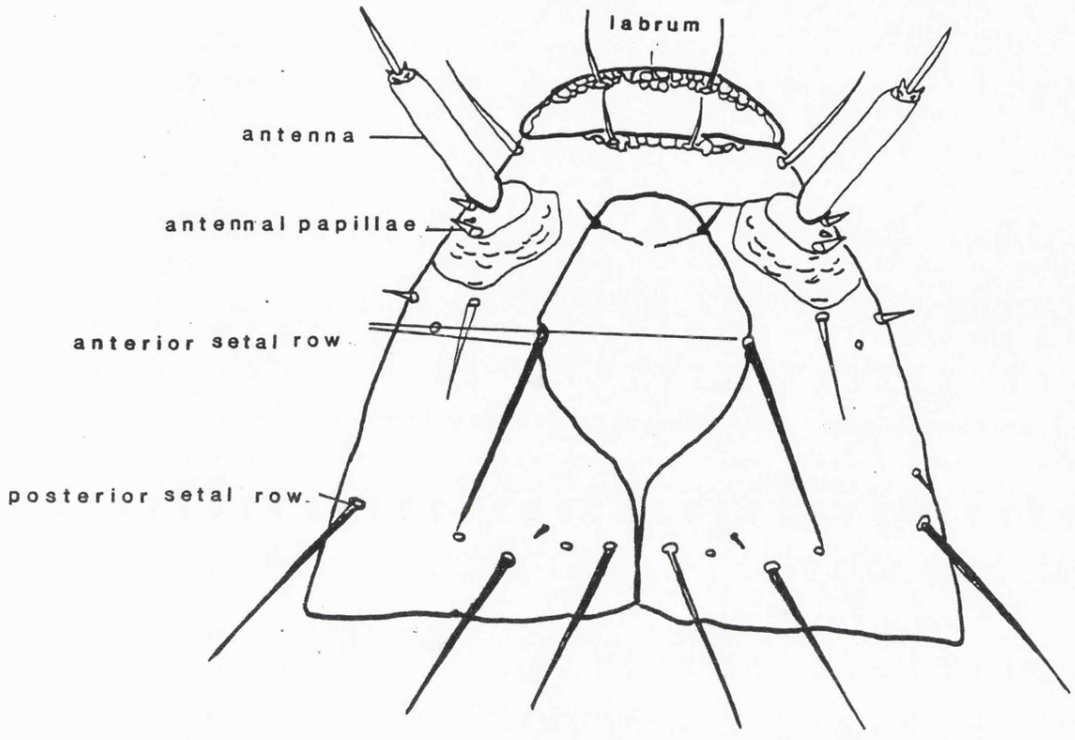
The mouth is nearly terminal in the lower half of the head; the most anterior part of the whole head is the labrum. Projecting from the mouth are the maxillary and labial palps. Each maxilla bears 2 sclerites, which form the posterior cardo separated by a chitinous thickening from the anterior stipes, which agrees with the descriptions of many flea larvae (*cf.* eg Sikes 1930). The cardo bears 2 setae and the stipes 1 seta posterior to the 2-segmented palp. the anterio-medial portion of the stipes below the mouth has a number of spines which is presumably what Bacot *et al.* (*op. cit.*) refer to as the maxillary brush.

The labium lies between the maxillae and bears a 1 segmented palp. Often obscured by the labrum are a pair of well developed mandibles, which possess 9 teeth in all 4 specimens of *C.hirundinis*. The number of teeth recorded for other ceratophyllid larvae varies. For example Stark *et al.* (*op.cit.*) records 6-7 teeth on the mandibles of *Monopsyllus anisus* Schrank and *Nosopsyllus i.iranius* (Wagner & Arg) whilst Kirjakova (*op. cit.*) records 7-9 teeth for both *Monopsyllus sciurorum* and *C.gallinae*.

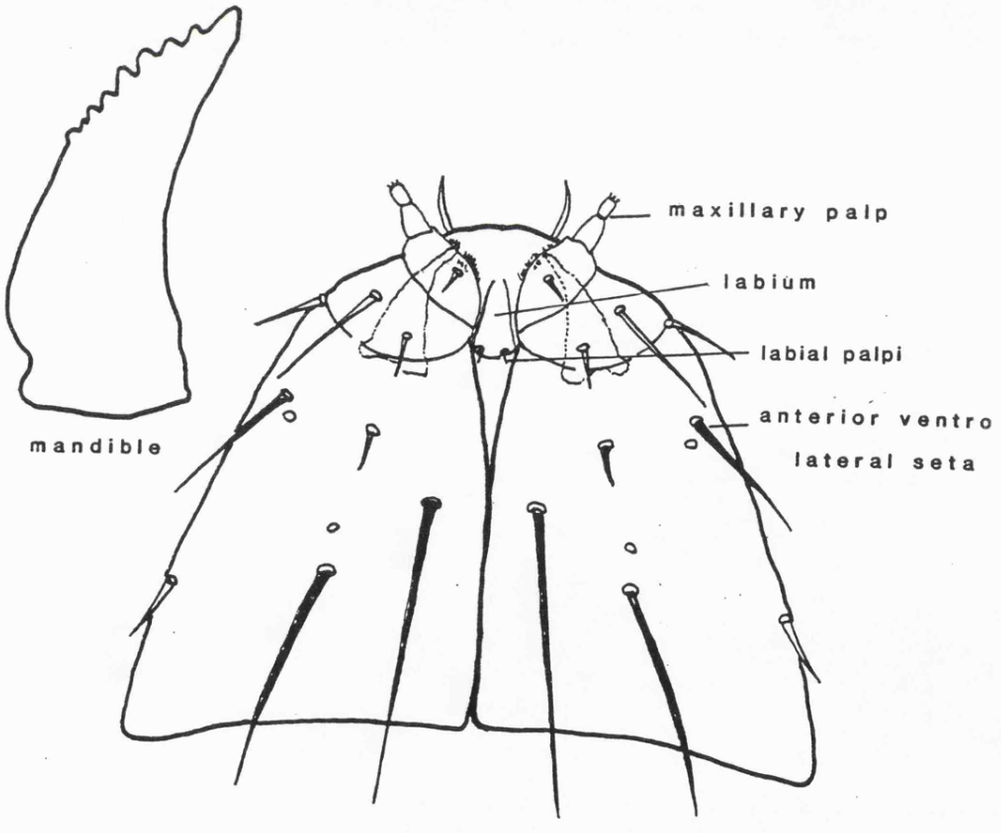
Antennae are the most prominent appendages of the head; each forms a cylinder which tapers slightly at

Figure 24

C.hirundinis larva



Head Dorsal



Head Ventral

0.1mm

the distal end. The top of the antennae bears a stiff seta surrounded by 4 minute projections. The whole antenna projects from a flattened dome. On which there are 3 pointed papillae interspersed with 3 much smaller papillae. This arrangement corresponds with Bacot *et al.* (*op.cit.*) type B larva. The larvae of *C.hirundinis* examined here appear to conform in all respects with the typical ceratophyllid larva. From Kijakovas's (*op.cit.*) description of *C.gallinae*, *C.hirundinis* appear to differ only in the minor setae. For example they do not have very small setae near the anterior edge of both dorsal and ventral surfaces of each segment .

Comparing the anal combs of *C.hirundinis* with Kirjokova's drawings of *C.gallinae*, *C.hirundinis* has a similar number of setae. There are more setae however, on the base of the anal struts in *C.hirundinis*.

Of the 905 larvae examined as well as the shed larval skins no consistent differences were found between individuals. In one larva 4 antennal papillae instead of 3 was found. As this was the only larva of this type out of so many examined from mixed populations it is considered to be an abnormality. It must be concluded that morphologically the larvae of all three species are identical although they could doubtless be differentiated with the advanced biochemical and genetic techniques now available. The head capsule measurements made to assess population structure could only be made therefore on the total number of larvae occurring in the nest regardless of species, and could only be used as a

rough guide to the overall composition of larval instars.

Larvae from nests taken at different times of the martin breeding season were mounted on slides in polyvinyl lactophenol. Elbel (1951) found that of the many measurements made of different parts of the body of *Ctenocephalides felis*, *Orchopeas leucopus* and *Nosopsyllus faciatus* (eg depth and length of head capsule, body length) the maximum width of the head capsule was the least variable although there was an overlap in these measurements between the 1st and 2nd instars. However, the 1st instar larva could be distinguished from the 2nd by the presence of the egg burster on the head. No overlap was found between the 2nd and 3rd instars. In this study in an attempt to assess how many larval instars were present in the nest at any one time head width measurements were made of mounted specimens using a compound microscope and a calibrated eyepiece graticule.

From the measurements made of the maximum head capsule width the smallest head capsule measured 0.26mm. All of these larvae possessed an egg burster on their heads (Plate 27) and were therefore obviously 1st instar larvae. The results of the head capsule measurements with larvae from nests just after the first brood of martins had flown and in recently vacated nests in the autumn (Figure 25) presents a confusing picture. Fleas have 3 larval instars and there is no reason to

Figure 25 Head capsule width measurements of flea larvae from house martin nests

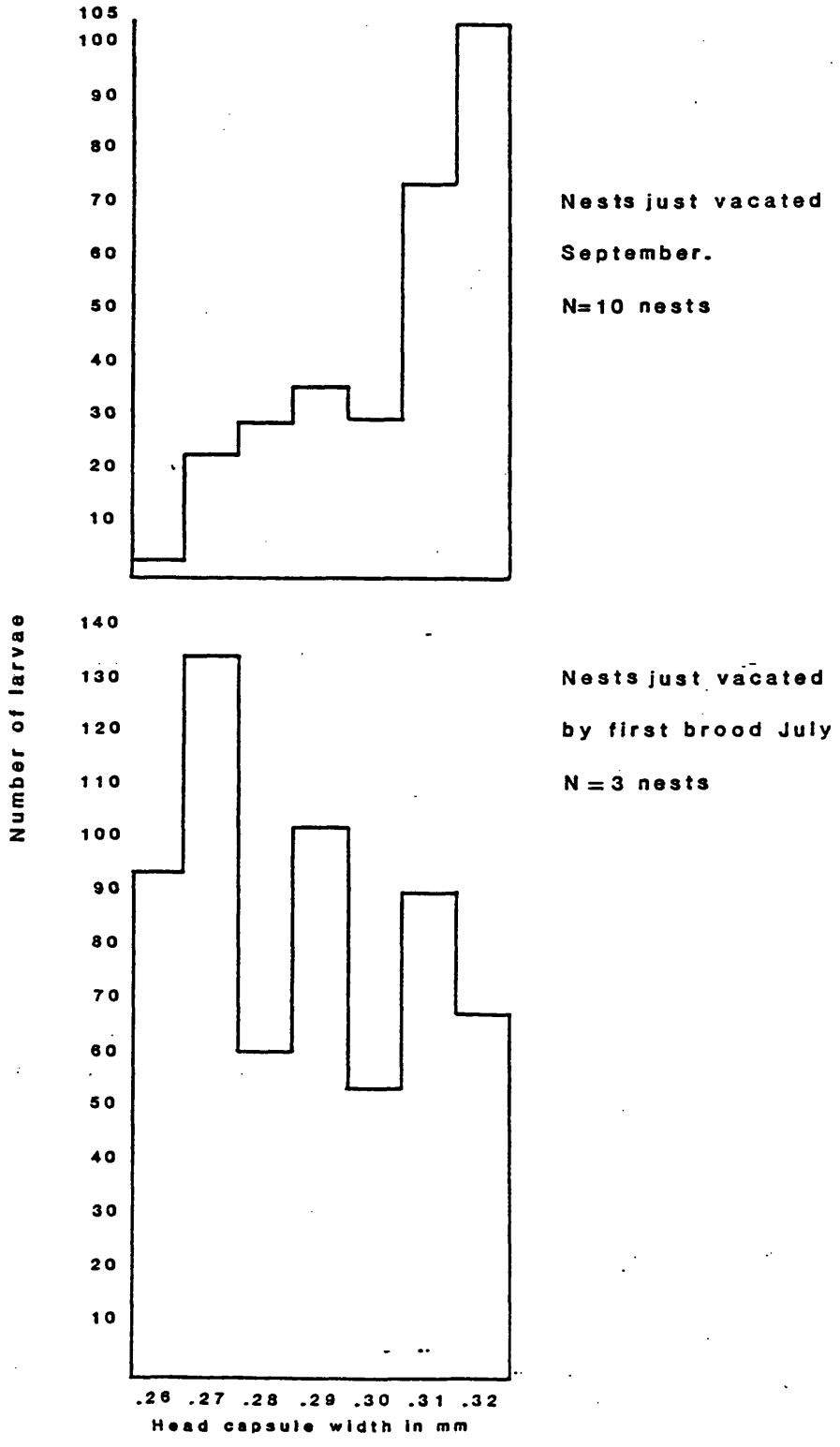
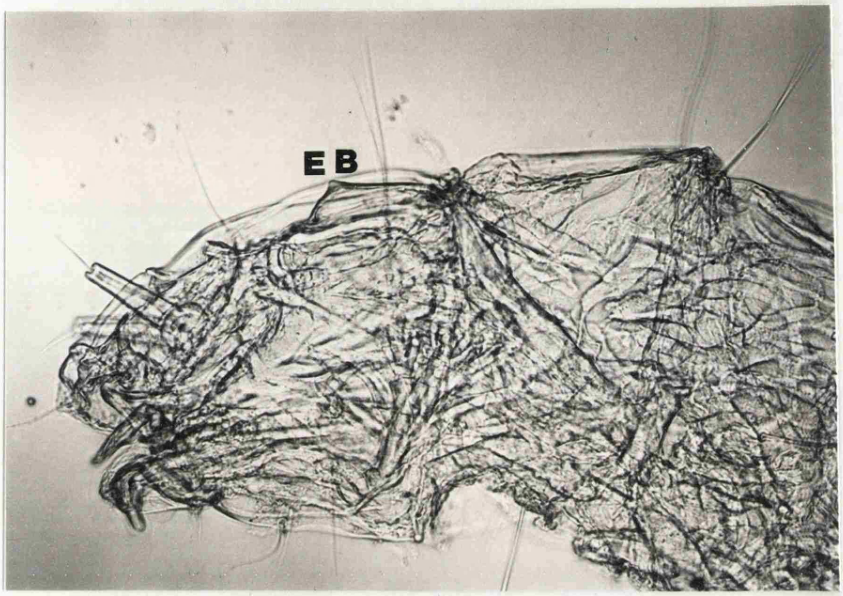


Plate 27.



