Some ASPECTS OF THE RELATIONSHIP BETWEEN

CERTAIN EPIFAUNISTIC INSECTS AND

THEIR ~~MAMMALIAN~~ HOSTS

BY

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ABSTRACT

Certain aspects of the relationship between small mammals and their epifaunistic communities were investigated in a habitat supporting three rodent species.

Preliminary studies indicated that, in an area of rough grass and bramble shrub, a community of rodents existed harbouring a wide range of flea ectoparasite species, as well as the apparently rare beetle *Leptinus testaceus* Müller.

Techniques were developed, and are described, for the accurate assessment of the level of epifaunistic infestation of rodents. The infestation of various host species, sex and age categories were compared during the different phases of the host's annual population cycle. The rates of re-infestation of hosts and the levels of infestation with fleas with respect to home range size and migratory/sedentary host categories were also investigated.

The underlying cause of certain observed similarities in the level of infestation of some host categories was studied by the use of mark and recapture of fleas. The possibilities offered by this method of study of ecto-parasites and their hosts are discussed.

In order to contrast the situation observed in the flea infestation of small mammals a study of the associat-ion between hibernating hedgehogs and their flea ectopara-sites was undertaken. A method was developed for the assessment of the alimentary relations of a flea population with its host and this approach, together with the use of other techniques, indicated certain behavioural modifica-

tions which allowed the fleas to successfully parasitise their hibernating hosts.

ACKNOWLEDGEMENTS

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CHAPTER 3

EXPERIMENTS WITH THE RELEASE OF MARKED FLEAS

EXPERIMENTAL SECTION II

CHAPTER 4

THE RELATIONSHIP BETWEEN HIBERNATING HEDGEHOGS AND ARCHAEO-

PSYLLA E. ERINACEI.

CHAPTER 1

GENERAL INTRODUCTION AND PLAN OF THESIS

Introduction

The study of the relationship between mammals and their epifaunistic communities is an area of zoology which has stimulated much interest and discussion. However, intensive studies have been almost exclusively concerned with species infesting commensal mammals or those that are disease vectors. Indeed, it was recently pointed out that our knowledge of the ecology of the epifauna of non-commensal small mammals is quite fragmentary (Ulmanen and Myllymäki, 1971).

The possible reasons for this neglect are several. Firstly, quite frequently the numbers of insects infesting individual small mammal captures are small and collecting techniques must be efficient if more than "rough estimates" of infestation levels are to be obtained. Secondly, it is the habit of almost all species of small mammal flea to spend some portion of its adult life in the nest of the host rather than on its body (Mead-Briggs, 1964a), this is probably also true of many other epifaunistic insects. Attempts to quantify the numbers of insects residing in small mammal nests, under natural conditions, have met with many difficulties. For example Davis (1934) stated that the essential stage of nest identification depends mainly upon circumstantial evidence. Thirdly, Cole and Keopke (1947) have shown that analysis of numerical results from studies of epifaunistic insects is often impossible by standard methods and, to date, no means of comparing levels of infestation of different host categories have been described that do not require transformation of results

(see for example Evans and Freeman, 1950 and Ulmanen and Myllymäki, 1971). Finally, and probably not least important, is the fact that investigators must apply both entomological and mammalogical techniques in order to obtain information on the ecology of the epifauna of small mammals. Flea collections are frequently made as a by-product of mammal studies and are then passed on the entomologists for examination. This procedure often divorces the insect data from valuable information concerning their hosts.

During a small-scale trapping experiment in 1970 certain areas of the grounds of the Department of Zoology, Royal Holloway College at Alderhurst in Surrey were found to support a mixed community of small mammal species with an interesting epifauna, including seven flea species and the infrequent Leptinid beetle *Leptinus testaceus* Müller. During the summer of 1971 a pilot study was performed to confirm these facts and to overcome some problems of technique and, in 1972 and 1973, a full scale investigation was undertaken into the relationships between certain epifaunistic insects and their mammalian hosts.

Plan of Thesis

The study falls into two major sections. Firstly, an
ecological study of a community of small mammals and the
members of the insect epifauna which they support. The
second section is a comparative study based on the relation-
ships between a hibernating host species, the European
hedgehog *Erinaceus europaeus* L., and on one of its ectopara-
sites, determined by enclosure and laboratory studies.

The nature of the project necessitates the introduction,
presentation and discussion of results from studies of both
mammals and insects. However, in both of the above sections
the mammal and the insect areas of study will be dealt
with by different methods because of the different purposes
for their presentation. The mammal studies should be
regarded as essential backgrounds to the insect work as it
is not possible to discuss, in detail, surveys of epifauna
in the light of results from other, previous mammal studies
from other localities. This is especially true in the case
of small mammals because the annual cycles of these animals
vary greatly from year to year and with geographical posit-
ion (Brown, 1966). The two studies must be synchronous,
both temporally and geographically, if it is to be possible
to relate them to each other. However, previous work on
the ecology of both small mammal populations and hedgehog
hibernation is extensive and an introduction to these areas
will form a major part of the introductions to Chapters 2
and 4. On the otherhand, the introduction to the biology
of the epifauna will be less comprehensive and its later
discussion, in the light of the information gathered

concerning the mammals, will be correspondingly more
thorough.

The major component of the rodent community at Alder-
hurst at the time of the study was *Apodemus sylvaticus* L.
This extremely ubiquitous species has received little
detailed attention with respect to its epifauna since the
investigations of Evans and Freeman (1950). It was hoped,
using efficient techniques for insect collection including
live trapping and full anaesthetisation of all captured hosts
for deinfestation, to make a study of the seasonal changes
in the levels of infestation of certain host categories.

Within the annual cycles of small mammal populations
it is possible to define three major periods. Firstly, the
overwintering period when little or no reproductive activity
can be detected. Secondly, the pre-breeding period when a
majority of the population are in a reproductive condition
and, finally, the breeding season when there is an influx
of juvenile animals and a sudden increase in population
density after the period of low density during pre-breeding.
At all stages the closest possible observations of both
host and insect populations was to be maintained in order
to determine, if possible, the effects of the changing
patterns of host behaviour on levels of infestation of
their epifauna during the three periods of the annual cycle.

The comparatively short length of the study made it
necessary to restrict the investigation to the annual
population cycles of the hosts rather than the long term
population fluctuations first described in detail by Elton
(1942).

The information concerning the ecology of the flea
species and *L. testaceus* was accumulated simultaneously by
the same techniques and from the same host material, there-
fore it was decided that separate presentation and discus-
sion of results was unwarranted.

During the summer of 1972 it became apparent that
certain similarities existed in the levels of infestation
of male and female *A. sylvaticus* with fleas during summer
which were not wholly expected on the basis of previously
published work (see for example Ulmanen and Myllymäki, 1971).
A means of further studying these similarities, as well as
the more expected similarities which were observed during
winter, was devised. This work and the extension of it,
which was suggested by the nature of the results obtained,
is presented in Chapter 3.

The fully active overwintering behaviour of British
rodent species is such that they present almost constantly
favourable conditions for their epifauna during winter in
"permanent nests" (Cotton, 1970). This is not always the
case among British mammals. The hedgehog, *E. europaeus*,
although occupying a winter nest or hibernaculum for long
periods, presents some interesting problems as a host for
epifaunistic insects. For long periods during winter the
hosts undergo hypothermia, when the body temperature falls
to only a degree or so above ambient. Indeed, Morris (1967)
has shown that the host's body may frequently be cooler
than ambient temperatures. The study of the hedgehog flea
Archaeopsylla erinacei erinacei Bouché has been neglected since

the behavioural studies of Sgonina (1935 and 1939). It was
thought that a study of the winter ecology of *A.e. erinacei*
would provide an interesting comparison with the situation
found among rodents and shed some light on the apparently
very specialised abilities of that species to infest the
hedgehog. Results from such a study are presented in
Chapter 4.

EXPERIMENTAL SECTION 1

(Chapters 2 and 3)

C H A P T E R 2

THE ECOLOGY OF SMALL MAMMALS
AND THEIR EPIFAUNA

1. Introduction

1.1. The Mammal Populations

(i) Population Fluctuations

All small mammal populations undergo periodic fluctuations in density. These cyclical fluctuations and the various behavioural changes which accompany them have profound effects on epifaunistic communities which live in close association with the small mammal hosts. Before a precise knowledge can be gained of the ecological relationships between hosts and their epifauna the nature of these fluctuations must be understood.

The varying density of small mammals, both on an annual and a long-term basis, is the outward manifestation of the combined effects of the environment and many internal (endogenous) changes which are constantly occurring within the bodies of the animals. These endogenous reactions may be elicited within the body as a direct result of external (exogenous) factors, for example, certain environmental conditions, or they may be a response to other endogenous factors. By whatever means they arise changes in population density have a serious effect on the lives of the ectoparasites and these animals, in order to be successful, must be able to adapt their behaviour to the various pressures placed upon them by their hosts.

It has long been understood that annual cycles are not the only population fluctuations which are undergone by mammalian species. Superimposed on this short-term cycle are long-term fluctuations, also cyclical in nature, often taking between two and five years to complete (Elton, 1942).

These long-term cycles, which involve a pattern of increase-
peak-decline (crash)-low phases, are incompletely understood.
They can only be studied by lengthy investigations. The
results of some such long-term studies have been published
recently (Krebs, Gaines *et al.*, 1973; Lidicker, 1973).

The precise nature of the causal mechanism of these
cycles is not known. Exogenous factors have been implicated
by various authors and it has been suggested that epidemic
diseases or the activities of predators may be responsible
for the sudden drastic decreases in population density
which have been observed during "crash" periods. However,
none of these theories have been supported by reliable
experimental evidence.

Recent American work has been summarised by Myers and
Krebs (1974) who have postulated that it is a combination
of various endogenous factors which cause the rapid
declines in rodent density. They have suggested that, in
Microtus ochrogaster and, perhaps, in other rodents, the pop-
ulation is composed of two distinct genetical types. One
type has a combination of high reproductive rate and an
inherited propensity for dispersal while the other type is
more aggressive but has lower reproductive potentials.
During the period of increase aggressive animals are at an
advantage and they thrive at the expense of the less
aggressive animals which tend to migrate rather than compete
in the increasingly overcrowded parent population. Finally,
at the peak of population density, the animals with high
aggression and low reproductive capacity predominate. How-
ever, these animals can no longer replace the losses imposed
by death and, very rapidly, the population density declines.

This model, only recently formulated, requires large-scale experimental investigation before it can be generally accepted or applied to other species.

Both the annual and the long-term cycles can profoundly effect the ecology of the ectoparasite communities of small mammals. It will probably be some time before the effects of the long-term cycles can be identified with respect to the relationship between hosts and parasites and this area merits more interest. However, in the present study, the very nature of the long-term cycles preclude them from the investigation although their occurrence must be noted.

Because of its apparent simplicity when compared to the long-term cycles, mainly due to its shorter duration, the annual cycle has received much more attention from mammalogists. Consequently our understanding of the processes which are involved is more complete. Observations have been made of the effect of the annual cycle on various internal organs (Clarke, 1953; Christian, 1956; Chitty, 1961; Tanaka, 1962); also its effect in altering the social interactions between individuals in a population of a small mammal species (Sadlier, 1965; Healey, 1967; Getz, 1972; Turner and Iverson, 1973), between different populations of a species (Foster, 1959; Brown, 1966) and between different species within a community (King, 1957; Andrzej-ewski and Olszewski, 1963; Colvin, 1973; Hoffmeyer, 1973; Petersen, 1973). The effects of the changes in social behaviour of the host on the ectoparasitic populations, which are brought about by the annual cycle, will be investigated and discussed in some depth in later sections.

The following account of the events within an annual population cycle is based upon work done on *A. sylvaticus* in this country and in Europe. However, the events within the cycle are not completely understood, for this or any other species of small mammal, and where reference is made to another species this will be indicated in the text. In general terms the annual cycle of *A. sylvaticus* is similar to that of the two microtine rodents under investigation in this study. Where significant differences have been demonstrated this will be mentioned at the appropriate time.

The winter period is a time when there is little sexual activity within the small-mammal population (Brown, 1969). The animals are therefore, behaviourally, fairly homogeneous although three main reproductive groups exist for each sex. Firstly, a small number of "old" animals are present who are overwintering for the second time, very few of these will survive to the following spring. Secondly, there are some animals, born early in the year, who matured to full breeding condition. Both of these groups have, therefore, regressed sexual organs; the males having ascended testes and the females closed (healed over) vaginae. Finally, a third group is comprised of those animals that were born later in the breeding season and did not enter breeding condition. These have, as yet, undescended testes and imperforate vaginae.

The social relationships within this overwintering population are probably fairly relaxed, the social and spatial pressures that existed during breeding no longer exist. L.E. Brown has contributed much to our understanding

of the social relationships within communities of *A. sylvat-icus* (Brown, 1954, 1956, 1966 and 1969). She has cast doubt upon theories involving mutually exclusive home ranges for each member of a population throughout the year and this is, doubtless, especially true during overwintering. In Brown's opinion a dominant male exerts its authority over a "super-family" or "clan". It probably patrols a large area, often ranging over up to six acres, only small parts of the area are used during a particular period. This area, however, does not conform to the definition of a "home-range" given by Dice (1952) who emphasised that the area should be used habitually in daily activities. A more widely accepted definition is that of Burt (1943) which was restated by Jewell (1966) as follows:- "home range is the area over which an animal normally travels in pursuit of its routine activities".