0.1mm

First stage larva of *C.hirundinis* showing egg burster (EB).

suppose that the three species of martin flea are any different. However, in Figure 25 there appears to be 4 instars present. To some extent this may reflect the relative crudeness of the measurements, however, it may be because the larvae collected include all three species. Adult *C.hirundinis* is the largest of the three species (2.25-2.75mm) with *C.farreni* and *C.rusticus* of a similar size (2.0-2.5mm). It may reasonably be expected therefore that the larvae would also differ in size although it is curious that all first instar larvae had the same head capsule measurements.

Adult males of each species tend to be smaller than females it would therefore be reasonable to expect larvae of each sex to also differ in size which may further confuse the picture. It is not possible therefore with these data to extract any information on abundance of larval instars for each species.

In the newly built nests, which with only 12 larvae are not shown in Figure 25, 9 were 1st instar larvae and the other 3 were 2nd instar. What is clear from Figure 25 is that there is a shift in the size distribution of larvae from one dominated by smaller instars at the end of the first brood of martins, although other instars are present, to one dominated by larger instars in the autumn nests. This indicates that egg production diminishes as the time for the martins to migrate approaches. This is also substantiated to some extent by the absence of eggs in three of the September

Cornwall nests and the low number of females with mature oocytes in all ten september nests (see Table 7:1). Why there should be a slowing down in egg production while the martins are still in residence is unclear. The age of the females is one possibility if they are reaching the end of their reproductive capabilities at this time. Another possibility is that although the martins are still using the nest at this time of the year it is usually only to roost in (*pers. obs.*). Therefore, the absence of the martins for long periods may also play a part in the cessation of flea egg production.

7.6 Results from nests collected for flea community structure.

The results (Table 7:2) show that in newly built nests the starting populations are low (<15 adults). However, at this time egg production is under way and larvae are already present, albeit in small numbers. Martins take on average 14 days to complete a nest (McNeil & Clark 1977), therefore either the oocytes mature in less than 14 days or they begin to mature as soon as the adult receives a blood meal. This presumably could be when the adult fleas first encounter martins returning from migration.

The one nest which was re-occupied from the previous year contained a larger number of fleas than the newly built nests, but only relatively few (<40%) had taken a blood meal and none of the females contained

Table 7:2.

Population structure from martin nests just built, after the first brood had flown and when the martins had just vacated the nest in September.

C.h= *C.hirundinis*, C.f= *C.farreni*, C.r= *C.rusticus*, P= Present.

Locality	Nest condition	Date collected	Species present and sex	Number of females with blood in gut	Number of males with blood in gut	Number of females with mature oocytes	larval numbers	Eggs	Number of pupae	Dead fleas
Leicestershire										
Thurnby	Just built	May 1976	8♀, 2♂C.h	8	2	8	4	P	0	0
			2♀, 3♂C.f	2	3	2				
Thurnby	Just built	June 1978	3♀, 2♂C.h	3	2	3	2	P	0	0
			7♀, 5♂C.f	7	5	7				
Thurnby	Just built	June 1978	9♀, 4♂C.h	8	3	8	0	P	0	0
Whetstone	Just built	June 1976	3♀, 5,C.h	3	5	3	0	P	0	0
			4♀, 1♂C.f	4	1	4				
			2♀, 2,C.r	2	2	2				
Whetstone	Just built	June 1979	7♀, 2,C.h	7	2	7	6	P	0	0
Lincolnshire	Nest from	June 1979	45♀,13♂C.h	10	5	0	0	P	0	10♀ 8♂C.h
	previous		15♀,12♂C.f	8	11	0	0			20♀10♂C.f
	year		4♀, 5♂C.r	3	5	0	0			6♀ 6♂C.r

Table 7:2 continued

Leicestershire (including Rutland)										
Leicester City	After 1st.	July 1984	35♀,21♂C.h	26	18	13	117	P	23	3♀ 8♂C.h
	brood		43♀,16♂C.f	35	11	21				0♀ 4♂C.f
	New nest									
Leicester City	After 1st.	July 1985	62♀,18♂C.h	10	16	6	174	P	13	4♀ 6♂C.h
	brood		7♀, 6♂C.f	2	11	1				2♀ 2♂C.f
	New nest									
East Goscote	After 1st.	Aug. 1982	21♀,15♂C.h	17	15	5	315	P	54	1♀11♂C.h
	brood		4♀, 7♂C.f	4	6	1				1♀ 8♂C.f
	New nest		2♀, 3♂C.r	2	3	0				
Cosby	Martins	Sept 1979	49♀,15♂C.h	8	26	0	60	P	43	11♀ 8♂C.h
	just left		5♀, 7♂C.f	4	2	1				1♀ 1♂C.f
	Previous years nest									
Cosby	Martins	Sept 1979	35♀, 2♂C.h	14	2	0	24	P	10	3♀ 4♂C.h
	just left		6♀, 5♂C.f	6	5	2				
	Previous years nest									
Whetstone	Martins	Sept 1978	73♀,26♂C.h	10	23	0	100	P	43	12♀11♂C.h
	just left		26♀, 8♂C.f	2	5	0				1♀ 8♂C.f
	New nest									

Table 7:2 continued

Thurnby	Martins	Sept 1979	78♀,23♂C.h	5	21	2	16	P	41	21♀22♂C.h
	just left		20♀,10♂C.f	1	8	0				18♀19♂C.f
	New nest single brooded									
Whitwell	Martins	Sept 1983	3♀, 5♂C.h	0	0	0	15	P	14	4♀ 8♂C.h
	just left		32♀,16♂C.f	7	5	2				9♀ 3♂C.f
	New nest		12♀,11♂C.r	3	3	0				2♀ 5♂C.r
Whitwell	Martins	Sept 1983	53♀,29♂C.h	15	7	3	26	P	28	14♀10♂C.h
	just left		28♀,16♂C.f	14	9	2				6♀10♂C.f
	New nest		32♀,23♂C.r	12	18	3				9♀12♂C.r
Cornwall										
Hayle	Martins	Sept 1982	16♀,14♂C.f	7	9	1	12	0	62	3♀ 4♂C.f
	just left		4♀, 1♂C.r	1	4					2♀ 2♂C.r
	New nest									
Hayle	Martins	Sept 1982	14♀,12♂C.f	0	2	0	10	P	36	5♀ 4♂C.h
	just left		4♀, 3♂C.r	0	1	0				1♀ 2♂C.f
	New nest									
St Ives	Martins	Sept 1982	8♀, 4♂C.h	0	0	0	20	0	20	1♀ 1♂C.h
	just left		17♀, 3♂C.f	1	0	0				3♀10♂C.f
	New nest									
St Ives	Martins	Sept 1982	17♀, 9♂C.h	0	2	0	16	0	16	5♀ 5♂C.h
	just left		9♀, 7♂C.f	1	0	0				2♀ 1♂C.f
	New nest		3♀, 2♂C.r	0	1	0				

Plate 28.

100µm

Eggs of *C.hirundinis*, some of which have hatched.

mature oocytes. This observation agrees with the findings from the overwintering trials where not all fleas took a blood meal and not all females matured oocytes.

To try and get some idea of the duration of each stage in the life cycle of martin fleas a few of the females removed from nests taken after the first brood had flown were kept alive on moist filter paper where eggs were deposited. But even though kept under what was considered suitable conditions of temperature and humidity and under subdued lighting conditions only a few eggs were laid. The eggs were laid in batches of 2-4 eggs at one time. When egg laying had ceased the fleas were offered a blood meal on the ear of a rabbit to see if egg production could be maintained. Although they readily fed on the rabbit ear the maintenance of egg production was never achieved.

Only eggs from *C.hirundinis* were obtained in this way. They were cemented to the substrate (Plate 28). Workers (eg. Cotton 1970) on other species of flea, for example *Ctenophthalmus nobilis* (Rothschild) a common flea of the wood mouse (*Apodemus sylvaticus*), also found that eggs were laid in batches but in this species a faecal pellet was deposited beside them, presumably so that the newly hatched larva would have an immediate supply of food (Cotton *op.cit.*). *C.hirundinis* was not seen to do this in this study.

The eggs were white and measured 300µm long and 50µm in diameter. At 20^{o}C these eggs took 3-4 days

to hatch and the larvae kept on a blood/mud mixture took 21-25 days to reach the pupal stage. The 1st stage larvae moulted within 2 days with the 2nd and 3rd stages taking 10-11 days each. Thirty-two larvae were reared in this way.

Adding these development times from egg to adult together would come to around 32 days. The time it takes the martins to build their nests and raise a single brood takes about 50 days ;the individual development times for both martins and fleas are presented in Table 7:3. By the time the 1st brood has fledged all stages of the fleas life cycle would therefore be expected and were indeed found in the nests removed after the 1st brood of martins had left (see Table 7:2). As well as eggs, 1st,2nd and 3rd instar larvae and pupae were found in these nests together with both old fed/reproducing and newly emerged adult fleas (older fleas can generally be differentiated by a much darker colour than newly emerged individuals).

An attempt to find dead fleas in these nests was made to assess mortality. The numbers found were only a rough guide as other nidicoles, for example histerid beetles (Rothschild *et al.*(*op.cit.*) and flea larvae (Kirjakova 1963) may feed on dead fleas. Further, dead fleas are difficult to see amongst the nest debris. The indication is that mortality occurs throughout the martin breeding season, presumably mainly amongst those fleas that formed the initial populations. In the recolonised nest considerably more dead fleas were found

Table 7:3.

Development time for martins	Development times at 20^0_C for *C.hirundinis* and *C.farreni* in martin nests.
Nest building 14-15 days	egg 3-4 days
incubation 14-15 days	1st-3rd instar larvae 21-25 days
Brooding young 19-22 days	pupal stage 3 days
	Maturation of female oocytes circa 14 days. (Data from those fleas bred on quail, see Chapter 8)
Total days 50.	Total days 46.

than in the newly built ones; presumably these resulted from deaths of the previous season's adult populations.

Martins often raise a second brood after the first has departed but in the nests collected in September the number of broods raised in the majority of nests could not be determined. However, in one nest taken from Thurnby Rectory, Leicestershire in September 1979 it was known that only one brood had been raised. The flea biota in this nest was comparable with the other nests collected at that time some of which may have had two broods during the season. The nest at Thurnby was used by both the adults and fledged young for roosting until they migrated. It seems therefore that providing martins are occupying the nest, whether they themselves are breeding or not, the fleas continue to reproduce until shortly after the nest is vacated.

The presence of reproductive hormones in the blood of the host has been shown to play an important role in the reproduction of the *Spilopsyllus cuniculi* (Rothschild & Ford 1966 & 1973). The indication from the Thurnby nest where gravid female fleas were found in a nest only used for roosting, is that the host's reproductive hormones are not playing any part in the reproduction of martin fleas.

As the females of *C.hirundinis* and *C.farreni* laid only a few eggs after removal from the nest no measure of the number of eggs laid in the life of a single individual could be made. The stimulus for maturation of oocytes and egg laying would seem to come

from the martins alone. Sections of *C.hirundinis* and *C.farreni* females removed from the nest in September and after egg laying had ceased in those removed from nests after the 1st brood showed regression of the oocytes. These, as described by Williams (1986) in the cat flea, appear as blue bodies in the ovariole and are the degenerated nuclei of oocytes, indicating reproductive failure (Plate 21).

7.7 Discussion

These results, although based on a small number of nests, indicate that all three species of martin flea reproduce throughout the time that the nests are occupied by the martins. Gordeyeva (1969) studied the life cycle of *C.farreni* in both barn swallows nests and by feeding newly emerged *C.farreni* in the spring on a variety of small rodents in the laboratory. The number of eggs laid by an individual *C.farreni* is not given but the development times for all stages are as follows: egg stage 19-25 days, three larval instars 30 days, and pupal stage 5-6 months, while adults lived for a maximum of 3 months. The temperature at which the eggs developed is also not given but the time period is considerably longer than the 3-4 days at 20^{o}C found in this study, suggesting a lower temperature.

The larval development time of 30 days is approximately the same whilst a pupal stage lasting 5-6 months is far beyond the time found here. It is possible that the timing is for the adult contained in the

cocoon, but in those reared in the laboratory emergence due to disturbance and higher temperatures would be expected well inside 5 months.

An adult life of 3 months is certainly within the time found in this study. The adults of all three species appear to survive from October to the next July, well into the martin breeding season, a period of about 10 months. The presence of both reproducing and non-reproducing adults in the nests taken at the end of the first brood, given the development times from egg to pupa, would indicate that many of the overwintering adults survive up to the fledging of the first brood of martins.

There is little information on the development times for other species of bird flea. Cotton (1970 c) determined a development time for *C.gallinae* of 28 to 49 days from egg to adult at 21^{o}C. The development time for *C.hirundinis*, and given the number of fed and reproducing females of the other two species in nests at different times of the martin breeding season (Table 7:2), also appear to fit this timing. Little information is also available in the literature on the numbers of eggs laid by individual fleas. In this study gravid females removed from the nest laid only a few eggs which made it impossible to assess reproductive capability. However, a very rough estimate can be made by dividing the mean number of gravid females in newly built nests into the number of larvae and pupae found in the three

nests removed after the first brood had flown. Using a mean of 8.8 gravid females from newly built nests gave values of 10 and 15.5 eggs/female for the two Leicester City nests and 13.1 eggs/female for the East Goscote nest. These figures of course take no account of the number of eggs in the nest. Also by the end of 50 days, the time taken from the beggining of nest building to the first brood flying, adult fleas from the first eggs deposited during nest building would probably be contributing to the numbers of early instar larvae.

Host reproductive hormones would appear to play no part in the maturation of martin flea oocytes. In bird breeding cycles the stimulus of nest building encourages the ovarian follicles to grow and produce oestrogen leading to oviduct development and egg laying (Murton & Westwood 1977). In house martins the female gains weight steadily during the 10 days prior to egg laying (Bryant 1979). During this period the nest is being constructed and the various hormones associated with ovulation would be at a maximum. Therefore fleas feeding at this time would imbibe increased levels of reproductive hormones. However, the fact that the fleas in the nest collected from Thurnby in September were still laying eggs in a nest which had been used only for roosting for a considerable period of time would suggest that the levels of reproductive hormones in the blood of the host are not playing a part in the maturation of oocytes of the fleas. The frequency of nest use by the

martins, however, may be playing a part in egg production as it appears that this declines in nests used only by the martins for roosting.

The steady build up of the population of each species during the time the nests are occupied by the martins contrasts with the closely related *C.celsus* in the nest of *H.pyrrhonota*. This species lays only a few (*sic*) single eggs and exhibits high mortality at all stages of development being particularly vunerable to dessication (Loye & Hopla 1983). *C.hirundinis*, *C.farreni* and *C.rusticus* appear quite long lived and, as far as can be seen from these data, each has similar reproductive cycles.

Chapter 8

Feeding and reproduction

8.1 Introduction

No accurate assessment of the number of eggs laid by an individual flea could be gained from the field data. Since the reproductive capabilities of each species will to some extent determine autumn and overwintering populations, it seemed appropriate to attempt to examine these under laboratory conditions. Further, since the major component of larval diet is blood contained in the faeces of the adults it also seemed appropriate to examine adult feeding behaviour and faecal output.

House martins are insectivorous, feeding entirely in flight and therefore could not be kept in the laboratory. Consequently alternative hosts would have to be found. Humphries (1963) attempted to keep *C.styx* on chicks of the domestic chicken, but they were rapidly predated by the chicks. He also introduced *C.styx* into occupied pigeons' nests, but no breeding success was achieved. Gordeyeva (1969), however, claims to have reared *C.farreni* on a variety of small mammals, therefore there seemed some hope of establishing cultures on unusual hosts.

8.1.1 Methods

As Gordeyeva (*op. cit.*) had had success with small mammals and laboratory mice were available the

first attempts at establishing cultures of each species of martin flea was made with these. Initially 10 male and 10 female *C.hirundinis* were liberated on a white mouse (*Mus musculus*) contained in a glass tank. At once the mouse started grooming and in a short space of time (3-4 min) appeared to have removed them. Examination of the bottom of the tank revealed a number of mutilated flea bodies. When the mouse was 'defleaed' (*cf* Chapter 5), no fleas were found. Those fleas not accounted for were assumed to have been eaten by the mouse. Another trial was performed, this time using *C.farreni*, but the result was the same.

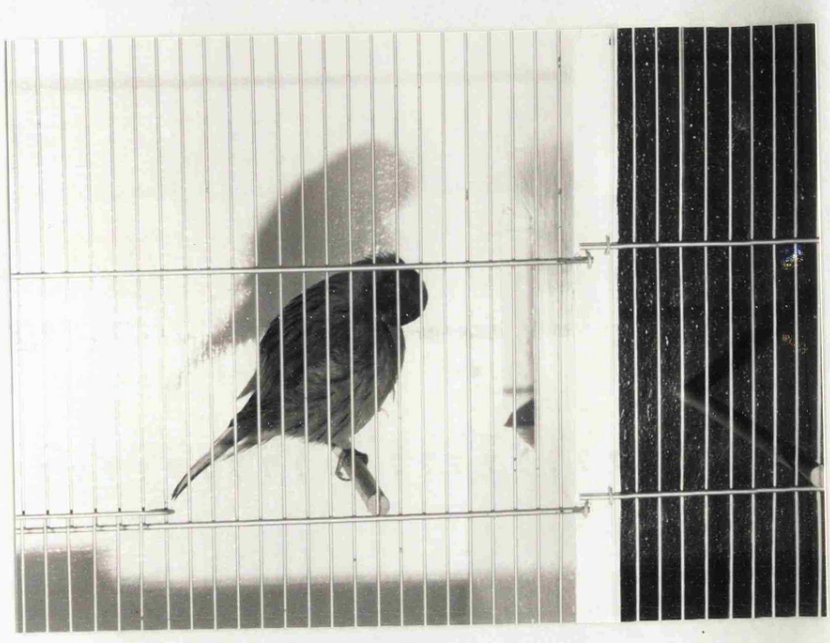
It was felt that perhaps fleas were more obvious in a white pelage, although grooming in the mice appeared to be tactile rather than visual. It seemed worthwhile repeating these trials using brown mice but the same result was obtained for both species of flea. It was concluded that mice are very good at catching these species of flea and that the flea species naturally occuring on mice, eg. *Leptopsylla segnis*, must have quite different behaviour patterns. It was therefore decided to abandon small mammals and look to various species of bird as potential hosts.

A number of bird species are available locally. Of these the two species that were used were the zebra finch *Taeniopygia castinotis* and the canary *Serinus flaviventris*. Individuals of both species were seeded with *C.hirundinis* by tipping individuals from a tube

onto their backs while held in the hand. The two birds were then released into separate cages and observed. In both species preening began at once and after 5 minutes or so ceased. Both birds were removed from their cages and exmined for fleas using the previously described method. No fleas were found on the birds but a number of mutilated bodies were recovered from the bottom of the cages, indicating that both species of bird were very efficient at catching *C.hirundinis*. This trial was repeated with *C.farreni* with the same result. There were insufficient numbers of *C.rusticus* available for these trials. The way in which both species of bird preened was by probing the feathers with the bill and then working up individual feathers using the bill as a pair of forceps (see Plates 29 & 30). Rapid scratching with the feet was also used particularly under the wing. The results of these trials showed that neither of these bird species were likely to be of any use in culturing martin fleas.

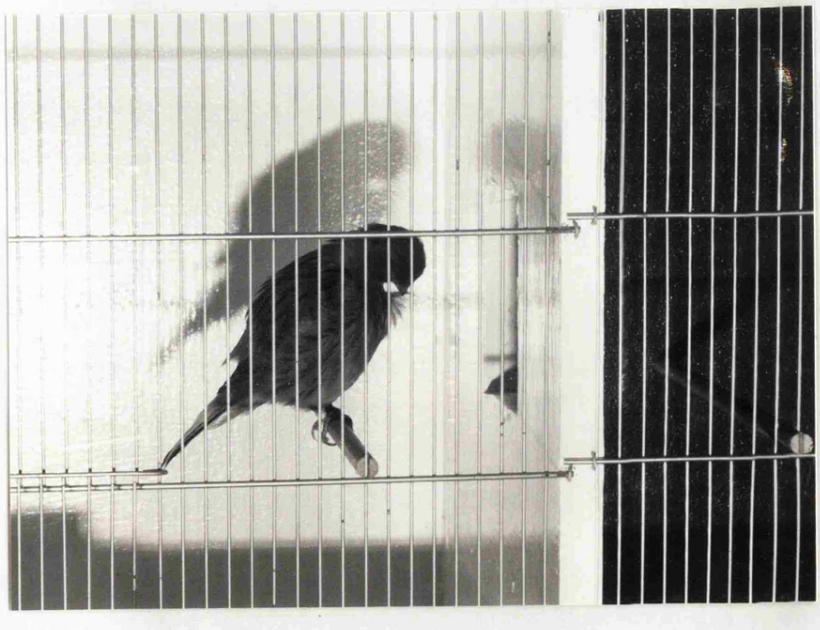
The house sparrow (*P.domesticus*) often occupies nests of martins, as discussed earlier, and several workers, for example Gordeyeva (*op. cit.*) have found engorged individuals of *C.hirundinis* in sparrow occupied martin nests before the return of the martins. This implies that house sparrows may act as alternative hosts although the findings in this study suggest that martin fleas are adversely affected by the presence of house sparrows. As house sparrows are one of the few British birds that may be trapped wild and kept in

Plate 29.



Preening by probing feathers.

Plate 30.



Preening by using the bill as a"pair of forceps".

Plate 31.

Quail in nest box.

captivity without a licence, it seemed therefore, that this species was worth trying as an alternative host. Two females and one male sparrow were caught and each kept in individual cages. Each sparrow was seeded with 10 males and 20 females of a single species of flea, a different species on each bird in the same way as the zebra finch and canary had been seeded. The sparrows appeared to preen in much the same way as the previous bird species. Preening lasted approximately 10 minutes and, as before when preening ceased they were removed from their cages and examined for fleas. No living fleas were recovered and only mutilated remains were found. These trials were repeated three times with the same result as on the first occassion.

In view of the fact that Gordeyeva (*op. cit.*) had found engorged individuals of *C.hirundinis* in sparrow occupied martin nests these results were a little surprising, although in this study the indication was for a reduction in the numbers of martin fleas in sparrow occupied nests. It was thought at this stage that under natural conditions the fleas would move onto the bird from the nest lining material and that a fairer test would be to seed lining material with fleas and allow them to gain the bird in their own way. Nest boxes were attached to the outside of the cages, access into these boxes was through a 6cm hole in the side of the cage. The boxes were lined with grass and feathers and were left unseeded until the sparrows had accepted the

boxes and were using them for roosting, this took about six days.

The lining material was then seeded with fleas, a single species in each box. The boxes were removed and the lining material examined for fleas after 24 hours. In all three boxes only dead and damaged individuals were found and no living fleas were recovered from the bodies of the sparrows. Seeding the nest boxes was repeated on several further occasions but with the same results as before. These results therefore show that *C.hirundinis*, *C.farreni* and *C.rusticus* taken from the Midlands of England are not capable of feeding or reproducing on house sparrows and cause Gordeyeva's results to be regarded with suspicion. These results would also go some way in explaining the reduction of martin fleas in sparrow occupied nests.

A great variety of other captive species of bird are commercially avialable. If martin fleas were to be successsfully cultured in the laboratory a species of bird whose preening activities were not as efficient at removing these species of flea had to be found. All three birds tried so far were predominantly seed eaters, and have similarly shaped bills. It seemed worthwhile trying a species of bird from a group of more generalised feeders. Bob White Quail (*Colinus virginianus*) are generalised feeders and are easily obtained and kept. Two of this species, one of each sex, were purchased and kept in separate cages.

Each quail was provided with a nest box. The

nest boxes were lined with feathers and grass (Plate 31) and each seeded with 30 male and 50 female *C.hirundinis*. These and subsequent batches of fleas used in the feeding and breeding trials were removed from house martin nests in that autumn 1981. Only fleas that had freshly emerged from their cocoons and had not previously fed were used. The cage, containing the quail and the nest box, was placed over a plastic tray containing water to catch any departing fleas outside the nest box. The initial trial ran for four weeks. At the end of each week all fleas were removed from the nest lining material and the state of maturity of female flea ovaries assessed by dissecting no more than two females at a time so that the maximum number of fleas could be returned to the nest box with the new lining.

The results , which are fully described later in this chapter, showed that some of the fleas were capable of surviving on the quail for a number of weeks and therefore other shorter term experiments to answer other questions, could be tried. The main questions were (1) how long does each species take to feed? and (2)as the type of lining material appears to exert some influence on the fleas, is the duration of feeding affected by the presence and the type of lining material?

In an attempt to answer these questions 15 female and 15 male individuals of each species, using one species at a time, were placed onto a quail which

was confined to a nest box containing either grass, feathers or no lining. The lining material was replaced every 30 minutes over a period of four hours and was examined for fleas. Four replicates were performed for each species and each treatment. At the end of four hours the quail were 'defleaed'. To test the no lining situation the nest box was left empty and examined every 30 minutes. These trials were performed in both autumn and spring to examine further the effects of overwintering.

8.1.2 Results

Breeding of fleas on quail.

The results of the attempt to establish monocultures of each species of flea on quail are given in Table 8:1. These show that *C.rusticus* did not survive beyond 7 days with *C.farreni* fairing only a little better at 14 days. No gravid females of *C.farreni* or *C.rusticus* was found. Of the three females *C.farreni* found at 14 days two were dissected and one was returned to the nest box, but could not be found at 21 days. For *C.hirundinis* mature females were found from 14 days through to 28 days when only two females were left and were dissected for an assessment of maturity.

Males of all three species survived for a shorter period of time than the females with *C.rusticus* males surviving the shortest time, and none survived longer than 14 days. The cages containing the quail were

Table 3.:

Results of the survival and breeding trials on quail with 30 male 50 female of *C.hirundinis*, *C.farreni* and *C.rusticus*.

Species	7 days		14 days		21 days		28 days	
	Male	Female	Male	Female	Male	Female	Male	Female
C.hirundinis	6	14	3	8(-2)	0	4(-2)	0	2
C.farreni	6	15	1	3(-2)	0	0	0	0
C.rusticus	2	11	0	0	0	0	0	0

of moulded plastic which afforded no hiding places for fleas. Further since the cages were kept over trays (60cm X 46cm) containing water any flea leaving the cage would almost certainly end up in the water. No fleas were found in the water, though fleas have some ability to swim it is considered that, with regular examination, fleas in the water would have been detected. It is therefore concluded that the loss of fleas was attributable to the preening activities of the quail.

At the end of 21 days, 12 second stage larvae of *C.hirundinis* were recovered from the lining material and these were kept in the same way as larvae from martin nests descibed in the previous chapter (Chapter 7). At 28 days a further 2 second stage larvae were recovered. Of the fourteen larvae only 8 passed into the third larval instar, 4 of these were preserved for morphological examination (see Chapter 7) and 4 pupated, taking 8-12 days at $20^{o}C$.

The first females with mature eggs were found after 14 days and the first larvae at 21 days. The time from egg to second stage larva would appear to be around 7 days. With a further 8-12 days to pupation. This would give, taking the greatest number of days, a development time of around 19 days. This figure is close to the time found for egg to pupa for eggs laid by *C.hirundinis* taken from martins' nests (see Chapter 7).