Within this area - the "home-range" of the clan - the dominant male tolerates the presence of adult males not in breeding condition and it is probable that the animals exhibit true communal behaviour, sharing nest and feeding sites. Morris (1968) observed three adult *A. sylvaticus* sharing an old nest of a hedgehog, *Erinaceus europaeus*. It is probable that this behaviour is quite common in more usual nest sites during overwintering, and this behaviour would have important implications for ectoparasite popula-tions.

During winter, food is fairly abundant in the form of nuts, seeds and acorns. *C. glareolus* and *A. sylvaticus* feed readily on these foods (Gorecki and Gebczyńska, 1962). Even a blanket of snow hardly effects the life of the animals

in their complex runway systems below soil level (Frank, 1964 for *Microtus arvalis*). During exceptionally mild winters, or even in some normal winters when the seed crop is very heavy, some breeding may occur and various authors have noted breeding activity under these circumstances (Baker,1930 and, Newson, 1963 for *A. sylvaticus*; Zejda, 1962 for *C. glareolus*). This phenomenon is, however, uncommon and when it does occur litter sizes are often significantly reduced (Smyth, 1966).

In spring a degree of dispersal occurs within the communities. The cause of this dispersal is incompletely understood but depletion of available food may be instrumental. It results in very low trappable population densities which do not increase again until breeding reaches its peak in late summer and early autumn.

Miller (1958) found that the average range of a male *Apodemus* from March to May was four times as large as the September to November ranges. Dominant males remain in their favoured positions but increased antagonism between them and other, now sexually mature males, results in a movement of animals (Brown, 1966). This dispersion serves to spread the animals over wide areas into regions of comparatively low population density and it results in maximum utilisation of available habitat. These movements will be seen to have an important effect on the ectoparasites. The "lull" in the trapping frequency of animals, at this time, is not due entirely to dispersal. The death rate of overwintered animals goes up in spring (Chitty and Chitty, 1962 for *Microtus agrestis*), probably because of a

shortage of food. Several authors have noticed a reduction in the trappability of animals (Miller, 1958; Kikkawa, 1964; Tanton, 1965). This period of great activity within the small mammal communities may be termed the "pre-breeding" period.

The timing of the onset of breeding is governed by the maturation of the females (Baker, 1930). Males come into breeding condition in March, although this may be rather later in *Clethrionomys* (Southern, 1964). However, the first pregnancies are rarely detected until late in April as the females come into breeding condition some time after the males.

At this stage small litter sizes and high mortality of young result in low recruitment into the population and continuing sparse population densities despite apparent high breeding activity (Baker, 1930; Brown, 1966; Sadlier, 1965 for *Peromyscus*). As breeding continues the older, dominant overwintered males die out and the younger males are able to become established. This probably results in a breakdown of the "clan" system at the height of breeding, although Brown (1966) suggested that the animals continue to seek to fit into a social hierarchy. At this time, usually in late July and August, population densities rapidly increase. Competition for the available space within the dense communities results in home ranges becoming much smaller. Brown (1966) recorded densities of three animals per acre during spring pre-breeding increasing to seventeen animals per acre in late summer and autumn.

As breeding reaches a peak the breeding females fiercely

defend an exclusive "breeding home range" (Brown, 1966 and 1969) in order to afford their unweaned young a measure of protection from the competition for space operating within the community as a whole. In Brown's opinion these ranges are the most fiercely defended of all. In *Microtus* (Frank, 1957), and no doubt in other small mammal species, the males are only allowed near these breeding territories when the female is in oestrus. Many authors have observed the extreme aggression of the breeding females in small mammal species (Crowcroft and Rowe, 1963 for *Mus;* McCabe and Blanchard, 1950 and Sadlier, 1965 for *Peromyscus*). During weaning there is some evidence that the female may guide her young until they are acquainted with safe territorial boundaries (Howard, 1949 for *Peromyscus;* Crowcroft, 1966 for *Mus*).

Breeding slows down in late autumn and usually ceases during November. The duration of the breeding season for British small mammals is outlined in Southern (1964). Cessation of breeding is not due to lack of food, which is usually most plentiful at this time; it is probably due to subtle interactions of several external factors including temperature and day length. The reproductive organs of the breeding adults regress, the testes of the males become abdominal and the vaginae of females heal over with scar tissue. The breeding behaviour patterns imposed by high blood hormone levels are no longer maintained and mutual tolerance becomes greater at this time (Brown, 1966). Usually a dominant male asserts itself and the presence of mature, though sexually inactive individuals of the same sex, is tolerated establishing a firm "clan". It is at this

time that a social hierarchy is most evident within the
society. The individual home ranges of all the animals
coalesce into the area used by the "clan" and patrolled by
the dominant male. The population has returned to its
"asexual" overwintering condition.

(ii) Habitat Preference and Feeding

Southern and Linn (in Southern, 1964) summarised the
habitat preferences of the mouse and vole species concerned
in this study. They stated that *C. glareolus* is most common
in deciduous woodland and scrub and in banks and hedges,
usually in thick cover. *M. agrestis* is usually found in rough
grassland, whereas *A. sylvaticus* inhabits woodland, fields,
gardens and sometimes grass and heather where lack of cover
makes the habitat unsuitable for *Clethrionomys*. It has been
suggested that the presence of the field vole inhibits the
invasion of grassy areas by the wood-mouse (Brown, 1954).

The reasons for these preferences are self evident.
Microtus is, almost exclusively, a vegetarian feeding on
grass roots and succulent stem bases (Godfrey, 1953). The
bank-vole and wood-mouse are more opportunist in their
feeding habits; they take a wide variety of vegetable and
animal food depending on availability. *Apodemus* usually
takes more animal food than *Clethrionomys*, (see Miller, 1954
for *A. sylvaticus* and *C. glareolus*; Hološová, 1960 and Kikkawa,
1959 for *A. sylvaticus*; Turcek, 1953 for *C. glareolus*).

An overlap in feeding habits occurs between the two
species but its effects are reduced by the fact that the
greater speed and agility of *Apodemus* allows it to utilise
more open habitats. However, that is not to say that *A.*

sylvaticus does not frequently inhabit grassland. Indeed, Hoffmeyer (1973), who presented *A. sylvaticus* with a choice between beech-wood and grassland habitat, in large outdoor pens, found that the mice prefered the grass to the wooded areas. Fairley (1967) recorded that more *Apodemus* were captured in the parts of his trapping area covered by heather than those covered by grass. It is most probable that the response of *A. sylvaticus* to a grassland habitat is dependent on the amount of cover offered by it.

(iii) Survival

Relatively little is known about the age structure of populations and survival of small mammal species. The construction of life tables is difficult due to the very rapid turnover of the population. The appearance of new individuals on an experimental area may be explained by immigration as well as by recruitment of newly weaned animals, and disappearance of animals is as easily explained by emigration as by death. These problems usually make estimates of length of life by mark-recapture methods unreliable.

Pucek, Ryszkowski and Zejda (1969) calculated the age of *C. glareolus* by the length of tooth roots and went on to determine the length of life of the bank-vole by two methods: 1) "shrinkage between successive age classes" (Deevey, 1947; Ryszkowski and Petrusewicz, 1967) and 2) "kill curve" (Quick, 1963). They found that the estimated average length of life of voles depended on the type of habitat and the type of trap used to take the sample. Furthermore, the time of birth significantly affected mean

length of life. Animals born in autumn and spring tend to
live longer than animals born in the summer. The lowest
average length of life was observed in a *Pinetum* (1.339
months) and the highest in a *Tilio-Carpinetum* (3.869 months).

Dapson (1972) used biochemical changes in the eye lens
protein to determine the absolute age of specimens of *P.
polionotus*. He used similar methods to those of Pucek,
Ryszkowski and Zejda (1969) to obtain median ages of 49-84
days and maximum ages of 181-297 days.

No similar studies have been carried out for *A. sylvat-
icus* although Brown (1966) stated that the life span of
mice is "usually much less than ten months, (and) for many
it is less than ten weeks". This assumption seems to fit
quite well with results from other small mammal species
based on experimental evidence.

(iv) Home Range and Centre of Activity

It has long been recognised that the majority of
mammalian species restrict their activities to a defined
tract or area of ground for most of their lives. Seton (1910)
described "home regions" or "home grounds" for various
mammals while later authors wrote of an animal's "territory"
(e.g. Darling, 1937). Burt (1943) reviewed early literature
on these aspects of mammalian ecology and discussed defini-
tions of home range and territoriality. He decided on a
distinction between the two terms, which up to that time,
had been almost interchangeable, by stating that a
territory is a defended area whereas he suggested, in his
paper, that home range is: (a) "that area traversed by the
individual in its normal activities of food gathering,

mating and caring for young" and (b) "the area, usually around the home site, over which the animal normally travels in search of food". These definitions have been almost universally accepted, modifications by Jewell (1966) and Dice (1952) have been discussed previously.

The concept of home range and its practical determination for various mammalian species has received much attention from mammalogists since its early definition by Burt. Many methods have deen described for the measurement of home ranges. The use of a mark-recapture system of live trapping has been most widely used and probably a majority of contemporary studies concerned with home range calculation still rely on this device (e.g. Madden, 1974; Briese and Smith, 1974). Hayne (1949) described a method of calculating home range area from trapping data and Stickel (1954) has critically compared the method of Hayne and other authors for estimating home range dimensions from mark-recapture data.

Recent studies have suggested that live trapping is not an entirely reliable method for accurate assessment of home range.. The presence of traps tends to restrict penetration of the mammals to the periphery of their home range areas because movement is curtailed when the mammal is captured (Kikkawa, 1964; Jewell, 1966). Furthermore, there appears to be a differential response to the traps by mammals of different age, sex and species categories (Young, Nees and Emlen, 1952; Tanton, 1965; Brown, 1969). Therefore, various other methods, not requiring the capture of the animal, have been developed for home range size assessment. Justice (1961) individually marked mice by toe

clipping and detected their absence or presence at various points by footprints left on smoked kymograph paper. More recently Randolph (1973) has developed a tracking technique where marker bait containing identifiable fibres was fed to animals and later recovered from faecal pellets which the animals deposited in a grid of cartons.

In the present study a precise measurement of the size of home ranges was not sought. It was recognised that the computed areas did not represent the full home range; usually the calculated areas were underestimates. The obtained areas, therefore, are referred to as "areas of observed activity" and should not be taken to define the actual home range size of the animal, although they correspond quite closely to some home range estimates for *A. sylvaticus* (Brown, 1966).

Hayne (1949) introduced a measurement termed the centre of activity which was the calculated geometric mean of all the captures of a particular animal, an example of a calculation was given by him. The validity of the concept of centre of activity has been questioned by Smith, Boize and Gentry (1973). They pointed out that the assumption that the centre of activity is close to the nest or home site was not true for *Peromyscus polionotus*. However, Hayne (1949), when introducing the concept, specifically noted that it is not possible to identify the centre of activity with the home site of the animal concerned. In the present study the centre of activity was used to define a particular point about which the observed activity of the animal was

most intense. Proximity of the centres of activity of two
individuals indicated that portions of their home ranges
were overlapped or, at least, very close to each other.

(v) Movement_and_Migration

During the period of peak reproductive activity there
is a considerable reduction in the amount of space available
for each individual within the area inhabited by the pop-
ulation. This causes dispersal which is usually most
intense among sub-adults and juveniles (Brown, 1966).
Furthermore, temporary movements of small mammal populations
have been observed to correspond to local farming activities
(Miller, 1958; Rowe *et al.*, 1963 for *Mus*.). Seasonal
migrations are a normal pattern of behaviour. For example,
in winter, animals tend to congregate for warmth in dry
habitats and return to their home sites in spring (Curry-
Lindahl, 1956 for *Apodemus* and *Microtus*). The spring
dispersal has already been discussed. All these movements
result in changes in the spatial distribution and settlement
of individuals and a multitude of other factors combine to
ensure that, for much of the year, a proportion of any small
mammal population is composed of non-resident or migratory
animals that do not remain long in the area and, hence,
construct no permanent nest-site. These animals have
complicated relationships with their nidicolous ectoparas-
ites and present a challenging habitat for their epifauna.

1.2. The Flea Populations

Several standard entomological texts carry adequate
descriptions of fleas or Siphonaptera (e.g. Imms, 1925).
Indeed, such a well defined and homogeneous order, containing
so few aberrant forms, requires little initial description
so far as body shape and general biology is concerned.
However, some basic information, of direct importance to
this study, may be desirable before more specific aspects
of flea ecology are introduced in the following pages.

Fleas are small, wingless (apterous) insects with
holometabolous metamorphosis; that is they have life cycles
with egg, larva, pupa and imago stages. Their markedly
laterally compressed bodies are usually heavily sclerotised
giving them dark-brown to blackish colouration. Only the
adult stage is parasitic, the larvae being legless, eyeless
and elongated with biting mouthparts, living in the nest
or close to the home area of the host and feeding on organic
matter. Adults spend a varying amount of time on the host,
which is usually avian or mammalian, some flea species
spend most of their adult lives on the body of their host
while others spend only enough time there to obtain a meal
of blood before leaving to return to the nest. The free
pupa is contained in a coccoon.

Until the pioneer study of Evans and Freeman (1950)
our knowledge of the biology of British flea species under
natural conditions was limited to a series of geographical
records and host distributions. Indeed, more generally
throughout the world, detailed knowledge of the host

relationships of small mammal fleas was restricted to those
parasite species involved in epidemiological studies of
plague and other flea-borne diseases. Ulmanen and Myllymäki
(1971) have pointed out that the biology of the oriental
rat flea, *Xenopsylla cheopis* (Roths.), vector of plague,
Spilopsyllus cuniculi (Dale), vector of myxomatosis, and
Nosopsyllus fasciatus (Bosc.) a cosmopolitan rat flea, is very
well known. However, information about the ecology of fleas
of non-commensal small mammals is quite fragmentary.

(i) Variations in the level of flea infestation

Variations in the level of infestation of animals are
very common. Infestation differs within a population on a
yearly cycle basis. At any one time infestation may vary
with the sex or age of hosts. Depending on their social
position mice may be resident (sedentary) or non-resident
(migratory) on any given area and these factors bring about
further changes in infestation level.

(a) Yearly infestation cycles

The occurence of annual peaks of flea population
density on small mammals is well documented. Cotton (1970)
summarised the information available for *Ctenophthalmus nobilis*
(Roths.), infesting *M. agrestis*, the most common flea species
to be found in the present study, he stated that the flea
appeared on the body of voles in spring, it attained a
summer infestation peak and declined in the autumn; the
exact timing of this cycle differing with geographical
position and between years. Evans and Freeman (1950);
George and Corbet (1959); Cotton (1965) and Cowx (1967)

have worked on this ubiquitous flea. Of the above authors
only Evans and Freeman collected significant numbers from
A. sylvaticus, the other studies were mainly concerned with
voles as hosts.

Similar data for other British small mammal fleas is
almost entirely lacking; this is almost certainly due to
the overwhelming numbers of *C. nobilis* specimens which
assume prime importance in almost all studies. However,
Cotton (1965) gives information about the annual abundance
of *Megabothris turbidus* (Roths.), *Megabothris walkeri* (Roths.)
and *Hystrichopsylla t. talpae* (Curtis). Cowx (1967) gave
figures for population density for *Peromyscopsylla silvatica
spectabilis* (Roths.) as well as *C. nobilis, M. walkeri* and
H. t. talpae. He found that peaks of *P. sylvatica spectabilis*
coincided with low densities of *C. nobilis,* while peaks of
C. nobilis and *M. walkeri* were synchronous. He observed no
defined yearly population cycle for *H. t. talpae* but noted
that periodic peaks were associated with wet environmental
conditions. Both the above workers captured *M. agrestis*
almost exclusively.

Workers in Europe have discovered similar patterns of
yearly infestation cycles. Ulmanen and Myllymäki (1971)
collected fleas from *M. agrestis* and obtained comparable
results for *C. agyrtes fennicus* Peus. This flea species is
the ecological counterpart of *C. nobilis* in Southern Finland.
They noted distinct spring and autumn peaks separated by a
period of lower infestation in that species.

It would be premature to discuss the causes of these
fluctuations at this point. Cowx (1967) observed that they
may be associated with behavioural differences in the

mammals, rather than in the fleas. This is almost certainly the case and the precise nature of the relationships between the behaviours of both host and parasite species merits further studies.

(b) Infestation of the two sexes

The different levels of infestation with fleas of male and female hosts, at any given time, is a concept that has been discussed by many authors (George and Corbet, 1959; Janion, 1961; Smit, 1962; Haas, 1965 and 1966; Cowx, 1967; Brink-Lindroth, 1968; Ulmanen and Myllymäki, 1971). There can be little doubt that such variations do exist in some species, although the precise reasons for these observed differences remain somewhat obscure.

Buxton (1948) thought it probable that *X. cheopis* requires a mammalian sex hormone in order to complete its reproductive maturation; this phenomenon is well documented in the case of the rabbit flea, *S. cuniculi,* (Mead-Briggs and Rudge, 1960; Mead-Briggs, 1964; Mead-Briggs and Vaughan, 1969; Rothschild and Ford, 1964,1966,1969 and 1973; Rothschild, Ford and Hughes, 1970). Buxton's suggestion was put forward as an explanation of the higher infestation of male small mammals in Scotland by George and Corbet (1959), and may be acceptable, provided that the hormone concerned is an androgen. Cowx (1967) similarly observed that mature male small mammals have larger flea burdens and used this to show that hormones are not involved in the breeding cycle of *fleas* of these hosts, he ignored the possibility that the required hormone may be an androgen.

It is highly significant, however, that the rabbit

flea, the only species proven to be dependent on mammalian

hormones for its successful reproduction, requires a female

hormone. Furthermore, Smit (1962) observed that the prepo-

nderance of fleas on male small mammal hosts is not

confined to the fleas' breeding cycle and, hence, ecological

rather than physiological factors are more likely to be

responsible for the popularity of males.

It has been suggested that the variations of the sexes

may be due, in part, to the size differences between male

and female animals (Mohr, 1961; Phillips, 1966). They

believed that surface area plays a major role in the infest-

ation of hosts with parasites. Males, being usually larger

than females, display a larger surface area to the parasites

and, consequently, "pick up" is more intense. However,

the small differences in surface area between male and

female mice and voles hardly explains the very large

differences in the levels of their flea infestation.

Furthermore, these differences in infestation are seasonal, and

at certain times of the year males and females are similarly

infested whereas size does not vary in the same way.

(c) Infestation of different age groups

Variation in flea infestation according to reproductive

category or absolute age of the mammalian host has not been

recorded frequently. Generally, the level of infestation

of adult or older animals is higher than that of immatures

or juveniles. Bakeyev *et al.* (1956) recorded more fleas

on adult *Meriones tamariscinus* than on juvenile animals and,

similarly, Darskaya (1957) recorded fewer fleas on juvenile

Ochotona daurica. Smit (1962) noted, however, that in some

host species juveniles may be more heavily infested than adults (e.g. Eskey, 1934 for *X. cheopis* on *Rattus exulans;* Morlan and Utterback, 1952 for *X. cheopis* on *R. rattus*). Brink-Lindroth (1968) collected fleas from *Clethrionomys rufocanus* and found that juvenile males carried more fleas than adults of both sexes as well as juvenile females. Also, in her samples, juvenile *M. agrestis* and *C. glareolus* were as heavily infested as adults. Ulmanen and Myllymäki (1971) pointed out that her collections were made during late summer and autumn and that the decreasing differences between males and females may have been due to the predominance of sub-adults in overwintering populations. In their own samples Ulmanen and Myllymäki noted that older animals were usually more heavily infested than young ones.

(d) Infestations of sedentary and migratory animals

It is often stated that the infestation of mice primarily takes place in the nest (Janion, 1960; Vysotskaja, 1964). With such an obviously nidicolous group as the Siphonaptera this is almost certainly the case. It follows, therefore, that animals with long established nest sites, providing constant replacement of fleas by breeding, will be more highly infested than transient animals with no nest site. This concept has formed the basis of the work by Janion (1960, 1961 and 1962). He has shown that with both commensal and non-commensal host species the degree of infestation with fleas increases when animals become established and that sedentary mice are more heavily infested than migratory mice. However, this situation did not exist during a period of "mass occurrence" of *Apodemus*

agrarius (Janion, 1962). The generally "unsettled" nature
of the population resulted in no clear distinction between
migratory and sedentary hosts.

(ii) Re-infestation of mice

Meyer (1938) has shown that deinfested rats regained
many fleas within a very short time. Evans and Freeman
(1950) observed that the flea infestation of *A. sylvaticus*,
from which all fleas had been removed, was the same twenty
four hours after defleaing as after one month. That is,
individual hosts from which the flea population had been
removed acquired, in a day or less, as many fleas as when
they were first examined. Evans and Freeman also showed
no decrease in infestation of animals occured even after
deinfestation on four successive days. Rychman (1971)
recorded similar results when working with the flea fauna
of *Citellus beecheyi* in America. He found that for most flea
species the index on recently deinfested hosts was actually
higher than on control animals. He attributed this to the
maturation of pupae in the nest during the absence of the
host for defleaing, which was for periods of up to nine days.
He collected the astonishing number of 49,000 fleas from
just 143 squirrels during two two-month trapping periods.
It is possible that his results may have been affected by
a "mass outbreak" of fleas since Holdenried *et al.*
(1951) took only 64,000 fleas from 2,300 animals of the same
species over a study period of three and a half years.

Nevertheless, it is widely accepted that there is a
large pool of fleas inhabiting the nest and, depending on
the behaviour of the species, spending a certain proportion

of the time on the host for feeding. To support this theory Davis (1934) counted as many as ninety-two fleas in thirty-eight nests of *Microtus*. However, in a similar study, Cotton (1970) examined eighty-seven nests of the field vole and collected a mean number of 5.1 fleas per nest.

It is often stated that infestation is independant of deinfestation (Janion, 1960). However, the mammal's nest will not furnish an unending supply of fleas when they are being constantly removed. Depletion of the flea numbers will eventually result in lowered infestations on the body of hosts. This may occur, in the short term, if emergence of fleas from cocoons cannot keep pace with removal of fleas from the host or, in the longer term, when fewer eggs have been deposited into the nest resulting in a lowering of the actual numbers of fleas emerging. Thus, it may be possible to determine the state of the fleas nest population by investigating the rate of re-infestation. This would avoid all the difficulties and disadvantages of studying nest material.

However, the animals nest is not the only site of re-infestation of hosts, although it may be the major one. Fleas falling from hosts into the undergrowth or the tunnel systems may be picked up by other animals that utilise that particular area. In populations with mutually exclusive home ranges this origin of re-infestation would be relatively unimportant. Abandoned nests with large numbers of cocooned adults are probably disturbed by investigating animals and may result in the very high individual infestations occasionally observed. Nestlings and weanlings

obtain some fleas from the mother. All these and other
factors must be taken into account when considering the
re-infestation and build up of infestations on certain host
categories.

Study of re-infestation has been neglected as a method
of investigation of ectoparasite population dynamics. The
rate of re-infestation is proportional to the number of
fleas that encounter the animals between deinfestations.
At times of population peaks complete re-infestation would
be very rapid, at times when fleas are less abundant the
time taken for complete re-infestation would be longer.
This mechanism has several possibilities as a method for
study of the relationship between fleas and their small
mammal hosts.

(iii) Sex ratio of fleas

Variation in the sex ratio of fleas has been reported
by a large number of authors. Some of these fluctuations
have shown seasonal patterns (Cole, 1945) although the
patterns may not be reproduced in succeeding years (Morlan,
1955). Morlan suggested that "observed changes in sex ratio
may be primarily associated with seasonal changes in reprod-
uctive activity, which, in turn, are probably influenced
by climatic conditions". Parker (1958), who, like Morlan,
worked with fleas of ground squirrels (*Cittellus* sp.), showed
that male fleas tended to predominate in samples when
infestation rate of hosts was low. Other authors have
failed to show any seasonal pattern of sex ratio (Amin,
1966 for *Ctenocephalides f. felis* (Bouché), *C. canis* (Curtis)
and *Pulex irritans* L. on *Canis domesticus*; Cotton, 1970 for

C. nobilis on *M. agrestis*).

A general feature in almost all reports of sex ratios of fleas is that females almost always outnumber males. Table 2.1 summarises some of the more recently published records for fleas of mice and voles in Europe.

There has been some variation in the method of presentation of sex ratio results. Evans and Freeman (1950) recorded numbers of males per hundred females although most recent authors prefer percentage males per hundred fleas. This variation has resulted in some confusion. Ulmanen and Myllymäki (1971) state that "Evans and Freeman (1950), quite astonishingly, report a surplus (67.9%, n = 1016) of male *C. agyrtes* (= *C. nobilis*)". In fact, Evans and Freeman's data (67.9 males per 100 females) gives a result of about 40% males per 100 fleas, this result is quite normal and in no way "astonishing".