8.1.3 Feeding rate of fleas on Quail.

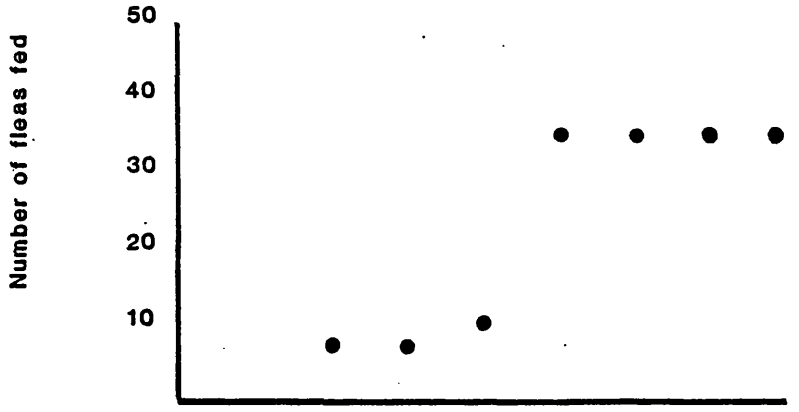
The rate at which the fleas fed and left the bird in each treatment was examined using linear regression analysis. Although significant correlation coefficients were obtained in all cases it was clear from graphing the values for each species and sex that the regressions were not adequately describing the data (see Figure 26). Therefore any comparison between treatments using regression coefficients would have little meaning.

To examine the effects of lining material on the fleas feeding on quail over time a three-way analysis of variance on the percentage fed (arcsin transformed) was performed on the numbers at 2hr and at 4hr by which time all fleas had left the quail regardless of treatment.

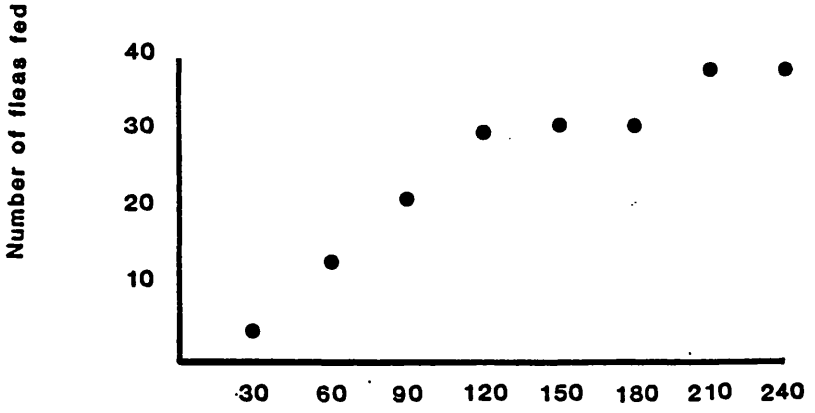
The analysis of variance on the 2hr results (Table 8:2) gave significant F values for species($P<0.001$), sex ($0.001<P<0.01$), season($P<0.001$) and lining ($P<0.001$). In the first order interaction significant F values were obtained for species/season ($0.001<P<0.01$) and season/lining ($P<0.001$) only. A Student-Newman-Keuls range test was performed on the means in each of these.

The result for species showed that fewer *C.hirundinis* had fed and left the quail than *C.farreni* or *C.rusticus* which were not significantly different from each other. The result for lining material showed that all three lining treatments were significantly

Figure 26 Two examples of the rate at which fleas fed and left the body of the quail in the presence of different nest lining treatments.



C.rusticus female, grass (Autumn).



C.rusticus female, No lining material (Autumn).

Table 8:2

Results of the analysis of variance with the percentage fleas which had fed on and left the quail after 2hr.(arcsin transformed) with species, sex, season and lining.

Main effects	F	DF	P
Species	17.996	2,108	P<0.001
Sex	5.571	1,108	0.001<P<0.01
Season	135.679	1,108	P<0.001
Lining	18.820	2,108	P<0.001
Species/Sex	1.299	1,108	P>0.05
Species/Season	6.023	2,108	0.001<P<0.01
Species/Lining	2.445	4,108	P>0.05
Sex/Season	2.551	1,108	P>0.05
Sex/Lining	0.391	2,108	P>0.05
Season/Lining	46.342	2,108	P<0.001

Species	Mean		
	C.hirundinis	C.farreni	C.rusticus
	26.85	32.01	34.05
SNK		———————	

Sex	♂	♀
	32.16	29.77

Table 8:2 continued

Season	Mean	
	Autumn	Spring
	36.85	25.08

Lining	Feathers	No lining	Grass
	34.29	31.78	26.83

All significantly different.

Species/Season	Mean	SNK
C.f. Autumn	39.83	|
C.r --	37.62	|
C.h. --	33.11	
C.r. Spring	30.47	
C.f. --	24.19	
C.h. --	20.58	

Season/lining	Mean	SNK
Autumn Feathers	43.72	|
-- No lining	41.00	|
Spring Grass	27.00	|
Autumn Grass	25.84	|
Spring Feathers	24.86	|
-- No lining	22.57	|

different from each other with least quitting the host on the grass lined and most in the feather lining. In the sexes significantly more males had fed and left the quail, while there were significantly more fleas feeding and quitting the quail in autumn than spring.

In the first order interaction species/season significantly more autumn *C.farreni* and *C.rusticus* had fed and left than all of the other treatments but each of the other treatments were significantly different from each other. The results for the season/lining interaction showed that significantly more fleas had fed in the autumn feathers and no lining treatments. These two treatments were not significantly different from each other and all of the other treatments were not significantly different from each other.

The results (Table 8:3) for the 4hr analysis of variance gave significant F values for sex ($0.001<P<0.01$), season ($P<0.001$) and lining ($0.001<P<0.01$) in the main effects with no significant first order interactions. For the lining material a Student-Newman-Keuls range test showed that significantly more fleas had fed in the no lining treatment than in the feather and grass treatments which were not significantly different from each other. The means for species, season and lining for both 2hr and 4hr are presented in Table 8:4.

8.2 Fleas fed on rabbit ears.

Although the quail proved more satisfactory

Table 8:3

Results of the analysis of variance with percentage fleas fed on quail (arcsin transformed) with species, sex, season and lining at 4hr.

Main effects	F	DF	P
Species	0.1108	2,108	P>0.05
Sex	12.0851	1,108	0.001<P<0.01
Season	52.2256	1,108	P<0.001
Lining	6.9060	1,108	0.001<P<0.01

Sex	Male	Female
	39.44	45.30

Season	Autumn	Spring
	48.46	36.28

Lining	No lining	Feathers	Grass
	46.75	40.77	39.60

Table 8:4

Means for fleas fed on quail by species, season and lining at 2hr and 4hr.

Two hours		Autumn	
		Lining	
	No lining	Feathers	Grass
Species			
C.hirundinis	35.46	43.78	20.07
C.farreni	45.78	39.24	34.45
C.rusticus	41.75	48.14	22.98
		Spring	
C.hirundinis	19.01	17.47	25.27
C.farreni	21.07	25.93	25.55
C.rusticus	27.61	31.17	32.64

Four hours		Autumn	
C.hirundinis	50.90	48.40	43.81
C.farreni	54.32	45.34	49.38
C.rusticus	55.56	50.45	38.00
		Spring	
C.hirundinis	40.89	28.00	38.93
C.farreni	38.56	36.72	32.16
C.rusticus	40.26	35.67	35.31

than the other hosts, there was still a high rate of predation. It was decided to examine the feeding behaviour further by feeding fleas on rabbit ears. This had the advantage of allowing feeding behaviour to be observed.

Two questions could be answered by feeding fleas in this way. First, does the density of each species affect feeding rates (intra-specific competition)? and, since the adult fleas' faeces form a major component of the larval diet, is the rate of defaecation affected by density? Secondly, does the presence of more than one species affect feeding and defaecation rates (inter-specific competition)?. In the first of these experiments three different densities of a single species were allowed to feed on the rabbit ear one at a time. These comprised 15 of each sex (total 30), 25 of each sex (50) and 40 of each sex (80). As the number of fleas was limited it was decided to run both sexes together in equal numbers which, as shown in the field data, is atypical as there is generally an imbalance in the sexes in favour of females. The actual numbers used were well within the range found in martins' nests. In the trial with 30 individuals seven replicates were used for each species but at the other densities only three replicates could be used for each.

To examine the second question 15 of each sex of all three species were fed on the ear at one time and the data compared with the data for 30 individuals of a single species used in the previous trial as a

comparison. Of course, the results could be confounded by the increase in the density of fleas but there seemed to be no other way of examining the effect of each species on each other. To examine further the effects of overwintering both experiments were carried out on unfed fleas in the autumn and again in the spring after the fleas had been overwintered under as near natural conditions as possible.

If the density or the presence of the other species affects feeding behaviour this may be reflected in the length of time spent feeding. The rate of feeding was therefore measured in three ways. First, the time taken from the first flea to start feeding to the first to finish: second, the time from first flea feeding to the maximum number of fleas feeding at one time: third the time from the first flea feeding to the last finishing. In practice, however, particularly at the higher densities, it was not possible to count accurately the numbers feeding or fed using the first two time variables. Therefore only the time variable first flea feeding to last finishing was used. However, although the time spent feeding could be measured, the time spent feeding at the highest density was always likely to be longer than at the lower density and thus no meaningful way of analysing the data could be found.

For the defaecation rates the number of faeces deposited during feeding and the number deposited during the 24 hours post feeding was counted. However, it was observed that there was considerable variation between

individuals in the number of blood spots produced while feeding. This was due to the fact that discret faecal pellets were not produced whilst the flea fed but semi-digested or undigested blood or both were ejected from the anus so that each ejection was separated into a number of individual spots which varied in number from one ejection to another. Therefore although blood spots could be counted any comparison in faecal output between treatments would have little value.

At the end of each trial the fleas were anaesthetised with CO_2 and examined under a compound microscope where the numbers of males and females that had fed were counted.

8.2.1 Single species at three densities.

In the analysis of variance (Table 8:5) on the percentage fleas (arcsin transformed) fed with season, species and densities, significant F values were obtained for season ($P<0.001$) and sex ($0.001<P<0.01$) only in the main effects. In the first order interaction only density/season ($0.001<P<0.01$) and season/sex ($0.01<P<0.05$) gave significant F values. No significant F values were obtained for density or species which indicates that no intra-specific competition occured at these densities. Comparing the means for sex shows that significantly more females fed than males and for season significantly more fleas fed in the autumn than in the spring.

Table 8:5

Results of the analysis of variance on percentage fleas fed (arcsin transformation) on rabbit ears with season, sex, and species at densities 30,50 and 80 with Student-Newman-Keuls range tests on those giving significant F values.

	F	DF	P
Species	1.325	2,120	P>0.05
Density	0.080	2,120	P>0.05
Season	142.298	1,120	P<0.001
Sex	41.740	1,120	P<0.001
Species/Density	0.684	4,120	P>0.05
Species/Season	0.389	2,120	P>0.05
Density/Season	3.640	2,120	0.001<P<0.01
Species/Sex	0.581	2,120	P>0.05
Density/Sex	0.269	2,120	P>0.05
Season/Sex	4.444	1,120	0.01<P<0.05

Sex	Mean
♂	♀
50.54	61.77

Season	Mean
Autumn	Spring
66.57	45.74

Table 8:5 continued.

Density/Season		Mean	SNK
80	Autumn	71.10	|
50	--	66.88	|
30	--	64.49	|
30	Spring	47.48	|
50	--	44.94	|
80	--	42.48	|

Season/Sex		Mean	SNK
Autumn	♀	70.34	
--	♂	62.79	
Spring	♀	53.19	
--	♂	38.28	

All significantly different.

A Student-Newman-Keuls range test on density/season showed that there was a very clear seasonal difference, as had already been shown in the main effects, with a greater proportion of fleas feeding at each density in the autumn than in the spring. In terms of the interaction it is noteworthy that the highest density(80) had proportionally the highest mean fleas fed in the autumn but the lowest in the spring, which suggests that an intra-specific factor may be operating in the spring.

In the first order interaction season/sex, each sex both within and between seasons was significantly different from each other. The difference in means between males and females in the spring is approximately twice that between sexes in the autumn (spring= 14.91, autumn= 7.55) which suggests that males are affected by overwintering to a greater extent than females.

8.2.2 Mixed species.

To examine inter-specific competition the data with 30 individuals of each species fed separately and with all three combined (7 replicates 90 individuals) were examined in the same way as the previous data set using analysis of variance and Student-Newman-Keuls range tests on interactions. In the analysis of variance with percentage fed by species, sexes, density and season (Table 8:6), the numbers of each species and sex fed at the higher density were counted at the end of each trial and compared with the single species data.

Table 8:6

Results of the analysis of variance and Student-Newman_Keuls range tests with single and mixed species on percentage fleas fed (arcsin transformed) on rabbit ears, with species, season, density and sex.

Main effects	F	DF	P
Season	90.380	1,144	P<0.001
Sex	33.577	1,144	P<0.001
Species	0.251	2,144	P>0.05
Density	0.650	1,144	P>0.05
2-way interaction			
Species/season	4.030	2,144	0.01<P<0.05
Species/sex	4.550	2,144	0.01<P<0.05
Season/sex	5.766	1,144	0.01<P<0.05

Season	Mean	
Autumn	Spring	
63.84	46.84	

Sex	Mean	
♂	♀	
50.03	60.49	

Species/Season		Mean	SNK
C.h	Autumn	66.67	|
C.r	--	64.90	|
C.f	--	59.94	|
C.f	Spring	49.25	|
C.r	--	47.34	|
C.h	--	43.44	|

Table 8:6 continued.

Species/Sex		Mean	SNK
C.r	♀	64.82	|
C.f	♀	59.52	| |
C.h	♀	57.11	|
C.h	♂	53.00	| |
C.f	♂	49.66	|
C.r	♂	47.42	|

Season/Sex		Mean	SNK
Autumn	♀	66.90	
--	♂	60.77	
Spring	♀	54.07	
--	♂	39.28	

All significantly different.