Table 2.1

The sex ratios of some flea species infesting small mammals based on recent surveys

Author(s)	Flea Species	Host Species	% males per 100 fleas	No. of fleas
Evans and Freeman (1950)	C. agyrtes = C. nobilis	A. sylvaticus and C. glareolus, pooled	40	1016
George and Corbet (1959)	H. talpae	A. sylvaticus, C. glareolus and M. agrestis, pooled	36	126
	C. nobilis	"	42	632
	P. silvatica	"	44	112
	M. penicilliger	"	39	359
	M. walkeri	"	41	115
Cotton (1970)	C. nobilis	M. agrestis	42	2168
Ulmanen and Myllymäki (1971)	C. agyrtes	M. agrestis	45	771
	C. uncinatus	"	40	284
	M. walkeri	"	52	918
Varma and Page (1966)	C. nobilis	A. sylvaticus, C. glareolus and M. agrestis, pooled	415	108
	M. walkeri		52	31

1.3. *Leptinus testaceus*

The taxonomic and ecological status of the beetle
Leptinus testaceus has stimulated wide discussion and provoked
disagreement among entomologists since its initial descrip-
tion. P.W. Müller (1817) is generally accepted as the
original author of the genus, *Leptinus,* and of the species
L. testaceus. However, Hatch (1957) has stated that Crotch
and not Müller is, in fact, the author. Park (1929) consid-
ered that *Leptinus* is closely related to the beaver parasite
Platypsyllus castoris Ritsema, 1869, which is a member of the
Platypsyllidae. He also regarded it as morphologically allied
to the Silphidae. Jeannel (1922) went further than this
and, in a most informative paper, suggested a new taxonomic
arrangement. After comparing, in detail, the morphology of
L. testaceus with that of *P. castoris* he concluded that they
were very closely related and included them both in the
family Silphidae. He erected a new sub-family of the
Silphidae, the Leptininae, to include both genera as well
as *Leptinillus.* He further·abolished the Leptinidae and
Platypsyllidae as families in their own right. Recently
Claassens and O'Rourke (1964) and Fairley (1965) assigned
L. testaceus to the Silphidae, although they did not discuss
the reasons for this. More generally the taxonomic assert-
ions of Jeannel have been disregarded, most notably by
Parks and Barnes (1955) who reviewed the genus *Leptinus*
and, despite liberal translations and quotations from
Jeannel concerning the biology of *L. testaceus,* completely
ignored his taxonomic suggestions. In the present study
the family Leptinidae is accepted as valid, although its

very close affinities to the Platypsyllidae are recognised, and the taxonomy of the genus *Leptinus* described by Parks and Barnes (1955) is used.

The family Leptinidae is a comparatively small one comprised of 3 genera. Olsufiev (1923) described these and constructed a key for their separation; however, at that time, only four species were known. Since then three more species have been described or separated from synonymity and, in a comprehensive paper, Parks and Barnes (1955) discussed their taxonomy, biology and distribution.

The name *L. testaceus* has had a complicated history. *Leptinus caucasius* Motschoulski, 1840, and *Leptinus americanus* Leconte, 1866, became synonymous with *L. testaceus* (Hamilton, 1891; Jeannel, 1922). Werner and Edwards (1948) removed *L. americanus* from synonymity after a detailed comparison of the external morphological features and the structure of the aedeagus of American material with confirmed specimens of *L. testaceus* from Europe; this re-established *L. americanus* as a distinct species. In an attempt to clarify this confusing situation Parks and Barnes (1955) concluded that references to *L. testaceus* in the Nearctic are, in fact, attributable to *L. americanus* and that authentic records of *L. testaceus* are probably confined to the Palaearctic region. Despite this clarification confusion continues and, for example, Maser and Hooven (1971) listed seven host species of "*L. testaceus*" in Oregon, U.S.A.

It is very difficult to decide upon the exact ecological status of *L. testaceus* from the literature. Specimens of the beetle have been found in many different habitats and workers have consequently suggested a free-living

existence, association with various hymenopterous insects and also parasitic, commensal and phoretic relationships with certain vertebrate animals.

Rye (1890) discovered the insect under dead leaves and in rotten wood. Imms (1925) and Linssen (1959) also regarded rotten wood as its habitat. However, later editions of Imms (e.g. 1964) do not include such reports. Hardy (1848) took the insect under chalk flints. Fauvel (1863) believed reports of ectoparasitic habits of *L. testaceus* to be erroneous but thought that some relationship with rodents existed stating that they fed on fungi which "invariably are found to line burrows of the nests of rodents". This opinion was shared by Hamilton (1891) who thought the insect to have a "frequently inquilinious" association with small mammals.

Eichhoff (1866), Rye (1866), Gorham (1869) and Lesne (1896) published records of *L. testaceus* taken from the nests of wild bees. These authors came to the general conclusion that the beetles were inquilines feeding on honey and pollen and that if association with rodents did exist it was only a phoretic one. Park (1929) discovered several populations of *L. testaceus* (now regarded as *L. americanus*) in the nests of the mound-building ant, *Formica ulkei* Emery, in Illinois, U.S.A. He concluded that although "honey" was a possible food source, reports of carnivorous, omnivorous or even ectoparasitic habits could not be disregarded. Wheeler (1923) and Cumber (1949) are among the more recent workers to suggest an association with hymenopterous insects.

Various mammalian species have been suggested as possible hosts of *L. testaceus,* although true ectoparasitic

behaviour has yet to be demonstrated. Early investigators regarded insectivores as primary hosts and the beetle was reported from *Sorex araneus* L. in both Poland (Waga, 1857) and France (Olivier, 1909). Champion (1907) regarded the mole, *Talpa europaeus* L., as a host of the beetle and Sainte-Claire Deville (1912) captured *L. testaceus* in the nests of moles in France. However, Ruschkamp (1914) explored hundreds of moles' nests near Hamburg in Germany but failed to find any beetles; he found them in great numbers in the nests of *Clethrionomys glareolus* and in lesser numbers in the nests of the water vole, *Arvicola terrestris amphibius* L., and the wood-mouse, *Apodemus sylvaticus*. Ruschkamp regarded all these species as "normal hosts".

In Great Britain *L. testaceus* has been found most commonly associated with the wood-mouse, *A. sylvaticus*. Reid (1942) found both adult beetles and larvae in a nest of this animal and many other British and Irish authors have identified the insect from specimens taken on the body or in the nests of wood-mice during ectoparasite surveys (O'Mahony, 1945 and 1947; Fairley, 1963; Claassens and O'Rourke, 1964; Fairley, 1965). Elton, Ford and Baker (1931) took *L. testaceus* on the bank-vole, *C. glareolus*, as well as on *A. sylvaticus*. Claassens (1965) recorded specimens from *Rattus norvegicus* Berkenhout and *Mus musculus* L.

Infrequently specimens of the beetle are found in birds' nests. Buck (1951) reported one individual taken from an old nest of the Barn owl, *Tyto alba* Scop., and Claassens (1965) took the beetle from the nests of a blue tit, *Parus caeruleus obscurus* Prazack, and a wren, *Troglodytes t. troglodytes* L.

Of the authors quoted above only Ruschkamp (1914), Park (1929) and Claassens (1965) attempted any experiments on the feeding of the beetle. The results of Park (1929) are limited and his conclusions are qualified by a statement that his results do not allow the preclusion of any previous observations. Ruschkamp (1914 and 1922) concluded that the beetle feeds on mites either on the body or in the nests of hosts; however, Claassens (1965) attempted to reproduce Ruschkamp's results without success.

A broad basic knowledge of a species is essential before detailed laboratory experimentation can be carried out to full advantage. Much of this basic knowledge about the biology of this curious insect was lacking. It was the aim of this study to elucidate some simple ecological points concerning *L. testaceus* and the large sample size allowed statistical analysis of data; an approach which had been completely neglected in previous investigations largely due to insufficient information. The host preferences of *L. testaceus* within a mixed community of *A. sylvaticus, C. glareolus* and *Microtus agrestis* are discussed and variations in the host/beetle index within the monthly samples allowed annual peaks of abundance to be deduced.

2. The Study Area

The grounds of Royal Holloway College, Department of Zoology at "Alderhurst", Englefield Green, Surrey (Grid. ref. 41/996697) were used for all field experiments and samplings of the animal communities. The areas used for field work were parts of the Small Field, the Orchard, the Tennis Courts and Alderhurst Copse (Fig. 2.1). Grid A was operated as a pilot experimental area during seven months of 1971 and a full year study of the small mammals and their epifauna took place on Grid B from spring 1972 to spring 1973.

No management of the study area had taken place since the arrival of the Department of Zoology at Alderhurst in 1963, except for a short period of cattle grazing in the Small Field. There is some evidence that certain parts of the area, especially the tennis courts, had been neglected for some time prior to 1963. Therefore, in most places, the ground layer had reverted to a natural grass sward and some small oak seedlings had become established where a tree canopy was not already present. Mature ornamental and natural trees formed a canopy in some places with much of the western part of the area covered by mature fruit trees. Alderhurst copse, a dense *Rhododendron* coppice, limited the extension of Grid A to the east.

The results presented in later sections are derived from data obtained on Trap Grid B. Consequently, a more complete description of the habitat in that area is presented. The grid could be divided into three main sections

Fig. 2.1 Sketch map of field study areas.
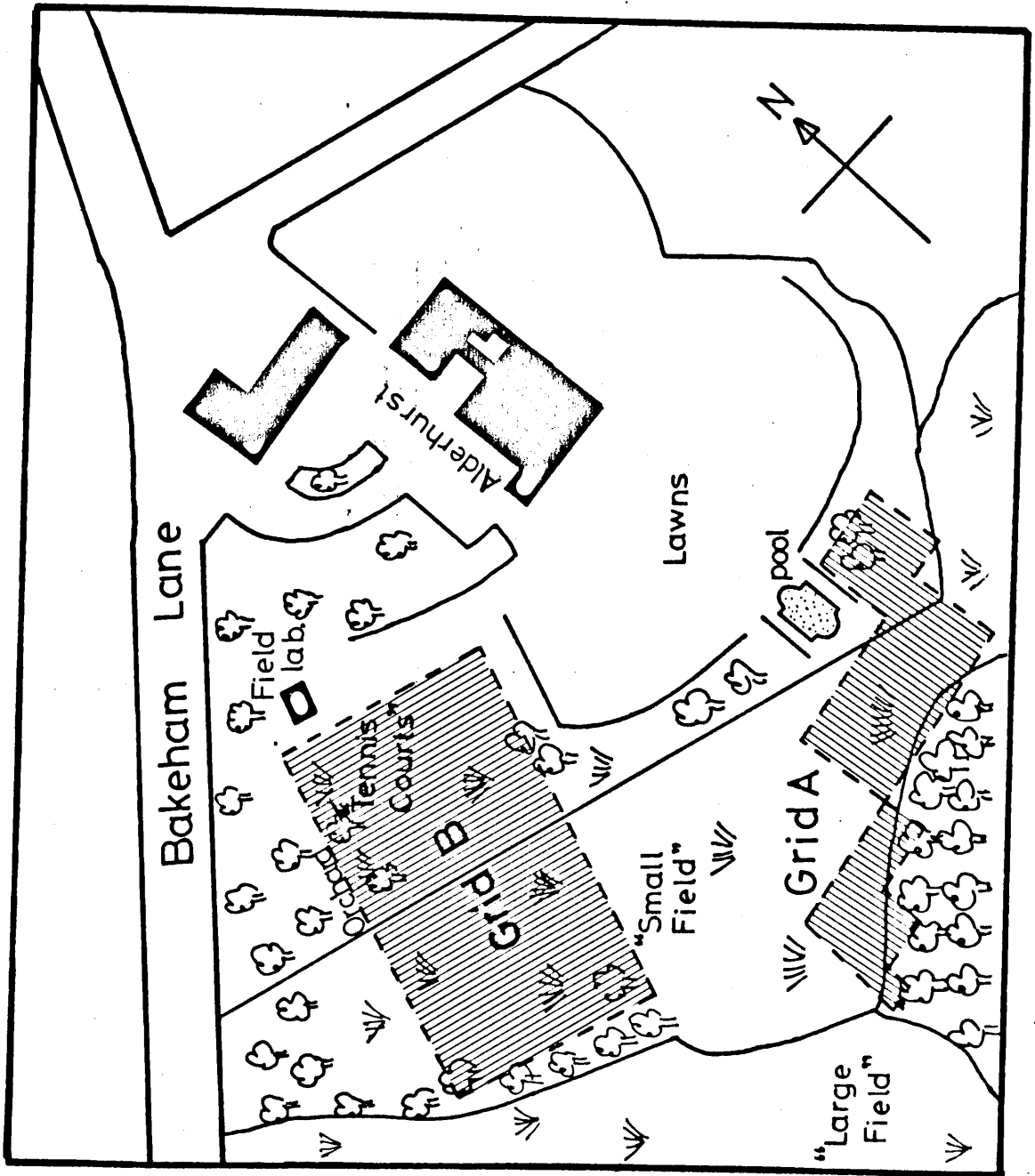
with regard to its suitability as a habitat for small
mammals. These three sections are shown in Fig. 2.2.

Grassland (A_1, A_2 and A_3) covered a large portion of
the grid and the area was dominated by the tussock forming
grasses *Arrhenatherum elatius* and *Dactylis glomerata.* Various
species of the genus *Poa* were found on paths and in the
more shady areas. During the summer the tussocky grasses
grew luxuriantly to a height of 1½ - 2 m. and then died
back in winter. However, the nature of the tussocks meant
that a covering layer of dead grass stems remained through-
out the year giving almost complete cover to about 30 cm.
The new grass grew out from this old layer during spring.
The grassy areas were not all alike. Area A_1 had arisen
from the overgrowth of a tennis "hard-court" and a much
fragmented layer of gravel remained at between five and
ten centimetres below the surface. In this area the grass
tussocks were much more intermittant and *Festuca ovina* was
abundant. Thus, the complete cover that the grass tussocks
offered in A_2 and A_3 did not exist in A_1.

In areas B_1 and B_2 mature trees formed a canopy. *Poa*
spp . offered sparse ground cover below the tree canopy and
a fairly rich herbaceous flora thrived during spring and
summer.