In this analysis only season and sex ($P<0.001$ in both cases) produced significant F values in the main effects. In the first order interaction significant F values were obtained for species/season, species/sex and season/sex only ($0.001<P<0.01$ in all three cases).

The lack of any significant difference between the two densities enabled other comparisons, such as those between species, to be made. No significant difference was found between species, therefore, there is no evidence of inter-specific competition. This is further supported by the lack any significant differences for species/density.

The result of the comparison between seasons showed that significantly more fleas fed in the autumn than in the spring which agrees with the single species trials. In the first order interaction a marked seasonal difference was found, as had already been found in the main effects, with significantly more of each species feeding in the autumn. In the interaction it is worth noting that *C.hirundinis* proportionally had the highest mean number fed in the autumn but the lowest in the spring suggesting some inter-specific factor may be operating in this season. A similar trend was however found in the single species data, therefore this result has little value.

The result of the first order interaction species/sex showed that overall proportionally more females fed than males except that *C.hirundinis* males did not differ significantly from either *C.hirundinis* or

C.farreni females, or from any other males.

The results for season/sex are similar to those obtained in the single species trials with each sex differing significantly from each other both between and within seasons but with the greatest difference between the two sexes in the spring (spring= 14.79, autumn= 6.13). This supports the view expressed earlier that males are affected by overwintering more than females.

8.3 Amount of blood taken during feeding by adult fleas.

In these trials it was not possible to determine the amount of blood taken or defaecated. This was because with so many fleas together in each trial an after feeding weight could not be matched to an initial weight for any individual. In order to get some measure of the amount of blood taken separate feeding trials were performed with single fleas only. Ten replicates of each sex of each species were fed on the ear of a rabbit in the autumn and the experiment repeated in the spring. Not all fleas fed particularly in the spring. The trials were therefore repeated until ten replicates of each sex and each species was achieved.

Each flea was weighed before and after feeding on a micro-balance. Some, but not all, of the fleas defaecated whilst feeding; consequently the amount of blood taken by these individuals is greater than would be indicated on a before and after feeding weight

difference. Since the blood passed during feeding dried rapidly, its fresh weight could not be determined for inclusion with the weight difference. Faecal material was scraped from the rabbit ear and weighed after each trial. This material weighed between 0.001mg and 0.002mg, but as it was drying the weights are neither dry or fresh. As some fleas defaecated in all trials it was decided to perform the analysis on the increase in weight without trying to take into account any faecal material.

The increase in weight in mg with species, sex and season was analysed using an analysis of variance with Student-Newman-Keuls range tests. The results (Table 8:7) gave significant F values for species ($P<0.001$) and sex ($P<0.001$) only in the main effects and for sex/season in the first order interaction. The results for sex showed that females took significantly more blood than males, in fact on average twice as much. For species both *C.hirundinis* and *C.farreni* took significantly more blood than *C.rusticus* but were not significantly different from each other. The result of the range test for sex/season showed that in both autumn and spring females imbibed significantly more blood than males in either season. No significant differences were found within sexes between seasons although females took more blood in spring, and males more in autumn.

8.4 Discussion

Although only a few female *C.hirundinis* were

Table 8:7

Results of the analysis of variance with weight of blood meal (mg), species, sex and season with a Student-Newman -Keuls range test on the interactions.

Main effects	F	DF	P
Species	8.8082	2,108	P<0.001
Sex	337.1838	1,108	P<0.001
Season	2.2563	1,108	P>0.05
2-way interaction			
Species/sex	1.1906	2,108	P>0.05
Species/season	0.3730	2,108	P>0.05
Sex/season	3.9704	1,108	0.01<P<0.05

Sex	Mean
♂	♀
0.09	0.18

Species	Mean	
C.hirundinis	*C.farreni*	*C.rusticus*
0.14	0.14	0.12

SNK _____

Table 8:7 continued

Sex/season		Mean	SNK
♀	Spring	0.19	|
♀	Autumn	0.18	|
♂	Autumn	0.09	|
♂	Spring	0.08	|

obtained with mature eggs it shows that this species is able to feed and to mature oocytes on an unusual host. As seen in the field data, considerable numbers of fleas are found in martin's nests, the high mortality of all three species found on quail and the other bird species tested, indicates the high level of adaptation to house martins. It has often been commented in the literature (see for example Rothschild & Clay 1952) that hirundines in general have a great number of different ectoparasites associated with their nests. This is generally thought to be because of particularly favourable microclimatic conditions prevailing in the nest. The fact that hirundines often use the same nest or nest site year after year and that their nests provide stable conditions cannot be denied. However, I would speculate that both the specialised bill of the hirundines, adapted to feeding on the wing, and their rather weak feet, may reduce their efficiency at removing ectoparasites. The development time from egg to adult for *C.hirundinis* was similar to that found for larvae reared from eggs laid by *C.hirundinis* removed from martins nests. The small number of larvae recovered from the lining material may have been due to only a few eggs being laid or to low survival due to conditions prevailing in the nest box. The quail had the unfortunate habit of defaecating in the nest box, which by the end of a week made for very messy conditions, quite unlike those found in house martin nests.

A variety of factors, both internal and

external to the animal influence egg production. Nutrition is probably the most important single factor in most insect species. Other factors in addition to feeding are known to influence egg laying in many species. For example, light, temperature and humidity may not only interfere directly with egg production but may also have an effect on feeding and mating. Aging also accounts for a decrease in egg production. In the flea *Echidnophaga myrmecobii* Rothschild egg production declined with age (Mules 1940) presumably because of the increasing number of degenerating follicles.

Accumulated data gained from scanning literature on insect reproduction shows that there is great variability in egg production even amongst species of the same genus (Englemann 1970). Quality of food has a definite effect on egg production for *Culex pipiens* with canary blood seemingly to have a higher nutrient value than human (Tate & Vincent 1936). Woke (1937) also found that this species laid twice as many eggs when fed on a canary than on other hosts. The flea *Xenopsylla cheopis* laid more eggs and matured them faster when fed on adult rather than baby mice (Buxton 1948). Given the above examples any results on reproduction on unusual hosts can only be taken as a rough guide.

For the three species of house martin flea considered here their nutritional requirements are likely to be similar. The preening activities of the quail will clearly affect the feeding activity of the fleas but it is assumed that this will be the same for all species and trials.

The results of the analysis of variance at 2 hours showed that significantly more *C.farreni* and *C.rusticus* had fed and left the quail than *C.hirundinis*. This result was not repeated in the analysis at 4 hours and suggests that *C.hirundinis* spends more time feeding than the other two species. On comparing the means between 2 and 4 hours in Table 8:4 it is clear that in all three species the majority of fleas had fed and left the quail by 2 hours. Lining material, or lack of it, gave significant differences in both analyses with all three significantly different from each other at 2 hours with feathers giving the highest mean and grass the lowest. At 4 hours no lining material gave the highest mean which was significantly different from both feathers and grass which were not significantly different from each other. The suggestion here is that in the presence of feathers the fleas feed and leave the quail at a faster rate and tend to spend longer on the quail when no lining is present. This further suggests that the fleas are less vulnerable to predation when on the quail than in a no lining material situation. It should be noted, however, that in these feeding trials only around 30% of the fleas survived and fed in the 4 hour period. The major factors affecting feeding appear to be season and sex which had already been noted in the results from fleas fed on rabbit ears (see Chapter 5).

The conclusion from these data is that the type of lining material has an effect on the feeding behaviour of the adult fleas. The effect of a no lining

situation is understandable as a lack of hiding places would make them more vulnerable to predation or accidental damage by the activities of the quail. It is difficult to say, however, what the difference is between feathers and grass. It is possible that feathers provide more hiding places and better protection amongst the vanes of the feathers.

The results for both single and mixed species trials on rabbit ears indicate that little intra- or inter-specific competition occurs at the densities tested. In the single species results there is a hint that some intra-specific factor is operating at the highest density after overwintering. If the ability to take a blood meal is a measure of fitness then density may be more important to weaker fleas in competing for feeding sites.

In the mixed species trials however, no significant density/season interaction was found although the density was greater than the highest density in the single species trials. In this mixed species trial this density comprised all three species which would have reduced any intra-specific interaction.

Significantly more fleas fed in the autumn than in the spring which supports the findings for both the quail and previous feeding trials on rabbit ears that after overwintering many fleas do not feed in the spring. In the trials with single species only significantly more females fed than males but there was no significant difference between species. This was true

also in the mixed species trials. Similarly there was a very marked difference in the percentage of fleas fed in both the single and mixed species trials between seasons. At these comparatively high densities in a confined space around 50% of the fleas fed and therefore the conclusion is that in the field inter-specific competition for feeding sites on the host is not an important factor limiting population size.

The results from the increase in flea weight before and after a blood meal by individual fleas showed that females took significantly more blood than males with no significant difference for either sex between seasons. Presumably females who have to mature eggs would require more nutients than males. Bar-zeev & Sternberg (1962) showed starved females of *X.cheopis* when fed through a membrane, imbibed more blood than starved males and that older fleas of both sexes fed more than younger fleas. Warren-Hicks, Schroder & Bigelow (1979) also comment that *X.cheopis* females take on average 39% more blood than males.

The ages of the fleas in this study could not be determined although as far as possible only newly emerged fleas were used. However, inevitably the disturbance caused in removing a few fleas from the nest would cause mass emergence and this would mean that fleas used in susequent trials would be older in terms of being out of the cocoon than those used in earlier trials. This, however, does not seem to be of importance

in so far as the females of all three species used in these trials imbibed more blood than males and are therefore similar in this respect to the other species of flea.

The results of these trials can, of course, only be taken as a rough guide to the feeding patterns of these species. Quail are considerably bigger than house martins (lengths 240mm and 120mm respectively) therefore a larger potential feeding area would have been available to them on the quail. However, the rate at which the quail removed the fleas would have probably reduced the effective feeding area to those parts of the body least accessible. Preening activities in all species of bird seeded with fleas in these trials appeared confined to the body area beneath the wings. It has been shown that different species of both bird and mammal fleas have specific sites on the host's body. For example *Echidnophaga gallinacea*, a species that is not host specific and is found on both birds and mammals, is confined to the head region (Lindsdale & Davis 1956). The rodent flea *Leptopsylla signis* is also found mainly on the head region of the host (Krampitz 1980). Where more than one closely related species is found on the same host, as in the case of *X.cheopis* and *X.astia*, they are spatially separated on the host's body (Prasad 1972). On birds it is impossible to see the fleas once they have moved into the feathers and no satisfactory method was found to investigate this aspect. However, since preening activity was confined to the area beneath

the wing it suggests that, at least, on unusual hosts this is the favoured site.

The feeding experiments on rabbit ears greatly restricted the available feeding area and therefore the pressures of density would have been maximised. But since conditions were the same for all three species of flea these results can be taken as a guide to the effects of season, density, inter- and intra-specific interactions. Marshall (1981), considers that body fleas such as *Malaraeus telchinus* (Rothschild) and *Spilopsyllus cuniculi* respond to the size of the host's body whilst nest fleas, such as those in this study do not. These results would tend to support this veiw.

One other factor that may also affect the feeding behaviour of these flea species is the difference between the body temperatures of birds and mammals. Birds have a normal body temperature of 40^{o}_{C} whilst their young are often $4^{o}C$ cooler. Eutherian mammal temperatures range from $37^{o}C$ to $39^{o}C$ (King & Farmer 1961).

The major factor therefore affecting feeding is season with a consistent difference in feeding between sexes. Lining material appears to have an effect but this appears to be marginal. The results overall suggest that there is little intra- or inter-specific competition at the densities tried.

Chapter 9

General Discussion.

In this study, I set out to investigate the relationship that allows three congeneric and monoxenous species of flea to share the same host and inhabit the same nest suggesting as initial hypotheses that either intra-specific control is sufficiently strong to minimise inter-specific competition, or coexistence is permitted either by sufficient niche segregation or through extrinsic controls such as predation. Niche separation would include spatial separation while feeding, selection of different micro-habitats and temporal separation resulting in at least partial separation in breeding periods.

House martin nests, as shown in Chapter 2, provide a sheltered habitat with a comparatively stable micro-climate during the period when the martins are incubating eggs and brooding young ($22^{o}C$-$34^{o}C$; RH 55%-75%). During the winter months the nest temperature stays within 2 degrees of the ambient temperature, with any rapid changes in ambient temperature being buffered by the lining material in the nest as demonstrated in Chapter 5. The number of species of flea associated with the nests of *D.u.urbica* would suggest that overall conditions are particularly favourable for colonization by fleas.

Colonization of the nest by fleas relies on transportation by the martins and consequently the number of fleas arriving at a new nest will be variable

and is one source of the considerable variation found in the numbers of each species recorded in the field survey (Chapters 3 & 4). The time at which each species reaches and becomes established will affect the composition of the nest community unless there are strong inter-specific interactions. Consequently the autumn flea densities would vary considerably. The data for the number of fleas carried on the martins, although in agreement with the small amount of data in other studies, is very limited. In any future study it would be worthwhile making an effort to net a large sample of martins to see how many fleas are transported on them at different times of the year eg. entering Britain, during incubation, brooding young and emigrating. Since transportation on the martins is the only way nests are colonised by fleas this would show just how much movement there is between nests while the martins are in Britain.

The results from the field data (Chapters 3 & 4) showed that often each species was positively correlated with the other two which suggests that, at the densities encountered, little inter-specific competition was taking place. Further, it also suggests that conditions suitable for one species are also suitable for the other two. Evidence for differences in micro-habitat selection rests on differing responses to the wall material to which the nests were attached and the type of nest lining material.

Although the precise effect of wall material on each species could not be determined there is evidence that all three species performed better in nests attached to either brick or painted dash than those on stone surfaces on buildings. Rougher textures may provide more sheltering places while stone surfaces that have been faced, and are comparatively smooth, may present fewer hiding places. It is worth noting that all three species occur in nests on cliffs where rougher surfaces may present more sheltering places.