Large areas of the grid had been invaded by brambles,
(*Rubus fruticosus agg.*) i.e. areas C_1, C_2 and C_3. Beneath
the dense bramble covering, during the summer period,
various grasses were common (*Phleum sp., Poa spp., A. elatius*)
or occassional (*F. ovina*). In places the taller herbs
Epilobium angustifolium, Urtica dioica and *Heracleum sphondylium* had
established themselves. During summer the brambles offered

Figure 2.2.

A vegetation map of Trap Grid B. (Letters refer to the text)
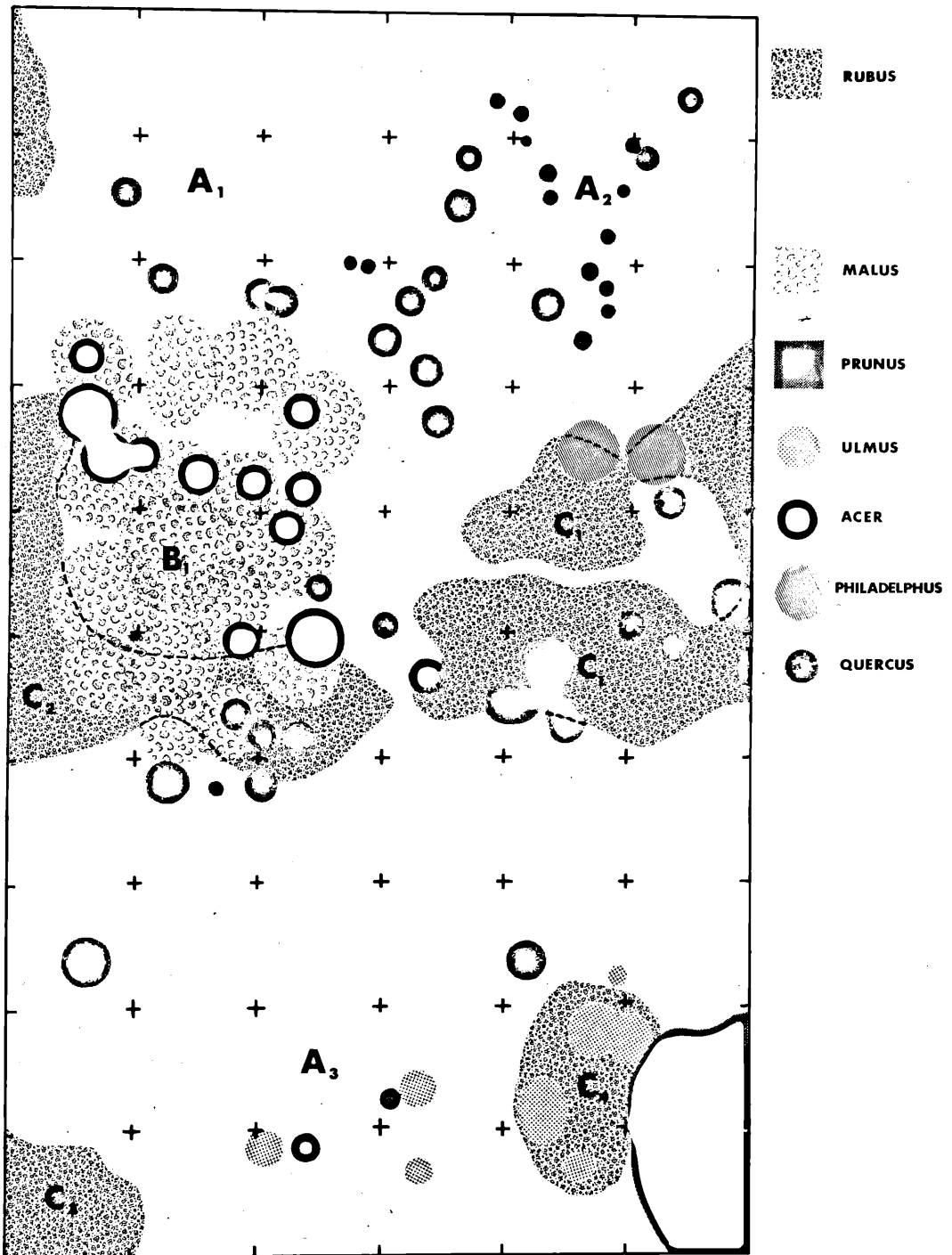
good cover to rodents but after leaf fall in autumn the sparse growth of herbs and grasses offered very little cover, much of the areas under the bramble canes were completely exposed at that time. However, the thick leaf litter layer provided some cover in semi-subterranean runways and burrows.

Table 2.2. gives details of the abundance of the plant species in the ground layer of grid B and indicates the nature of the tree canopy if present.

Table 2.2.

The abundance of herbs and the tree canopy of Trap Grid B.

Area	Canopy	Ground Cover	Abundance
A_1	Very sparse seedlings of Q.robur growing to a height of 2m.	Festuca ovina	A
		Dactylis glomerata	C
		Poa spp.	C
		Achillea millefolium	C
		Plantago lanceolata	O
		Cerastium cerastiodes	O
		Trifolium sp.	O
		Hieracium pilosella	O
		Veronica chamaedrys	O
		Arrhenatherum elatius	O
		Rumex acetosella	R
		Taraxacum sp.	R
A_2	Frequent seedlings of Q. robur growing to a height of 3-4m.	A. elatius	D
		D. glomerata	C
		Poa spp.	C
		Urtica dioica	R
		V. chamaedrys	R
		R. acetosella	R
		A. millefolium	R
		Trifolium sp.	R
		Taraxacum sp.	R
A_3	Very sparse seedlings of Ulmus procera to a height of 2m.	A. elatius	D
		D. glomerata	C
		Poa spp.	C
		U. dioica	O
		Taraxacum sp.	R
		Trifolium sp.	R
		R. acetosella	R

Table 2.2.(continued)

Area	Canopy	Ground Cover	Abundance
B_1		Poa spp.	D
		Narcissus sp.	C
		Anthriscus caucalis	C
	Malus sp. complete	Conopodium majus	O
	cover to 10m. Inter-	U. dioica	R
	mittent specimens of	Geum urbanum	R
	Acer pseudoplatanus	Endymion non-scriptus	R
	to 8m.	Tulipa sp.	R
B_2	Prunus sp. complete	Poa spp.	C
	cover to 15m. Some	much bare ground	
	Ulmus to 15m.		
C_1,	Some cover from	Rubus fruticosus (agg.)	D
C_2	Philadelphus sp. and	Phleum sp.	C
&	Q. robur in C_1. Much	Poa spp.	C
C_3	cover from Malus sp.	A. elatius	C
	in C_2 and Ulmus in	Heracleum sphondylium	C
	C_3. Brambles grew to	F. ovina	O
	1½m. and gave cover	U. dioica	O
	when in leaf.	Epilobium angustifolium	R

D = dominant

A = abundant

C = common

O = occasional

R = rare

3. <u>Materials and Methods</u>

3.1. <u>The Traps and Trapping Regime</u>

The Oxford or Longworth small mammal trap (Chitty and Kempson, 1949) was used for the capture of rodents throughout the study. This trap has proved an efficient device for the removal of small mammals from field communities since its initial introduction and has been used with success by many workers both in this country and, to a lesser extent, abroad (e.g. Ulmanen and Myllymäki, 1971). Some Scandinavian workers have used "net cage traps" for sampling small mammal populations in ectoparasite surveys (Brinck, 1966) and much use has been made of break-back traps. However, the escape of fleas from the captured host, whether alive or dead, is an important factor and may cause the loss of fleas from samples resulting in underestimation of flea numbers (Cole and Koepke, 1947; Jameson, 1947; Gross and Bonnet, 1949). Consequently, the Longworth trap is most effective for the capture of fleas in that the captured animal remains alive and the almost completely enclosed nest box ensures that few fleas, leaving the host during its residence in the trap, can eventually escape.

The spacing of traps is an important and interesting problem when sampling animals from a small mammal community composed of several species. Many factors must be considered when deciding on the distances between traps on a grid.

Traps that are too close together tend to restrict the movements of small mammals giving underestimates of the home

ranges of the animals because they encounter and enter traps before being able to reach the outer limits of their areas of activity (Davis, 1953; Justice, 1961). If traps are spaced too far apart animals do not encounter them with sufficient frequency to allow the accumulation of the large numbers of recaptures required to define home range boundaries.

It is generally recognised that voles have considerably smaller home ranges than mice (Kikkawa, 1964; Jewell, 1966; Brown, 1966). The aim of this study was to collect fleas from *A. sylvaticus, C. glareolus* and *M. agrestis* in the study area and to obtain some information about the areas of activity of the individuals present. It was important, therefore, that a trap spacing should be used that was compatible to the behaviour of all three species.

Brown (1954 and 1956) Kikkawa (1964) and Jewell (1966) have used approximately 10m. trap spacings for the study of vole species, although this distance is thought to be rather small for the study of mice.

Brown (1956) used 30yd. trap spacing; Jewell (1966) used 22yd. and Randolph (1973) 23m. during studies of *A. sylvaticus*.

The total area that could be trapped was limited to a 0.6h plot and, as it is important to have excess traps available, utilisation of the larger trap spacings would have resulted in the necessity of setting more than one trap at each point. Consequently, it was decided to use a 10m. trap spacing throughout the study and concede that any measurements of activity areas for *Apodemus* were, probably, underestimates.

The traps were placed in runs or in other likely localities and each trap was moved several times within a grid quadrat during a week's sampling period to prevent any particular animal from becoming habituated to one trap point. In grassy areas small portions of the underground burrows of *Microtus* were opened and the trap placed beside these, although not actually in the burrow. In the bramble and wooded areas the traps were placed in runs or near any obstacle that the animals might use for cover.

The activity rhythms of *Apodemus* and *Clethrionomys* have been extensively studied. Elton, Ford *et al.* (1931) showed that in both the field and the laboratory the activity of *A. sylvaticus* was dependant on the periodicity of daylight and darkness with a secondary rhythm during darkness dependant on feeding and digestion. Activity was at a peak at dusk followed by a lull with another peak around 01.00 to 02.00 hrs. continuing until dawn. These results are similar to those obtained by Brown (1956) for *A. sylvaticus*, who used a system whereby traps were checked at two hourly intervals. Kikkawa (1964) used similar techniques supplemented by the use of radioactive tagging of certain animals whose presence or absence within their nest sites were observed at fifteen minute intervals.

The activity patterns of *C. glareolus* are subject to some discussion. Brown (1956) considered that in a mixed community of *Apodemus* and *Clethrionomys* the two show almost mutually exclusive activity patterns, the mice being nocturnal and the voles diurnal. These results were not corroborated by Kikkawa (1964) who, in a similar situation,

observed considerable nocturnal activity by voles. It is
now generally agreed that both species show activity peaks
around dusk and dawn with the vole species exhibiting some
diurnal activity as well.

Davis (1933) and Brown (1956) observed dusk and dawn
activity peaks for *M. agrestis*. Davis was able to detect a
two to four hour cycle of activity associated with feeding
as well as the daily dusk and dawn peaks.

Many factors affect the diurnal and nocturnal activity
of small mammals. However, day length is considered to be
the most important single factor (Davis, 1933; Calhoun,
1945; Miller, 1955) although weather (Pearson, 1960), food
supply and hunger (Crowcroft, 1954; Brown, 1956), and
population density (Calhoun, 1945) as well as other behav-
ioural and physiological factors probably have profound
effects.

There is widespread agreement that the periods around
dusk and dawn are the time when small mammals are most
active. Consequently, throughout the present study the
traps were opened at about one to two hours before dusk and
emptied at one to two hours after dawn. The diurnal activity
of voles necessitated the traps being closed during the rest
of the daily cycle to ensure that the animals spent as much
time as possible in their natural environment.

When attempting to capture small mammals, for any study,
it is usual to utilise the procedure of prebaiting; that is
the traps are baited and opened but not "set", so that
animals have free access to the trap interiors.

Usually some bait is placed in the traps to act as an

attractant. Chitty and Kempson (1949) discussed the use of prebaiting and observed that "new object reaction", that is the avoidance by rodents of unfamiliar objects, could be cut down if pre-baiting took place. The animals became familiar with the traps during the period immediately prior to a sampling, without harm or unpleasant experience, and, in consequence, a larger proportion of the population was sampled when traps were actually set. Holišová (1968, a and b) further refined the technique of prebaiting and by using admixture of bait and dyed woollen threads during three "prebait" days, she effectively labelled the populations present so that when snap-trapping began, on the fourth day, she was able to distinguish between animals present on the grid during prebaiting and the immigrants that arrived during the snap trapping period to replace the dead animals. However, this work was followed by further studies (Zejda and Holišová, 1970) who showed that pre-baiting creates an unnatural circumstance within the small mammal community. When bait is put out the trophic conditions of the environment are improved so that its carrying capacity is increased. This increase in the number of animals that the area can support may be exploited by immigrants causing unnaturally high densities. Pelikan, Zejda and Holišová (1972) have published further evidence to support this view.