Different types of wall material will vary in their thermo-insulatory capabilities, as demonstrated in chapter 5., which may also exert some influence on the fleas. Given the range of temperatures that each species is exposed to throughout the year (see Chapter 2) it is difficult to see how differences of only one or two degrees Celsius would significantly affect the fleas. Relative humidity may be of more importance and the evidence strongly suggests this is particularly so for *C.rusticus*, which appears to be more abundant on both sea cliffs and a stone cottage in Cornwall which, of the nests tested, had the highest humidities. Substantial populations of *C.rusticus* were found in the Leicestershire 1974 collection and by Dunnet *et al.* (1955) in NE Scotland, therefore the results for Cornwall are unlikely to be connected with the milder climate prevailing in SW Britain. Although it is probable that the micro-climate of the nest will be affected by orientation (direction) of the nest there is

no evidence that this has any effect on the population densities of fleas.(Chapters 3 & 4).

The response to nest lining materials, if they do reflect a difference in micro-habitat selection, is very variable. In the field data all three species were affected by the components of the nest lining material with higher numbers occurring in nests containing feathers. The total amount of lining material does not seem to be of importance to the fleas. *C.rusticus* was the only species showing a significant response to this variable in the regression analysis (Chapter 3) but only 2% of variation was accounted for. The size of the lumen of the nest also does not have a significant effect on the fleas or influence the martins in the amount of lining material they use as neither were extracted as correlates in the regression analysis.

Under experimental conditions (Chapter 5) which examined survival at different temperatures and humidities with different nest linings at least 50% of each species were able to survive for several months and were capable of taking a blood meal. The weakness of the laboratory experiments is that both temperature and relative humidity were kept constant. Hence these data give no clue as to the response to differing micro-climates. However, these results would suggest that each species is capable of surviving for quite long periods of time in a variety of conditions. However, the response to

different nest lining materials may be tactile, with

adult or larval fleas better adapted to moving within feathers.

In terms of metabolic activity (Chapter 6) the respiration rates of all three species of martin flea were significantly lower at 5°C than those recorded for small mammal fleas by Kondrashkina *et al.* (1964). The values at 25°C are closer to those obtained for small mammal fleas but only the respiration rate for *C.hirundinis* at 15°C is similar. The differences found in respiration rates between the three species of martin fleas and small mammal fleas at 5°C may reflect the difference between species where the host is absent during the winter months and those where the host is present. The reduction in the fresh weight in fleas that had overwintered cannot be explained, the reduction in dry weight over the same period although not significant indicated that some of the fat body had been used which agreed with the visual assessment (Chapter 6).

Too few males were available for each species for a meaningful comparison of respiration rates. However, from the data that are available it is noteworthy that per unit weight the males had a higher respiration rate than the females. Equally noteworthy are the results from the activity monitor (Chapter 6) where females were significantly more active than males. The data from both the respirometry and activity monitor suffer, as with other trials in this study, in not knowing the precise history of any individual flea.

Although as far as possible only newly emerged fleas were used, some of the variation in the data may be due to differences in age and physiological state.

The feeding trials on quail (Chapter 8) showed that the type of lining material influenced the length of time each species spent on the body of the quail. As a longer time was spent on the body when no lining material was present, lining material is perhaps more important when the martins are in residence.

As all three species were often found in the same nest no temporal separation of species appeared to occur. Within one geographical locality one species may dominate and this may change with time as demonstrated at Oadby, Leicestershire (Chapter 4) where the numbers of *C.hirundinis* and *C.farreni* varied significantly between years and at Coverack, Cornwall where *C.hirundinis* and *C.rusticus* also varied significantly between years. England lies well within the known distribution of all three species, hence any variation in numbers between occasions in one geographic locality is most likely to be due to the transportation of the fleas from one nest to another.

Variation in the numbers of each species within one locality may also be due to differential emigration between nests in close proximity or differential fecundity. However, no significant differences in numbers of fleas or species composition could be demonstrated between nests in colonies and those in isolation (Chapters 3 & 4). This suggests that

there was little interchange between nests in colonies. This was substantiated by placing sticky traps around colonial nests where only very few fleas were caught (Chapter 5). These results are in contrast to those of Darskaya (1964) who, in spring, found both *C.hirundinis* and *C.farreni* on the outside of nests. Therefore, the findings in this study (Chapter 5) indicate that the starting populations in new nests rely on transportation by the martins and this, based on the results for numbers of fleas removed from the bodies of martins, appears to involve only a few individuals at any one time.

The development times (Chapter 7) indicate that each species of flea only reproduces while the martins are in residence with egg laying ceasing and regression of oocytes occuring soon after the departure of the martins. From the small amount of data available from nests taken at different times of the martin breeding season there appears to be no differential fecundity. It apppears therefore that the number of broods the martin produces is not important to the fleas providing the nest is still occupied. Given low numbers of fleas capable of reproducing in the spring it is unlikely in most cases that the carrying capacity of the nest is exceeded and thus inter- and intra- specific competition is mostly avoided.

It is unfortunate that in this study only a few nests were obtained for information on how each species population develops throughout the martin

breeding season (Chapter 7). If artificial nests could be used successfully and if biochemical techniques could be employed to distinguish between the larvae of each species, then a more accurate picture of the population dynamics of each species could be obtained.

The number of fleas surviving the winter was high but more females than males survived which would account for the imbalance in the sex ratio in favour of females found in the field data. However, not all of those fleas surviving until the spring were capable of taking a blood meal, mating or reproducing. Female fleas imbibed significantly more blood than males (Chapter 8) which might be expected since they would need more nutients to mature their oocytes, with *C.hirundinis* and *C.farreni* taking significantly more blood than *C.rusticus* but not differing from each other. Although there was no significant difference within sexes between seasons females took more blood in the spring and males more in the autumn. Presumably females are in greater need of a blood meal in the spring after overwintering, probably again related to maturing oocytes. It is unclear why males should take more blood in the autumn.

The type of lining material again appears to have some influence with significantly more fleas feeding after overwintering in a nest lining, regardless of type, than in the no lining situation. As shown in the results in Chapter 5, when nest lining materials are present they tend to buffer changes in ambient temperature. This presumably is less stressful to the

overwintering fleas and means that they are in a better condition in the spring. In the presence of the martins the lining material would provide hiding places for all stages of the flea's life cycle and afford protection from the activities of the martins.

The starting populations in the spring in nests going into their second or third season, given mortality and the inability of part of the overwintering flea community to feed and reproduce, may result in a similar numbers of reproducing fleas as in newly built nests (Chapter 7). Of course new fleas would inevitably be brought to these old nests on migrating martins, but this would be compensated by the martin's "load" of fleas on moving on again. Given similar starting flea populations in the spring no significant differences in the numbers of each species would be expected and none was found (Chapters 3 & 4).

Evidence regarding larval survival is scarce, partly because each species of larva could not be distinguished and partly, because of the difficulty in obtaining larvae, only a limited number of trials could be performed. However, it would appear from the results of larval survival at different temperatures and humidities that a wide range is tolerated.

The results of the feeding trials on quail (Chapter 8) showed that all three species were capable of feeding on an unusual host and, at least in the case of *C.hirundinis* and *C.farreni*, of reproducing on unusual hosts. The successful breeding of these species on an

unusual host that itself was not in reproductive condition, also showed that reproductive hormones play no part in the maturation of the oocytes in these species. The major problem with the feeding trials is that as with other experiments fleas were used whose precise history was not known. In all trials an attempt was made to use only freshly emerged fleas, but inevitably some of these may not have been. It would be difficult, without maintaining laboratory cultures of each species, for the history of an individual to be determined. Clearly this would be desireable in future studies.

The high mortality amongst the fleas on unusual hosts suggests that either a large proportion of fleas in house martin nests are lost to the host, which may help to control species population density or, given that considerable numbers of each species are found in martin nests, that the martins are not particularly adept at removing these species of flea.

When martin nests are taken over by *P.domesticus* in the autumn and winter the fleas are subjected to a much greater nest temperature change (up to $34^{o}C$). This, plus disturbance of occupancy, at a time when the fleas would normally be quiescent, would almost certainly cause emergence from the cocoon. At this time it is likely that the fleas would seek a blood meal and, as demonstrated in Chapter 8, would then be killed or damaged by the preening activities of *P.domesticus*. This, as found in the field data (Chapters 3 & 4),

results in an apparent decline in martin fleas.

At any rate the results from the feeding trials on *P.domesticus* show that the decline in numbers of martin fleas in house martin nests taken over by this species is due to its preening efficiency.

No direct evidence was obtained on spatial separation between species whilst they are feeding on the host. However, the results of the mixed species feeding trials on rabbit ears (Chapter 8) where the effects of density were maximised showed that each species was having little effect on the others. Therefore it is unlikely that they would need to separate spatially on the martin whilst feeding to avoid competition. The study of preening efficiency of martins could be made by capturing and seeding them with known numbers of each species in the same way as with the quail. However, it may prove difficult to convince various bird organisations that the information gained was worth the stress placed on the martins.

Of the three species *C.rusticus* appears to be the most affected both by different types of lining materials and in its ability to feed after overwintering (Chapter 7). This species appears to be the most sensitive of the three species to relative humidity and was most abundant in the wetter habitats, particularly in nests on sea cliffs. The results from the flea activity monitor (Chapter 6) showed that *C.rusticus* was the least active. This presumably because this species has the greatest reduction in the pleural arch which

suggests a longer association with the house martin than the other two species. As discussed in Chapter 5 the behaviour patterns of the house martin appear to have reduced the need for unaided emigration away from old nests to new ones in these species of flea and hence the most modified species is likely to have the longest association. Also, the ancestral nesting sites for the house martin must have been cliffs, where *C.rusticus*, particularly on sea cliffs, was the most abundant species, although the other two species also occurred in the same nests. The results for *C.rusticus* therefore suggest that it is the
least adaptable of the three species which again suggests that it is more specialised and has had the longest association with the house martin.

To summarize, in this study the evidence for micro-habitat selection would seem to rest on different responses to nest lining material and the surface to which the nest was attached, but the evidence overall suggests that each species is able to tolerate a wide range of conditions. All three species appear to be reproducing only during the time that the nest is in regular use by the martins and therefore there would seem to be no separation in the breeding periods. It is not known to what extent the preening activities of the martins reduce the flea community but certainly it cannot be as efficient as that of *P.domesticus*. Other invertebrates occurring in the nest appear to be having no effect on the flea community. It would appear therefore that each species population rarely reaches a

sufficiently high density for inter-specific competition to be of importance, the size of the flea community being regulated to a major extent by the numbers involved in the colonisation of nests and by part of the overwintering populations inability to feed and reproduce.

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Appendix 1.

Arthropods other than fleas from house martin nests Leicester 1974.

L= Larvae, P= Pupae, PI= Pupipara, A= Adult.

		Lepidoptera Tineidae			Diptera Hippoboscidae		Coleoptera Adults/larvae	Hymenoptera	Other Diptera	Psocoptera Epipsocidae	Aranea	Acari
		L	P	A	PI	A						
Anstey	SK552086	23	3	4	30	30	0	0	0	0	0	0
Belton	SK815014	82	0	0	0	0	5	3	0	18	2	23
Belton	SK815014	1	0	0	22	1	1	0	4	3	1	29
Belton	SK816014	8	8	16	5	0	0	0	0	0	0	0
Belton	SK816014	8	2	0	3	0	0	0	0	0	0	11
Belton	SK816014	24	0	0	0	0	0	0	0	0	0	0
Birstall	SK595085	4	1	1	0	0	0	2	0	0	0	0
Coalville	SK451147	1	0	0	7	0	3	0	0	0	1	0
Cosby	SP547947	2	0	0	0	0	6	0	0	0	0	39
Cosby	SP547947	4	0	0	5	0	0	0	0	0	0	49
Cropstone	SK551110	102	23	0	0	0	0	0	0	9	1	0
Foxton	SP701898	0	0	0	24	0	0	0	0	0	0	0
Glaston	SK894029	0	0	0	0	0	0	0	0	0	1	44
Glenfield	SK555063	35	2	0	0	0	0	0	82	0	0	0
Houghton	SK678037	8	0	0	0	0	0	8	0	10	1	0
Houghton	SK678037	9	0	0	0	0	0	0	0	0	0	0
Houghton	SK678037	8	0	0	0	0	0	0	0	6	3	0
Ibstock	SK408102	32	0	0	54	13	1	0	0	0	2	0
Ibstock	SK408102	0	0	0	0	0	0	0	0	0	0	0
Ibstock	SK408102	0	0	0	15	0	0	3	0	9	0	0
Leicester	SK609030	0	0	0	0	0	0	0	0	0	0	0

Appendix 1 continued.

		Lepidoptera Tineidae			Diptera Hippoboscidae		Coleoptera Adults/larvae	Hymenoptera	Other Diptera	Psocoptera Epipsocidae	Aranea	Acari
		L	P	A	PI	A						
Leicester	SK609030	0	0	0	0	0	0	0	0	0	0	29
Lutterwth	SP545844	2	0	0	4	0	0	0	6	0	0	0
M.Harboro	SP737877	0	0	0	18	2	1	0	1	0	0	2000
Medbourne	SP800930	1	0	0	28	0	7	0	0	0	1	0
Medbourne	SP800930	1	0	0	0	0	0	0	0	0	1	0
Medbourne	SP800930	0	0	0	0	0	0	0	0	0	1	0
Medbourne	SP800930	32	7	0	63	0	0	0	0	0	0	12
Medbourne	SP800930	113	1	0	0	0	0	0	0	0	0	0
Medbourne	SP800930	3	0	0	14	0	0	0	0	10	0	0
Medbourne	SP800930	11	2	0	0	0	0	0	0	0	0	20
M.Mowbray	SK748199	0	0	0	3	0	3	0	0	0	2	0
M.Mowbray	SK748199	1	0	0	12	2	1	0	0	0	1	0
Narborough	SP540984	0	0	0	7	0	0	5	0	9	0	0
Narborough	SP540984	24	18	0	15	0	0	0	0	3	0	12
Narborough	SP540984	23	3	4	0	0	0	0	0	0	0	0
Narborough	SP540984	82	0	0	22	0	0	0	0	23	0	6
Narborough	SP540984	1	0	0	8	0	0	0	0	0	0	0
New.H'cort	SP638971	8	8	0	12	3	0	0	3	0	1	0
New.H'cort	SP638971	8	2	0	0	0	0	8	0	2	0	0
New.H'cort	SP638971	24	0	0	0	0	0	0	0	0	0	0
Oadby	SP628999	4	1	1	10	2	1	0	0	0	2	0
Oadby	SP622998	1	0	0	15	0	0	0	0	0	1	28
Oadby	SP622998	2	0	0	15	0	0	0	0	0	1	0
Oadby	SP631993	4	0	0	0	0	0	0	0	0	0	9

Appendix 1 continued.