However, in a study where a short trapping period (7 days) was used to sample a population; and this being taken to represent a complete month, it was imperative that a high proportion of animals present should be caught on the first few trap nights. Some form of prebaiting was, therefore, essential to overcome trap shyness. The introduction

of large amounts of food into the environment was thought
to be undesirable and hence, in the present study, the traps
were opened, unbaited, for two nights prior to the commence-
ment of trapping. Considerable amounts of faeces were often
found in the traps during this period indicating that the
animals did, indeed, investigate the open traps. They may
have been used as temporary refuge sites but they were not
used as nest sites and the carrying capacity of the area was
not increased in this respect.

The traps were then "set" for seven consecutive nights
and each was provided with bedding material in the form of
dry hay and excess food in the form of a mixture of wheat,
oats and sunflower seeds.

These week long trap sample periods were interspersed
by three weeks of entirely natural conditions for the small
mammals and their ectoparasites. It was thought that this
period was long enough to allow the animals to recover from
the disturbances of the sample period. Traps remained in
their positions but were not open.

3.2. Handling and Defleaing of Animals

The captured rodents were taken from their site of capture, still contained in the traps, and transported to the field laboratory in metal carriers accommodating twelve occupied traps. The traps were randomly stacked on a work bench where they remained until the captured rodent was to be examined. The traps were always kept in shady positions to avoid excessive heat stress to the animals.

The handling of these agile creatures required some care and a degree of skill. Wood-mice were particularly difficult in this respect although the two vole species were less exacting. Care was taken to ensure that captured rodents did not escape during handling.. This not only would have led to the loss of important data but may also have resulted in the permanent displacement of the animal from its home range and nest site.

To remove the animal from the trap the door was carefully opened to ensure that the rodent was not in the tunnel section, this was then freed from the nest box by releasing the catch mechanism. Simultaneously, the open end of the nest box was enclosed with a clean polythene bag and the box was inverted and its contents shaken down into the bag. The animal and all the bedding were pushed into the bag together with any fleas that had left the body of the host during its residence in the trap.

When they were in the polythene bag the rodents tended to move to the corners. They were then gripped by the scruff and removed from the bag for defleaing. The polythene bag and its contents were placed at one side for later examination.

Since the study of flea populations of small mammals
began many different methods of defleaing have been described;
they can be divided into two main categories, some requiring
that the animal is killed and others not. It seems reason-
able to assume that methods where the animal, and often its
ectoparasites, are killed are highly efficient in removing
all fleas. This method has been used in a great many studies
concerning the epidemiology of plague where the captured
hosts are pest species and would be destroyed in any case
(Yeh and Davis, 1950; Olson, 1969). However, the use of
this technique in the study of non-pest animals (George and
Corbet, 1959; Brink-Lindroth, 1968; Edler and Nilsson, 1973)
has little to recommend it as it would rapidly deplete
the populations required for further study. When small
mammal populations are to be studied in a certain locality
over a prolonged period the disruptive effect of the method
makes it wholly undesirable. Consequently, various tech-
niques have been described in which the animals can be
returned unharmed, after defleaing, to their site of capture
thus minimising the adverse effects of the study on the
community. These procedures are, obviously, not entirely
efficient at removing all fleas infesting an animal.

Methods where animals are not killed fall into two
groups, in some techniques the animals are immobilised with
an anaesthetic for defleaing and in the others they are not.
Evans and Freeman (1950), Cotton (1965 and 1970) and
Achuthan and Chandrahas (1971) simply blew through the fur
of the captured host while it was held by the scruff and the
base of the tail over a white cloth or enamel dish.
Balthazard and Eftekhari (1957) described this method in

more detail and were convinced of its effectiveness. An
alternative method to "blowing" is the sprinkling of the
host with an insecticidal substance, Janion(1960, 1961 and
1962) used ether to kill fleas while not anaesthetising
the host and, similarly, Ulmanen and Myllymäki (1971) used
pyrethrum. The latter authors compared this method with
killing the hosts and then searching the bodies. Mean flea
counts were 5.31± 1.82 with pyrethrum and 6.75± 2.00 with
killed animals. Assuming the latter figure to indicate the
entire flea population; spraying the living host with pyre-
thrum yielded 79% of the fleas present. Clearly a method
combining the advantages of both immobilisation and retaining
a living host is desirable.

Varma and Page (1966) lightly anaesthetised the hosts
and examined them for fleas, they gave no further details
of the methods used.

In the present study all captured rodents were anaes-
thetised, with ether, to immobilisation and then searched.
Although some of the methods outlined above have advantages,
for example the "blowing method" is quick and simple and
can be used where the animals cannot be examined in a field
laboratory, they are rarely completely efficient in collec-
ting all the ectoparasites present. It will become apparent
that, in most cases, the numbers of fleas obtained in the
present study exceed those where the "blowing" was used.
However, despite the fact that similar host species, parasite
species and habitats were involved other variations in
circumstances may partly explain these differences.

The ether vessel was a wide mouthed glass jar which allowed easy handling of the rodents within it. Its broad base was covered with about 1cm. of plaster of Paris to absorb the liquid ether, which was used as an anaesthetic, and to ensure that only ether vapour contacted the hosts and ectoparasites. Jars incorporating cotton wool or similar absorbtive materials proved unsuitable because fleas, which fell from the host, became entangled with fibres and this hindered identification.

The animals were placed in the jar and very lightly anaesthetised. With practice it was possible to estimate the length of exposure to ether compatible to the animal's species and body weight to give an immobility period of sufficient length for complete defleaing to be accomplished. *A. sylvaticus* generally required considerably longer exposure to ether than did *C. glareolus* and *M. agrestis*, the latter species often requiring only two or three seconds.

The animals were removed from the ether jar after the appropriate period, any fleas or beetles which had fallen from them during etherisation were carefully collected. The search for ectoparasites in the pelage was then carried out under a strong light source and small patches of fur were systematically pushed back against the lie, with the aid of a pair of fine forceps, to expose the hair shafts down to the skin. The search was continued in this way until no more fleas were found for two full minutes, at the end of that time the search was terminated. Any fleas falling from the host's body onto the work bench were collected and put into the specimen tube containing fleas

from that animal. This basic procedure was used throughout
the study.

3.3. The Measurement of the Animals

Many authors have shown that variations in the numbers of fleas infesting members of small mammal populations are partly dependant on age and sex differences (George and Corbet, 1959; Janion, 1961; Smit, 1962; Haas, 1965 and 1966; Cotton, 1965 and 1970; Cowx, 1967; Brink-Lindroth, 1968; Ulmanen and Myllymäki, 1971). Consequently in order to interpret observed fluctuations in flea indices it was important to collect all available information concerning the biology of the small mammal hosts. This involved measuring and weighing captured animals, recording their reproductive state and noting the state of the pelage.

Accurate and consistent measurements of small mammals are difficult to obtain. Measurements of a single animal may vary depending on the technique used and the different methods of applying the same technique used by different operators. Jewell and Fullager (1966) described the various techniques presently used in small mammal studies. They showed that the average measurements of the head and body combined, when two different individuals applied the same techniques to a sample of twenty wood-mice, could vary up to ± 6mm. Furthermore, several of the methods described by the above authors used the anus as a fixed point. It was shown that the position of the anus may vary considerably depending of the sexual condition of the individual. Males were found to be especially liable to this discrepancy as the descending testes tend to push the opening of the anus posteriorly during maturation. Due to these variations measurements are only directly comparable when the same worker has used

the same technique.

In the present study the animals were measured while still under anaesthetic. They were placed in a supine position and slight pressure was applied below the jaw. A stout needle was run up to the base of the tail, with the needle at right angles to the main body axis, until it met with resistance from the pelvic girdle. The tip of the nose and the base of the tail were marked on paper and measured to the nearest millimeter. This method closely follows the one described by G. Corbet (1964, in the Handbook of British Mammals) and was referred to as the British Museum (Natural History) "new" method in Jewell and Fullager (1966). Considering the discrepancies described above it was thought that measurement to the nearest millimeter was sufficiently accurate.

The tail was then measured in a similar manner excluding the length of any apical or terminal hairs. The length of the ears, from the "notch" to the tip, and the length of the hind foot from the heel to the tip of the longest toe, excluding the claw, were then measured.

The animal was then recorded as male, with testes scrotal or abdominal, or female with perforate or closed vagina. The pelage was noted as being immature or adult.

At this point the animal was weighed on the pan of a torsion balance to an accuracy of 0.1 gramme.

3.4. Marking of Animals

Various methods have been described for use in marking small mammals, these have been reviewed by Southern(1964). Chitty (1937) first described a technique using numbered metal rings and Linn and Shillito (1960) discussed the best specifications of rings for marking most British species of small mammals. Southern also considered the problem of applying metal rings. Short-term marks can be obtained by fur clipping and a limited number of permanent marks are available by ear notching, although this method is less useful with species with small ears, e.g. *M. agrestis*.

In the present study a combination of toe clips was used to give a large number of possible marks. Justice (1961) used toe clipping to enable animals to be tracked by leaving identificatory footprints on smoked paper. He used a combination involving two toes on one foot being clipped in a proportion of the animals. In the present experiments only one toe on any foot was clipped and a maximum of two toes of any one animal. When the combinations available with this technique were exhausted a small notch was put in the ear of animals and the combinations used again.

Ethyl chloride was used as a freezing agent applied to the foot of the animal to be marked and the animal itself was under general ether vapour anaesthetic. Only the distal phalanx was removed and this was done swiftly with a sharp pair of spring scissors. Southern (1964) regarded this method as relatively painless. Often little or no bleeding

occured in *A. sylvaticus*, although some blood was lost when the more fleshy toes of the vole species were clipped.

After being defleaed, weighed, measured and marked (when captured for the first time) the animals were released on the grid at their site of capture.

3.5. <u>Conclusions and Refinements of Technique</u>

The results from the first seven trapping sessions
(Trap Period A, March 1971 - October 1971) indicated that
a mixed community of small mammals existed in the study
area and they harboured an interesting variety of epifaunal
species.

Many refinements of technique were evolved during the
first trapping and these techniques were put into use during
Trap Period B (April 1972 - May 1973). However, the
refinements meant that the data from the two periods could
not be pooled. Consequently results from Trap Period A are
presented in Appendix I and all further presented results
were collected during the second trapping period.

The following points of technique were different in
the two trapping periods:-

(i) During Trap Period A a large number of the captu-
red rodents died in the traps (twenty five animals, 4.6%
of captures).

Corke (1967) showed that damp bedding greatly increases
trap mortality and that this could be reduced by changing
the bedding material inside the trap every night. Shaw and
Milner (1967) found that trap deaths could further be redu-
ced by fitting polystyrene insulating covers to the outside
of the traps. Both these methods are time consuming to
apply.

The number of trap deaths would have probably increased
if trapping had occurred during winter and such a loss of
animals could not have been allowed to occur. Consequently,
pieces of corrugated plastic were cut into squares (about

350mm x 350mm). These could be easily folded down their
corrugations and were placed over the traps. The trap
tunnel was allowed to protrude so that the cover did not
affect the behaviour of the animals at the trap entrance.
(see Plate 1). The covers prevented frost from settling
directly on top of the trap, they reduced the conduction
of heat out of the trap and also kept the nest box dry.

(ii) Fleas are active and elusive creatures and a
proportion of them leave the captured host during its period
of occupancy of the trap (Cowx, 1967). The construction
of the Longworth trap is not completely enclosed and it is
possible that some escape of fleas from the traps can occur.
During the later trapping period the interior of the trap
nest box was lined with a polythene bag (about 300mm x
300mm) the tunnel section was fitted separately and was
unlined. The presence of the polythene bag prevented, to
a large extent, any movement of fleas out of the trap. The
bag was occasionally damaged by chewing although rarely so
severely as to significantly reduce its efficiency. The
use of the polythene bag also made it easier to remove the
nesting material from the trap. Furthermore it reduced heat
loss by the animal by adding an insulating layer between
the animal and the metal trap sides.

(iii) The trap grid used in Trapping Period A was an
irregular shape. The large periphery resulting from the
irregular shape caused many of the estimated areas of acti-
vity of the rodents to be on the "edge" of the grid, this
introduced considerable inaccuracies. Trap Grid B was laid
out in a single, simple rectangular shape reducing the
proportion of periphery to internal area.

Plate 1

A Longworth trap assembled as in Trapping Period B.
(note corrugated plastic and polythene bag in position).

4. Results

4.1. The Mammal Populations

It is thought that the age and reproductive state of host animals indirectly determines, to some extent, the size of their ectoparasite burdens. Consequently, it was necessary to categorise the host animals with respect to these criteria. Mammalogists vary in their opinions as to the exact nomenclature of age and sex groups. Adults, reproductives, sub-adults, juveniles and immatures are some of the terms that have been used although no definitions exist for them. The following categories were used in the present study for *A. sylvaticus*. Similar categories were used for the vole species although the head-body length tended to be less reliable as an indicator of age.

a) Reproductive males:- males with scrotal testes and a visible cauda epididymis. . These animals exceeded 80mm. in total head-body length.

b) Reproductive females:- females with perforate vaginae and/or found, by palpation, to be pregnant or lactating. Similarly, these animals had head-body lengths of more than 80mm.

c) Sub-adults:- male or female animals with adult pelage and head-body length exceeding 80mm., but males with abdominal testes or females with imperforate vaginae. These animals were usually present on the grid during overwintering and were either reproduct-ives from the previous breeding season that had re-

entered asexual condition or were late recruits into
the population which had not become sexually mature
in their first year.

d) Juveniles:- males and females with head-body
length of less than 80mm. and usually weighing less
than 12gms. These animals were in juvenile pelage or
in the early stages of moult into adult pelage.

These categories are similar to those used by Ulmanen
and Myllymäki (1971) when studying the flea fauna of *M.
agrestis,* although they differ in several important respects.
The above authors regarded females to be reproductive only
when they were found, by palpation, to be pregnant or they
were seen to be lactating. However, pregnancy cannot be
determined by palpation in its early stages. These
criteria would also have excluded from the reproductive
female category, animals behaving as reproductives but which
were in oestrous or those which had just copulated. For
the purposes of this study it was assumed that all perforate
females were reproductives during the breeding season.
Furthermore, Ulmanen and Myllymäki only included as sub-
adults those animals of adult age "that had not yet entered
into reproduction". During overwintering the populations
were entirely composed of asexual (sub-adult) animals, and
no distinction could be made, using external morphology, as
to those that had reproduced during the previous breeding
season and those that had not.

There had been much discussion as to the advisability
of using body weight as a criterion of age indication

because, in live animals, the very variable weight of the
gut contents may play an important part in determining
total body weight. In the present study head-body length
was used as a less variable character. However, when the
average weight during a sample session and the head-body
length of animals were plotted as scatter diagrams (Figs.
2.3.and 2.4.) clear correlation was demonstrated. Hence,
when weight data is collected over a period of time for a
single individual and then averaged it may be a useful age
indicator.

The distinction set at 80mm. head-body length between
juveniles and the other classes, in *Apodemus,* was almost
precise. Only one animal during the study was shown to be
reproductive at a length of less than 80mm. Miller (1958)
used 15gms. as the point of transition between adults and
"immatures" in his study of *A. sylvaticus,* although he
observed that many mice weighing less than 15gms. were not
only sexually mature but reproducing. This was most
certainly the case in the present study.

(i) The Annual_Cycle_of Population_Density
        a) *Apodemus sylvaticus*

Within the twelve sampling periods there were marked
variations in the numbers of mice present on the grid.
Figure 2. 5. shows these fluctuations. The breeding peak
in late summer was clearly defined.

The separate male and female samples showed similar
trends. The ratio of males to females present on the grid
varied from sample to sample. However, neither the gross

Fig.2.3 Correlation between head-body length and weight in male _A. sylvaticus_. Trapping B. (1972/3)

r = 0.91, p < 0.001.

weight in grammes

head-body length in cms.
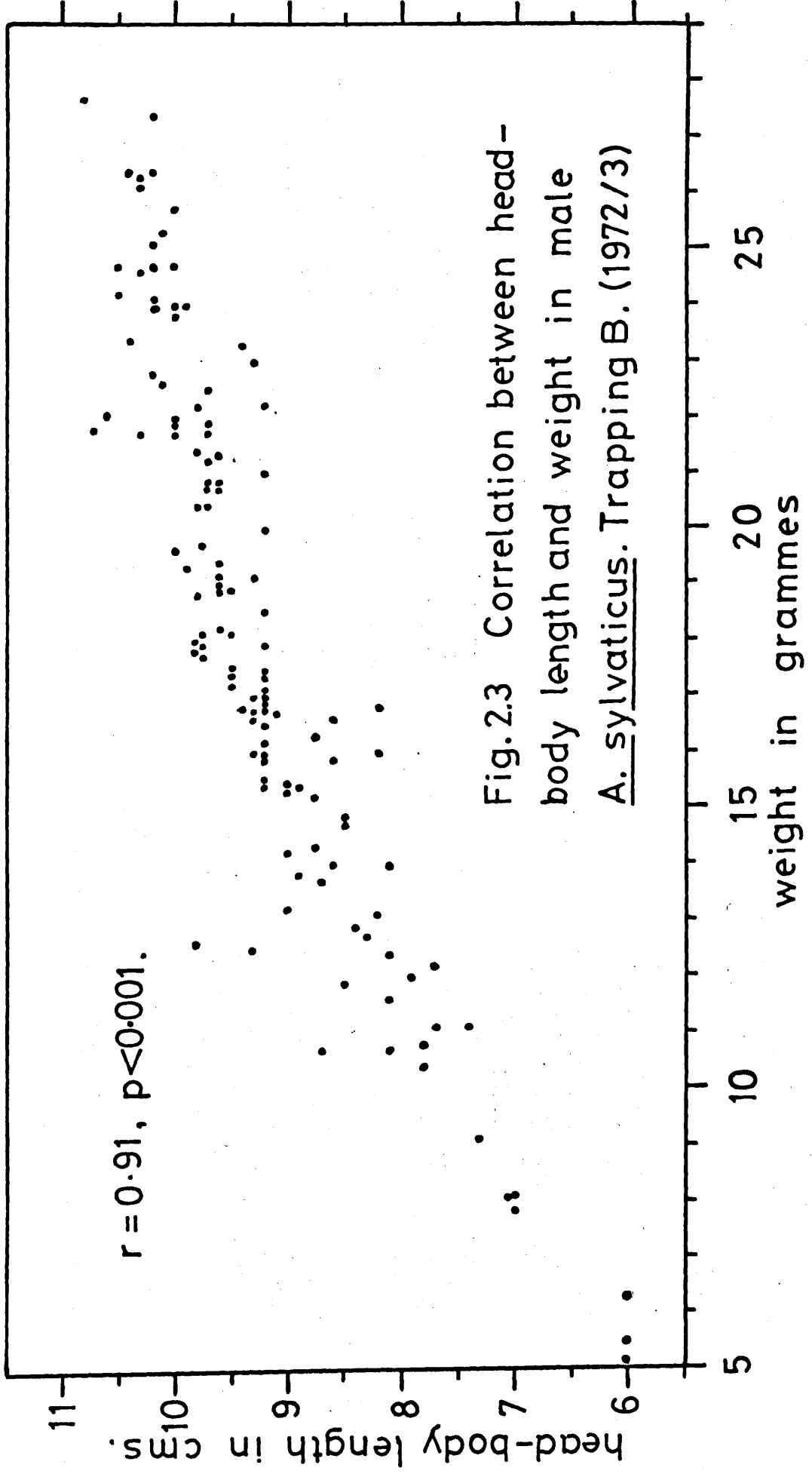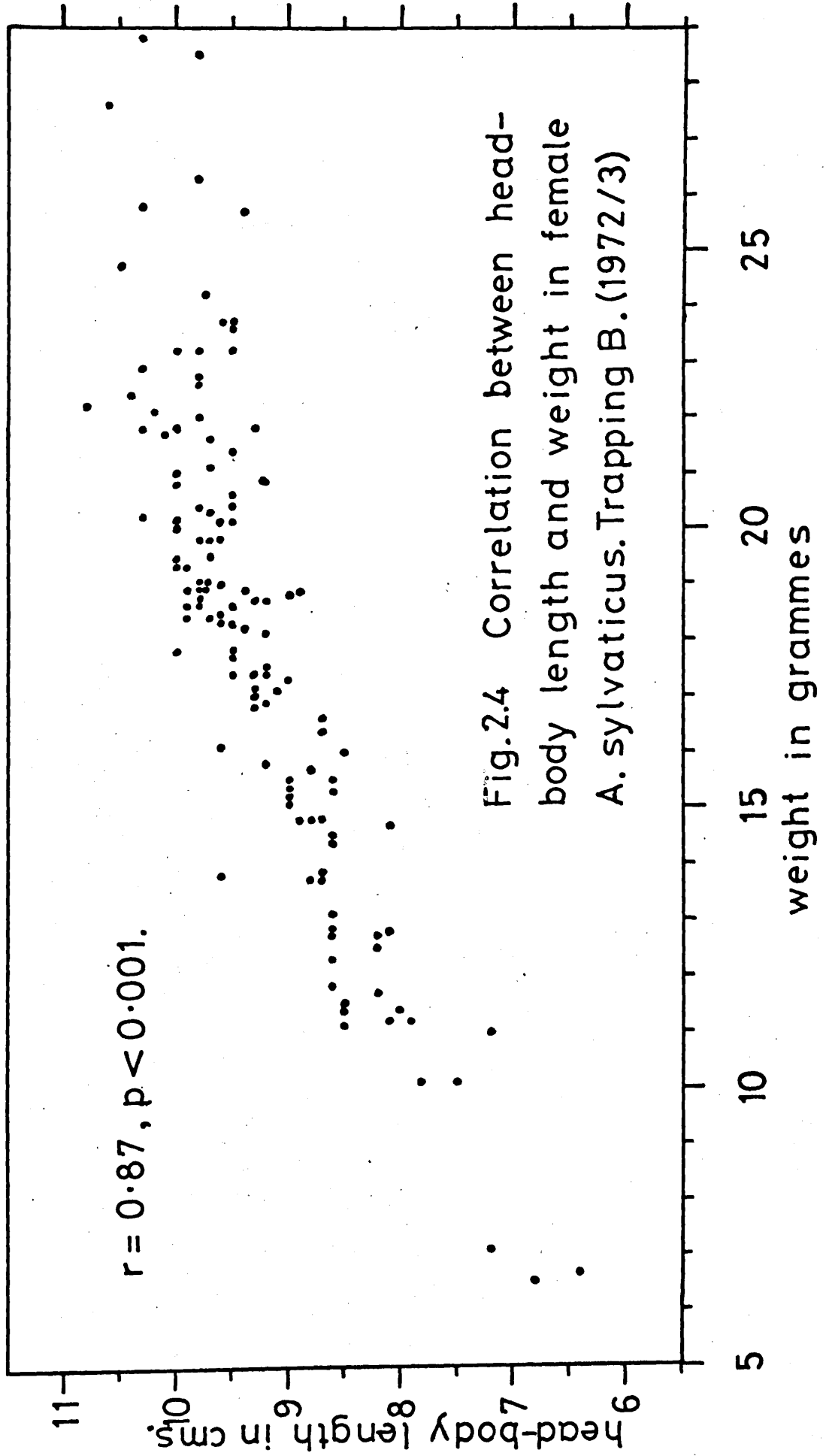
Fig.2.4 Correlation between head-body length and weight in female A.sylvaticus.Trapping B.(1972/3)

weight in grammes

head-body length in cms.

r = 0·87, p < 0·001.

Fig. 2.5. Numbers of A.sylvaticus on Trap Grid B. (1972/3)
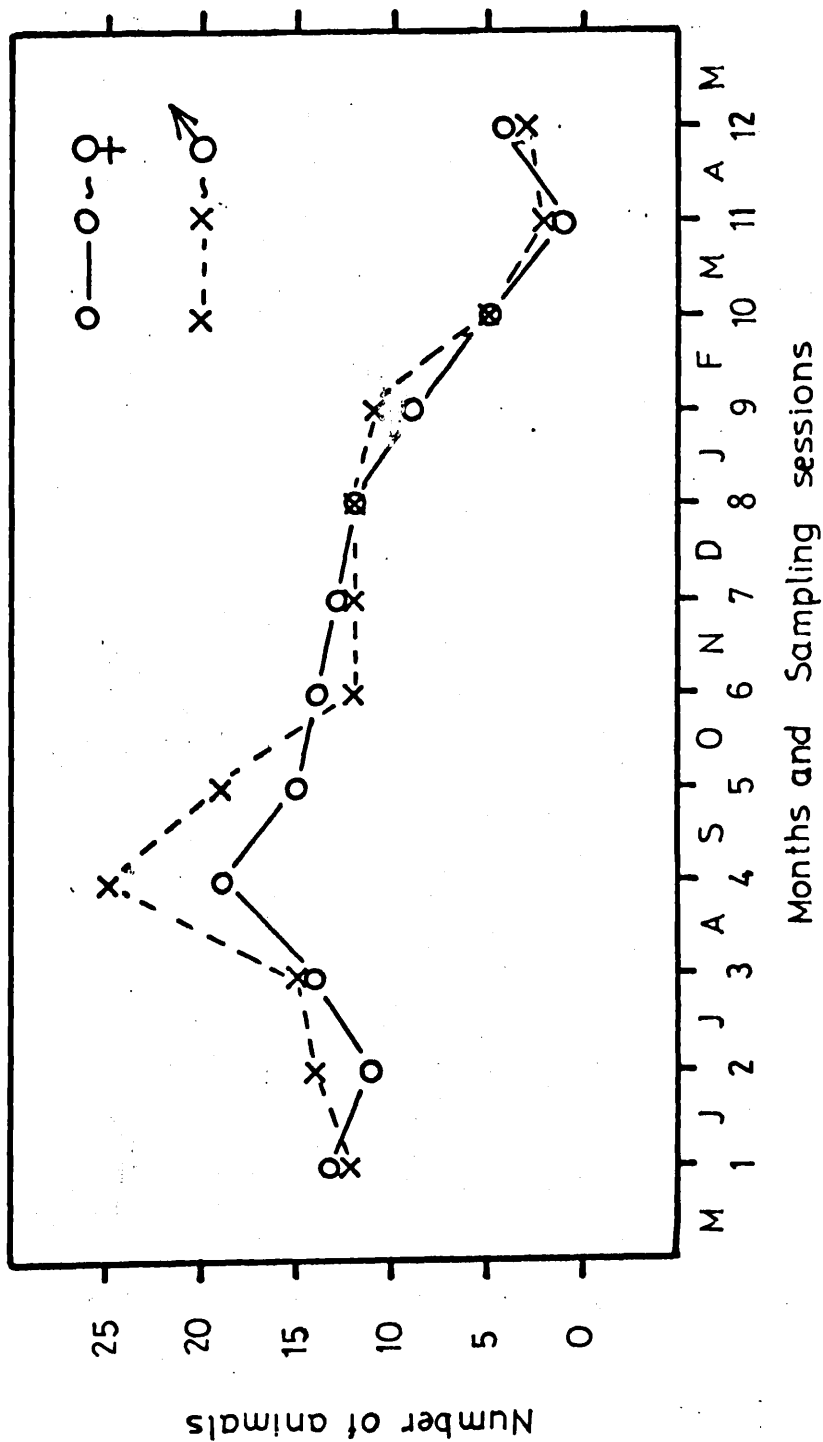
sample nor the individual samples varied significantly from a one to one ratio when compared by the method of X^2 analysis (X^2 always smaller than 3.84, p >0.05).