		Lepidoptera Tineidae			Diptera Hippoboscidae		Coleoptera Adult/larvae	Hymenoptera	Other Diptera	Psocoptera Epipsocidae	Aranea	Acari
		L	P	A	PI	A						
Oadby	SP631993	102	23	0	19	0	0	0	0	0	1	0
Oadby	SP631993	0	0	0	2	0	0	0	0	0	0	0
Oadby	SP631993	0	0	0	6	1	0	0	0	0	0	8
Oadby	SP631993	35	2	0	8	0	0	9	0	10	2	0
Oadby	SP631993	8	0	0	5	0	0	0	0	0	0	0
Oadby	SP632993	9	1	0	18	0	0	0	0	12	1	102
Oadby	SP632002	8	0	0	0	0	0	0	0	0	0	0
Oadby	SP629003	32	8	0	0	0	0	0	0	0	1	0
Oadby	SP624998	0	0	0	0	0	0	9	0	1	0	22
Oakham	SK861091	0	0	0	0	0	0	0	1	45	0	0
Packington	SK360146	0	0	0	0	0	0	0	0	0	2	0
Packington	SK358147	4	0	0	0	0	1	0	0	3	0	0
Packington	SK361145	2	0	0	0	0	0	0	0	0	0	6
Packington	SK361145	0	0	0	0	0	0	0	0	0	0	0
Queniboro	SK649120	1	0	0	10	0	1	0	0	0	2	0
Queniboro	SK640122	0	0	0	8	0	0	1	0	0	0	15
Queniboro	SK649120	32	7	0	0	0	0	0	0	0	0	4
Quorn	SK564166	113	1	0	0	0	2	0	0	0	0	0
Quorn	SK564166	3	0	0	13	0	0	0	1	0	0	0
Quorn	SK564166	11	2	0	23	0	0	0	0	0	1	0
Quorn	SK564166	0	0	0	0	0	0	0	0	4	0	0
Quorn	SK564166	1	0	0	0	0	0	0	0	0	0	0
Quorn	SK564166	0	0	0	0	0	0	0	0	0	0	0
Rearsby	SK651142	24	0	0	8	2	1	0	0	0	0	0

Appendix 1 continued.

		Lepidoptera			Diptera		Coleoptera	Hymenoptera	Other	Psocoptera	Aranea	Acari
		Tineidae			Hippoboscidae		Adults/larvae		Diptera	Epipsocidae		
		L	P	A	PI	A						
Rearsby	SK651142	9	1	0	4	1	0	0	0	0	0	0
Rearsby	SK651142	0	1	0	54	0	0	0	0	2	0	0
Rothley	SK576124	1	0	0	34	0	0	0	0	0	0	0
Rothley	SK576124	1	0	0	28	0	0	1	0	0	0	0
Rothley	SK576124	0	0	0	42	0	0	0	0	0	0	0
Sharnford	SP483920	0	0	0	19	0	0	1	0	0	1	0
Sharnford	SP483920	1	0	0	32	0	0	0	0	0	0	0
Sileby	SK610152	2	0	0	10	0	1	0	0	0	0	0
Sileby	SK610152	17	3	6	0	0	0	0	0	0	2	0
Sileby	SK610152	25	0	0	0	0	0	0	0	0	1	0
Sileby	SK610152	9	0	0	0	0	0	0	0	0	0	0
Sileby	SK610152	1	3	0	5	4	0	0	0	1	0	0
Sileby	SK610152	12	6	4	0	0	0	0	0	0	0	43
Sileby	SK610152	49	0	0	18	0	0	0	0	0	0	0
Stoughton	SK641022	17	0	0	11	3	0	0	0	0	0	5
Stoughton	SK641022	0	0	0	22	1	1	0	0	0	2	0
Stoughton	SK641022	0	0	0	0	0	0	0	0	0	1	0
Stoughton	SK642022	19	0	0	14	0	0	0	0	0	2	4
Stoughton	SK641022	2	0	0	20	0	0	0	0	2	5	8
Stoughton	SK641022	11	0	0	11	0	0	0	0	0	1	0
Stoughton	SK643022	98	8	0	61	0	0	0	0	0	0	0
Stoughton	SK642022	13	1	0	33	0	0	0	0	0	0	3
Stoughton	SK642022	16	12	0	0	0	0	0	0	0	0	0
Stoughton	Sk643022	0	0	0	0	0	0	0	0	0	0	0

Appendix 1 continued.

		Lepidoptera			Diptera		Coleoptera	Hymenoptera	Other	Psocoptera	Aranea	Acari
		Tineidae			Hippoboscidae		Adult/larvae		Diptera	Epipsocidae		
		L	P	A	PI	A						
Sutt Bonn	SK505254	3	0	0	9	0	0	0	0	0	0	0
Sutt Bonn	SK505253	23	9	4	16	0	0	0	0	0	0	0
Sutt Bonn	SK505253	3	0	0	0	0	0	0	0	0	0	0
Sutt Bonn	SK504255	1	0	0	15	0	0	0	0	0	0	0
Sutt Bonn	SK504255	13	0	0	12	0	0	0	0	0	2	0
Sutt Bonn	SK504255	22	0	0	14	0	0	6	0	0	0	0
Sutt Bonn	SK504255	8	2	0	21	0	0	0	0	0	0	0
Sutt Bonn	SK504255	6	0	0	39	0	0	1	0	0	2	8
Sutt Bonn	SK504255	3	3	0	12	0	0	0	0	0	1	0
Sutt Bonn	SK504255	19	0	0	44	0	0	0	0	0	0	0
Sutt Bonn	SK504255	24	6	12	27	0	0	0	0	0	0	0
Sutt Bonn	SK504255	8	3	1	29	0	0	0	0	0	0	42
Sutt Bonn	SK504255	0	0	0	0	0	0	0	0	0	0	0
Swithland	SK553130	0	0	0	38	0	0	0	0	0	0	0
Swithland	SK553130	10	10	16	14	0	0	0	0	0	0	0
Thurcaston	Sk567107	69	0	0	27	0	0	0	0	3	0	5
Thurnby	SK646039	25	0	0	13	0	0	0	0	0	0	39
Thurnby	SK646039	18	1	2	26	0	2	0	0	0	2	47
Thurnby	SK646039	0	0	0	17	0	0	0	0	0	0	13
Thurnby	SK646039	7	3	6	3	0	1	0	0	0	0	2
Thurnby	SK647039	33	15	2	11	0	1	0	0	0	2	0
Thurnby	SK646045	42	10	2	0	0	0	0	0	0	0	0
Whetstone	SP556976	13	0	0	0	0	0	0	0	0	0	0
Whetstone	SP556974	24	1	0	6	0	4	0	0	0	0	0
Whetstone	SP556974	18	0	1	0	1	0	0	0	0	0	0

Appendix 1 continued.

		Lepidoptera Tineidae			Diptera Hippoboscidae		Coleoptera Adults/larvae	Hymenoptera	Other Diptera	Psocoptera Epipsocidae	Aranea	Acari
		L	P	A	PI	A						
Whetstone	SP556974	16	10	0	23	0	1	0	0	0	0	0
Whetstone	SP556974	3	0	0	16	0	0	0	0	0	0	0
Whetstone	SP556974	0	0	0	0	0	0	0	0	0	0	0
Whetstone	SP556974	32	4	0	10	3	0	0	0	0	0	8
Whetstone	SP556974	12	5	0	22	0	0	0	0	0	0	0
Whetstone	SP556976	8	0	0	13	0	0	0	0	0	0	0
Whetstone	SP556976	2	0	0	0	0	0	0	3	9	0	54
Whetstone	SP556976	0	0	0	5	1	0	0	0	0	0	4
Whetstone	SP556973	42	10	0	0	0	0	0	0	0	0	0
Whetstone	SP556973	7	0	0	0	0	0	0	0	0	0	0
Whetstone	SP556976	1	0	0	10	0	0	0	0	0	0	0
Whetstone	SP556973	8	12	0	0	0	0	0	0	0	0	0
Wing	SK894029	33	14	0	10	3	1	0	0	0	0	9
Wing	SK894029	0	0	0	0	0	0	0	0	0	0	6
Wing	SK894029	0	0	0	0	0	0	0	0	3	1	28
Wing	SK894029	12	0	0	27	0	0	0	0	0	0	2
Wing	SK894029	1	0	0	11	0	0	0	0	0	0	0
Wing	SK894029	0	0	0	0	0	0	0	0	0	0	0
Wing	SK894029	16	32	1	48	0	0	0	0	0	0	0
Wing	SK894029	18	4	2	22	2	0	2	0	0	0	8
Wing	SK894029	15	0	0	5	0	0	0	0	0	0	0
Wigston	SP604989	3	0	0	24	0	0	0	0	0	0	0
Wigston	SP604989	0	0	0	8	0	0	0	0	0	0	0
Wood Hse E	SK531139	12	0	0	21	5	1	0	0	1	0	0

Appendix 1 continued.

		Lepidoptera			Diptera		Coleoptera	Hymenoptera	Other	Psocoptera	Aranea	Acari
		Tineidae			Hippoboscidae		Adults/larvae		Diptera	Epipsocidae		
		L	P	A	PI	A						
Wymeswold	SK605233	7	0	0	10	3	0	0	0	0	0	0
Wymeswold	SK605233	1	0	0	72	0	0	0	0	3	0	5
Wymeswold	SK605233	0	0	0	6	0	0	0	0	0	0	3
Wymeswold	SK605233	2	0	0	0	0	0	0	0	0	0	10

Appendix 1 continuued. Leicestershire 1977/78 collection.

		Lepidoptera Tineidae			Diptera Hippoboscidae		Coleoptera Adults/larvae	Hymenoptera	Other Diptera	Psocoptera Epipsocidae	Aranea	Acari
		L	P	A	PI	A						
Cosby	SP547947	18	6	0	3	8	0	0	0	0	1	64
Cosby	SP547947	9	1	0	10	2	0	3	12	16	0	0
Cosby	SP547947	21	14	0	0	0	0	0	0	12	0	0
Cosby	SP547947	13	0	0	15	0	3	0	0	0	0	0
Cosby	SP547947	2	0	0	26	5	0	0	3	3	2	12
Hoby	SK671176	0	0	0	13	0	0	0	0	0	0	0
Hoby	SK671175	0	0	0	12	0	1	0	0	0	0	0
Hoby	SK671175	13	10	5	8	0	2	0	0	1	0	13
Leicester	SK594021	7	8	0	2	0	0	1	4	0	0	0
Leicester	SK594021	10	2	0	0	0	1	0	0	8	0	0
Leicester	SK594021	8	0	0	0	0	0	0	0	0	0	64
Leicester	SK594021	14	3	0	9	0	0	6	0	0	3	0
Leicester	SK565044	29	10	4	14	0	0	0	0	0	0	0
Leicester	SK565044	8	3	0	18	0	3	0	0	10	0	0
Queniboro	SK649120	9	4	0	7	0	0	0	0	0	0	0
Queniboro	SK649120	38	4	0	0	0	0	0	0	0	0	0
Whetstone	SP556976	10	8	0	1	0	0	3	0	3	0	8
Whetstone	SP556976	0	3	32	0	0	0	0	0	0	0	0
Whetstone	SP558971	2	12	0	23	0	0	0	0	4	0	0
Oadby	SP697998	1	1	0	11	0	4	0	0	3	0	0
Oadby	SP697998	0	27	0	0	0	0	0	0	6	0	0
Oadby	SP630994	0	33	0	0	0	7	0	0	0	0	0

Appendix 1 continued.

		Lepidoptera			Diptera		Coleoptera	Hymenoptera	Other	Psocoptera	Aranea	Acari
		Tineidae			Hippoboscidae		Adult/larvae		Diptera	Epipsocidae		
		L	P	A	PI	A						
Oadby	SP630994	0	12	0	0	0	0	0	0	0	0	0
Stoughton	SK642023	3	48	0	10	0	0	0	0	0	1	0
Stoughton	SK642023	0	10	0	18	0	0	0	0	0	0	0
Oadby	SP633994	0	4	0	7	0	0	0	0	0	0	0
Oadby	SP633993	0	16	0	26	0	2	0	0	0	0	0
Oadby	SP634992	0	19	0	3	0	0	0	0	0	0	0
Oadby	SP629997	3	25	0	8	0	0	0	0	0	0	0
Oadby	SP629997	0	6	0	16	0	0	0	0	0	0	0

Appendix 1. Cornwall 1978/79/80.

		Lepidoptera Tineidae			Diptera Hippoboscidae		Coleoptera Adults/larvae	Hymenoptera	Other Diptera	Psocoptera Epipsocidae	Aranea	Acari
		L	P	A	PI	A						
October 1978.												
Coverack	SW785182	0	0	0	0	0	1	0	0	0	0	0
Coverack	SW785182	3	2	0	4	0	0	0	0	10	0	0
Coverack	SW785182	8	0	0	1	2	0	0	3	3	1	12
Coverack	SW785182	0	6	0	0	0	0	0	0	0	0	23
Coverack	SW785182	0	0	0	0	0	0	0	0	0	0	0
Coverack	SW783186	7	10	1	9	0	0	0	1	23	0	0
Coverack	SW783186	2	0	0	0	0	0	0	0	12	2	18
Coverack	SW783186	0	2	0	0	0	0	1	2	0	0	0
Coverack	SW783186	4	9	2	0	0	2	0	0	4	0	0
Mullion	SW681192	0	0	0	12	0	0	0	0	0	0	0
Mullion	SW681192	0	0	0	8	0	0	0	0	0	1	86
Mullion	SW681192	0	0	0	15	0	0	0	0	0	0	15

Appendix 1 continued.

		Lepidoptera			Diptera		Coleoptera	Hymenoptera	Other	Psocoptera	Aranea	Acari
		Tineidae			Hippoboscidae		Adults/larvae		Diptera	Epipsocidae		
		L	P	A	PI	A						
October 1979.												
Coverack	SW785182	0	0	0	5	0	0	0	0	0	0	0
Coverack	SW785182	8	1	0	0	0	3	0	1	23	2	31
Coverack	SW785182	2	0	0	0	0	0	1	0	9	9	42
Coverack	SW785182	0	0	0	0	0	0	0	0	0	0	0
Coverack	SW785182	0	5	0	0	0	0	0	0	0	0	14
Coverack	SW785182	12	4	1	8	0	0	2	0	26	0	81
Coverack	SW785182	0	0	0	0	0	4	0	4	17	1	11
Coverack	SW785182	7	0	0	0	0	0	0	0	0	0	0
Coverack	SW783186	18	12	0	0	0	0	0	0	24	0	8
Coverack	SW783186	3	0	0	16	0	0	0	1	0	0	0
Coverack	SW783186	0	0	0	6	0	1	0	0	56	0	24
Coverack	SW783186	0	0	0	0	0	0	0	0	0	0	0
Coverack	SW785182	0	0	0	8	0	0	0	0	0	0	0

Appendix 1 continued.

		Lepidoptera			Diptera		Coleoptera	Hymenoptera	Other	Psocoptera	Aranea	Acari
		Tineidae			Hippoboscidae		Adults/larvae		Diptera	Epipsocidae		
		L	P	A	PI	A						
October 1980.												
Coverack	SW785182	9	10	0	0	0	5	0	0	0	0	0
Coverack	SW785182	0	0	0	0	0	0	0	0	43	2	0
Coverack	SW785182	12	3	0	0	0	0	0	0	0	0	24
Coverack	SW785182	11	0	0	12	0	0	0	3	8	1	13
Coverack	SW785182	4	8	1	16	1	1	0	1	5	0	4
Coverack	SW785182	0	0	0	0	0	6	1	0	0	0	0
Coverack	SW783186	23	18	0	0	0	0	0	0	33	0	96
Coverack	SW783186	7	0	0	6	0	0	0	0	0	0	12
Coverack	SW783186	0	3	0	0	0	2	0	0	3	0	0
Coverack	SW783186	8	0	0	2	0	0	0	0	0	1	0

Appendix 1 continued.

Leicestershire 1984/85.

		Lepidoptera Tineidae			Diptera Hippoboscidae		Coleoptera Adult/larvae	Hymenoptera	Other Diptera	Psocoptera Epipsocidae	Aranea	Acari
		L	P	A	PI	A						
Walcote	SP567838	3	5	2	23	7	0	0	0	0	0	42
Walcote	SP567838	1	0	0	3	2	0	0	0	0	0	15
Walcote	SP567838	10	0	0	0	0	0	0	0	0	2	19
Walcote	SP567838	0	0	0	0	4	0	0	0	0	0	21
Walcote	SP567838	0	0	0	10	2	2	0	0	0	0	84
Walcote	SP567838	18	0	0	3	3	0	10	0	0	0	17
Walcote	SP567838	1	3	0	0	0	0	0	0	0	0	19
Walcote	SP567838	0	0	0	0	0	0	0	0	0	0	104
Cosby	SP547947	0	0	0	0	0	1	0	15	0	0	0
Cosby	SP547947	0	0	0	0	0	0	0	0	12	3	0
Cosby	SP547947	0	0	0	16	0	0	0	0	0	2	0
Cosby	SP548958	0	0	0	0	5	0	0	0	0	0	0
Cosby	SP548957	2	1	0	0	0	0	0	0	3	0	13
Cosby	SP547957	0	3	0	0	0	4	0	0	0	0	0
Whetstone	SP556976	1	1	0	0	0	0	0	0	0	0	0
Whetstone	SP556976	3	0	1	0	0	0	0	0	18	0	0
Whetstone	SP556973	0	0	0	2	0	1	0	0	3	0	0
Whetstone	SP557972	0	0	0	0	0	0	0	0	1	0	0
Oadby	SP631993	0	0	0	0	0	0	0	0	0	3	0

Appendix 1 continued.

		Lepidoptera			Diptera		Coleoptera	Hymenoptera	Other	Psocoptera	Aranea	Acari
		Tineidae			Hippoboscidae		Adults/larvae		Diptera	Epipsocidae		
		L	P	A	PI	A						
Oadby	SP631993	0	0	0	0	0	0	0	0	0	0	0
Oadby	SP622997	0	12	0	0	0	0	0	0	0	0	0
Oadby	SP632001	1	15	0	0	0	0	0	0	0	1	0
Oadby	SP628997	0	0	0	13	0	1	0	0	0	0	0
Oadby	SP628997	0	0	0	0	0	0	0	0	0	0	0
Oadby	SP630988	0	16	0	0	0	0	0	0	0	0	0
Oadby	SP625998	0	12	0	18	0	0	0	0	0	4	0
Stoughton	SK642021	1	8	0	3	0	5	0	0	0	0	0
Stoughton	SK642021	0	0	0	0	0	0	0	0	0	0	0
Leicester	SK608052	0	0	0	0	0	0	0	0	0	2	0
Leicester	SK608053	0	0	0	29	0	7	0	0	0	0	0
Whetstone	SP562978	0	0	0	0	0	0	0	0	0	0	0
Cosby	SP548952	0	0	0	0	0	0	0	0	0	0	0
Cosby	SP548952	0	0	0	0	0	0	0	0	0	0	0
Whetstone	SP559977	0	0	0	15	0	0	0	0	0	0	0
Whetstone	SP558976	0	0	0	3	0	0	0	12	0	5	0
E Goscote	SK644135	0	0	0	0	0	0	0	0	0	2	0
E Goscote	SK644135	0	5	0	0	0	0	0	0	14	0	0
Oadby	SP634996	0	0	0	0	0	0	0	0	2	0	0

Appendix 1 continued.

	Lepidoptera			Diptera		Coleoptera	Hymenoptera	Othera	Psocoptera	Aranea	Acari
	Tineidae			Hippoboscidae		Adult/larvae					
	L	P	A	PI	A						
St.,Harrold SK378209	0	0	0	18	0	0	0	3	1	1	0
St.,Harrold SK378209	0	0	0	0	0	0	0	0	1	0	0
St.,Harrold SK378209	0	0	0	0	0	2	0	0	0	1	0
ST.,Harrold SK378209	0	0	0	0	0	8	0	1	0	0	0

Appendix 2.

Methods and solutions used in the histology of fleas.

Duboscq-Brasil fixative.

Picric acid	1gm
80% alchol	150cc^3
Formalin(40%HCHO)	60CC^3
Acetic acid(glacial)	15cc^3

After fixation the fleas were wased in 90% aclohol, completely dehydrated in several changes of absolute alcohol and then cleared in Cederwood oil (8 hr). After these treatments the fleas were placed in moulten Paraplast, a high melting point wax (57^{o}C) under vacuum for 2 hours with a change to fresh Paraplast at one hour. At the end of this period the fleas were blocked in Paraplast. Sections were cut on a rotary microtome at a thicness of between 6-8,, then mounted on subbed slides, and after dewaxing in xylene were stained with Mallory triple stain.

Mallory triple stain cf Cason 1950.

Phosphotungstic acid	1gm
Orange G	2gm
Analine blue (WS)	1gm
Acid fuchsin	3gm
Distilled water	200cc^3

Appendix 2 continued.

Ingredients were added in the above order ensuring that each had dissolved before the next was added.

Staining.

1 Stain for 5 minutes.

2 Wash in running tap water 3-5 seconds.

3 Dehydrate rapidly in alcohols, clear in xylene and mount in Canada balsam.

Stains Nuclei - red; striated muscle blue-red; arthrodial membrane - blue; connective tissue -bright blue; tanned cuticle and chitin - yellow; untanned cuticle - red.

Method for embeding fleas in resin.

Fixation.

Fixation was carried out overnight (12hours) at $4^{o}C$ in Karnovsky's fixative (Karnovsky 1965). The fleas were then washed in phosphate buffer for twenty minutes. Acetone in a series of different concentrations was used to dehydrate the fleas prior to blocking, (30%, 50%, 70%, 90%, 100%). The fleas were left for twenty minutes in each concentration except for 100% in which they were left for one hour with a change of fresh 100% acetone at thirty minutes.

To prepare the bodies for the resin they were soaked in propylene oxide for 90 minutes, during which time the solution was changed once. After this time

they were placed in a 1:1 solution of araldite and propylene oxide for 12 hours under a slight vacuum. The fleas were then left in 100% araldite for 24 hours during which time the araldite was changed 3 times. Finally the fleas were placed in a mould with 100% araldite which was polymerised at $70^{o}C$ which took 24-48 hours.

Solutions.

Karnovsky fixative.

2gm E.M grade Paraformaldehyde in $25cc^{3}$ distilled water.

1-3 drops of NaoH warmed to $60-70^{o}C$ and then cooled.

Phosphate buffer.

M/15 $NaHPO4.2H_{2}O$ $8c^{3}$

M/15 $KH_{2}PO4$ $2c^{3}$

$10cc^{3}$ 25% Gluteraldehyde made up to $50cc^{3}$ with Po_{4} buffer pH 7.2.

Araldite.

Epoxy resin Araldite CY212 $50c^{3}$

Dodecenyl sussinic antydride $50c^{3}$

Dibutyl phthate $1.2c^{3}$

Appendix 2 continued.

These were mixed together by continuous agitation with a glass rod for 15 minutes. When thourghly mixed araldite can be stored for several weeks at -15^{o}C.

The polymerised blocks were roughly trimmed with a hacksaw to reduce the block face before mounting on stubs using household araldite as the adhesive. After polymerisation at 20^{o}C for 2 hours the block face was finely trimmed with a razor blade so as to leave as little araldite as possible around the flea and between the flea and the block face.

Saggital sections of each flea were cut on an LKB ultra microtome using a glass knife. One micron (µm) thick sections were cut with a fall speed of 1.0mm/second. Sections were collected from the surface of distilled water contained in a small boat attached to the glass knife and placed on subbed slides in a small drop of distilled water, then dried on a hot plate at 60^{o}C.

Appendix 2 continued.

Staining.

Sections were stained by flooding the slide, while still on the hot plate, with 0.25% filtered Toluidine blue, staining for 3 minutes. The stain was then removed and the slide was rinsed with distilled water and placed back onto the hot plate to dry. When completely dry the sections were covered with araldite and a cover slip and left on the hot plate for 2 days to polymerise.

Studies on three congeneric species of flea (Siphonaptera) from the nests of *Delichon urbica urbica* in England. By Frank Clark.

Abstract.

The house martin *D.u.urbica* builds an enclosed dome shaped nest of mud under overhangs on cliffs or buildings. Three species of flea, *Ceratophyllus hirundinis*, *C.farreni* and *C.rusticus* are commonly found in these nests. The relationship between these three congeneric and monoxenous species that permits coexistence on the same host and nest was investigated. This study comprised a detailed examination of some of the abiotic and biotic factors which might influence the distribution and abundance of these three species, as well as those factors which may control inter- and intra-specific competition. To achieve this the following aspects were examined.

1) The effect of different geographical localities within England and of nest site and nest characteristics on the flea community was investigated. Nests were collected and the numbers of each species from each nest recorded as were the characteristics of each nest. Analysis showed that the numbers of each species were often positively correlated suggesting that little inter-specific competition at the densities encountered was taking place. It further suggested that conditions suitable for one specie were also suitable for the others. Evidence of differing responses to the wall material to which the nests were attached and the type of nest lining material was obtained. All three species were more abundant in nests attached to brick or painted dash than those on faced stone surfaces. All three species were encountered in nests taken from cliffs where rougher surfaces may present more

sheltering places.

2) Nest environment (temperature and relative humidity) was measured in nests occupied by martins and throughout the winter months when the nests were unoccupied. In occupied nests the environment is controlled by the martins. During the winter months the environment is close to ambient although changes in temperature are buffered by the nest wall and lining material. Consequently overwintering fleas are exposed to a wide range of environmental conditions.

3) Flea emigration was examined by placing sticky traps around nests, by passing sticky cards over the front of nests and by netting and "defleaing" martins. Only two fleas were caught on the traps around the nests although they were left in position for two years and none on the cards passed over the nests. A few fleas were removed from the bodies of the martins. It is concluded that colonisation of new nests and re-colonisation of existing nests relied on transportation on the martins and that new nests were likely to be colonised by only a few fleas.

4) Survival of adult fleas in the absence of the martins was investigated with different nest lining materials at different temperatures and relative humidities. At least 50% of the fleas survived a range of temperatures and humidities over several months. However, when offered a blood meal not all individuals fed. Further, not all individuals would mate. Hence, despite surviving for long periods, not all fleas contribute to future generations.

5) Metabolic activity was investigated at different temperatures

using a Gilson Respirometer. Activity of each species was monitored in a flea activity monitor. The respirometry showed that there was considerable variation in the respiration rates both between and within species and between autumn and spring. Males had a significantly higher respiration rate than females. The activity monitor showed *C.rusticus* to be less active than the other two species with females overall more active than males.

6) Population dynamics was studied by the collection of nests at different times of the martin breeding season. Each species will only reproduce while the nest is occupied by the martins. The number of broods the martin had appeared to be of no importance in determining the breeding cycles of the fleas as long as the nest was used regularly for roosting. Data on the feeding rate, amount of blood taken and defaecated and the effects of density on these was obtained by offering each species a blood meal on the ear of a rabbit. Females took significantly more blood than males. At the densities tested little effect on feeding behaviour was observed. Using Bob White Quail, which was the least efficient species at removing fleas, the effects of different nest lining materials on the length of time the fleas spent feeding was examined. The results showed that in the presence of feathers a sigificantly shorter time was spent feeding with the longest when no lining material was present.