The criteria on which the hosts were grouped into reproductive categories have been described previously. Analyses of the structure of the wood-mouse samples caught in the twelve successive months of Trap Period B are presented in Fig. 2.6.

When trapping began all the captured male animals were sexually mature while a proportion of the females were still in their overwintering asexual condition. Baker (1930) stated that the time of maturation of the female determined the onset of breeding in *Apodemus* as they became fecund later than males. This appeared to be the case in the present study. During June some reproductive activity occurred resulting in the entry of a group of juvenile animals into the sample taken at the end of June. Some overwintered females remained imperforate, and therefore classed as sub-adults, until that late stage. The early breeding activity was not maintained and only a few juveniles were captured during the July/August sample, however some of the first litters had attained sub-adult status. Very high breeding activity during August resulted in a large number of juveniles appearing in the August/ September sample.

The fifth trapping session was a transitionary stage in the annual cycle of *A. sylvaticus*. Firstly, the high reproductive activity slowed down and fewer juveniles were detected on the grid. Secondly, some of the animals caught

Figure 2.6.

The composition of the *A. sylvaticus* population
during Trapping B. The number of mice of each category
is expressed as a percentage of the total grid population
for the session; males in the left hand column, females
in the right.

Reproductive adults.

Juveniles.

Sub-adults.

Fig.2.6
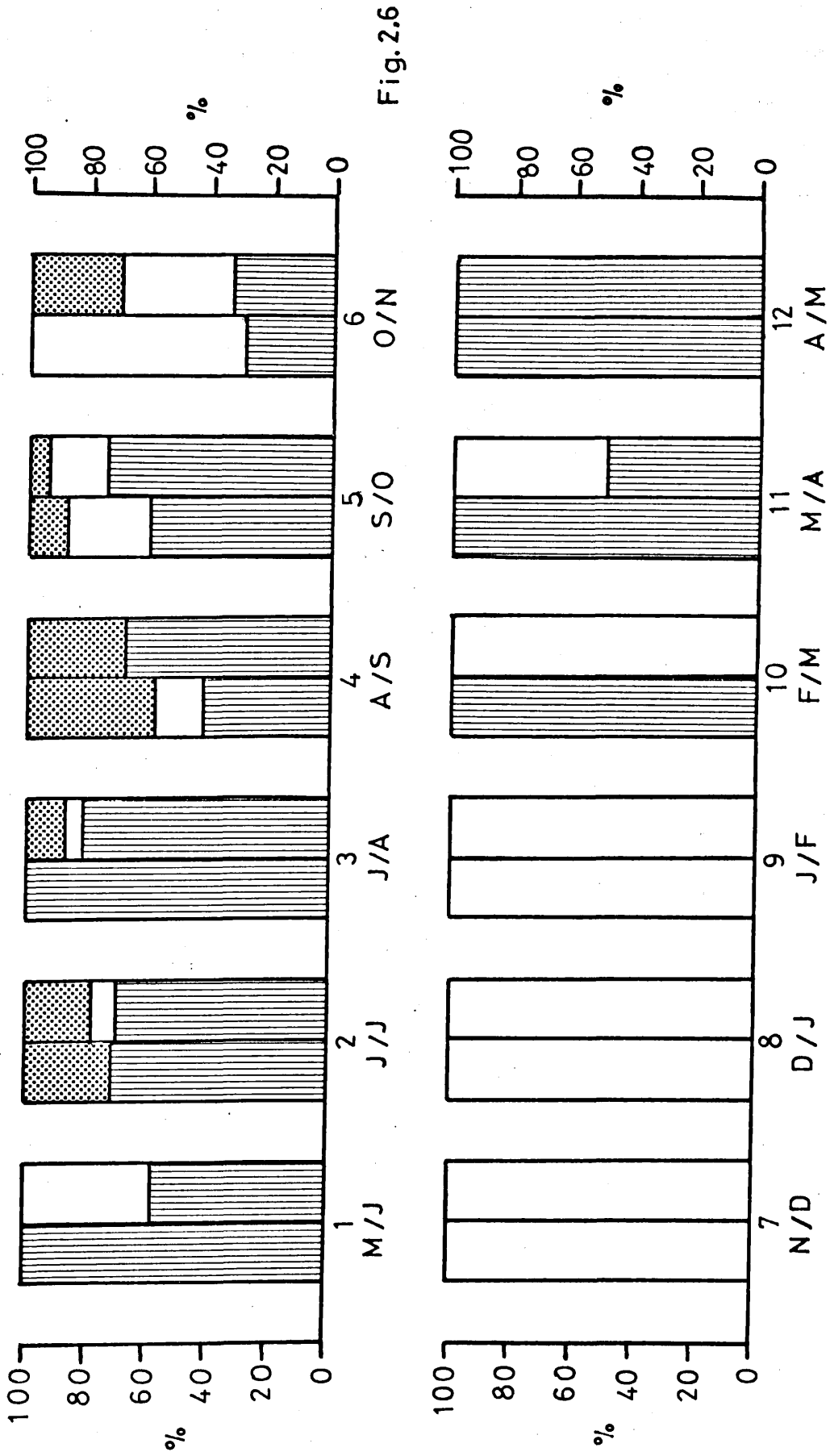
sampling periods and months

at that time, and classed as sub-adults, had previously been involved in breeding; the population had begun its change-over into the asexual overwintering phase. This trend was continued in the October/November sample and, finally, in November/December all the animals captured were in the sub-adult asexual state. A proportion of those animals had bred, and the male's testes had regressed or the females' vaginae had healed over, while the rest were late litters which had not entered breeding condition. During the winter period a steady population maintained itself on the grid.

In the February/March sample all the males had become sexually mature and the population that had remained at twenty to twenty-five animals all winter suddenly dropped to just ten animals. The possible reasons for this decline have been discussed earlier in the chapter. In the spring of 1973, as in the previous year the females matured later than the males so that in the March/April sample both adult and sub-adult females were present. The samples for this session were very small. More mice were collected in April/May and, in this final trapping session, all were sexually mature.

The onset of sexual maturity in females was observed to have been rather earlier in 1973 than in 1972, this was possibly due to the very mild winter. However, much larger samples would have been necessary before any definite conclusions could be made.

b) *Clethrionomys* and *Microtus*

There were considerably fewer *C. glareolus* and *M. agrestis*

present on the grid than *A. sylvaticus* during the trapping period. The number of voles captured is presented in Fig. 2.7. Because of the small sample sizes it is not possible to draw any definite conclusions from the data. However, some interesting trends were noted.

It seemed that two distinct peaks of numbers of *C. glareolus* density occurred, separated by a period of rather low density. The low coincided with the population peak of *A. sylvaticus*. Direct competition between the species may have resulted in this observation. It is also possible, however, that competition for traps caused this apparent decrease in *C. glareolus* and that, in fact, the population was maintaining itself at a higher level.

Small numbers of *M. agrestis* were found during all sampling sessions except one (the July/August sample). A small residual population was detected throughout the winter until, in spring, a peak was observed. It is interesting to note that high populations of *M. agrestis* had been found on the study areas in preceeding years. During the study period *M. agrestis* may have been at a low in its cycle of rise-peak-crash-low. In the grassy areas of the grid complex subterranean burrow systems could be found. The systems were little used as the new season's grass roots grew into the lumen of many of the burrows. However, their abundance indicated that there had been high levels of activity of *M. agrestis* in the area during previous years.

The actual numbers of captures of small mammals on the grid, as opposed to the numbers of different individuals, is shown in Appendix Figure III.

Fig. 2.7. Numbers of voles on Trap Grid B. (1972/3)
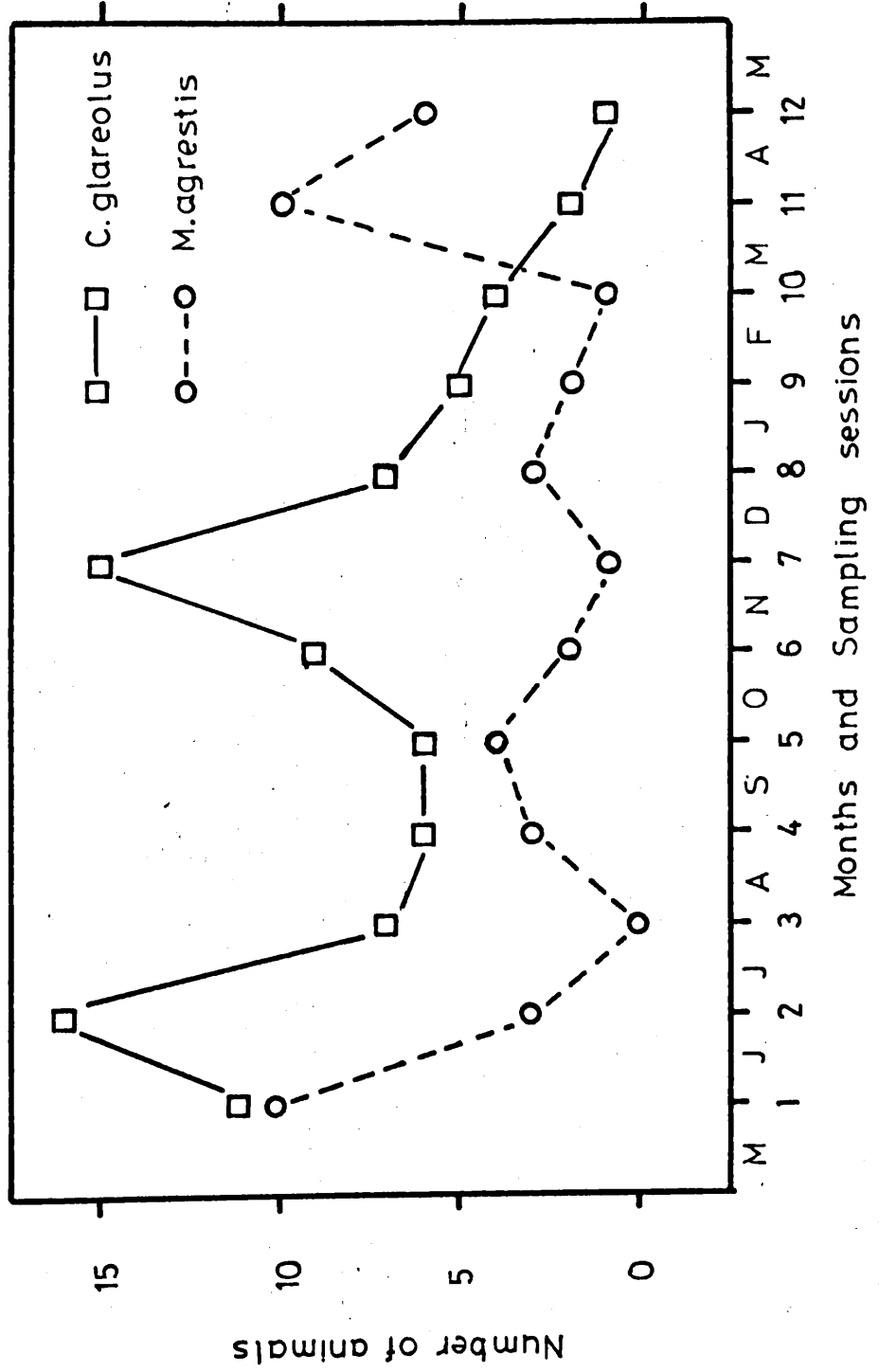
(ii) Annual Weight Variations

    a) *Apodemus sylvaticus*

Some interesting variations in the average weights of the population were observed during the trapping period (Fig.2.8.). In both males and females the onset of breeding activity appeared to bring about a general weight loss. Then, during the breeding season the average weight of female animals increased, mainly due to the pregnancy of some of the animals. The body weight of the males continued to decline throughout the breeding season. At first this was probably due to the actual loss of weight among breeding males and later it was due to the influx of smaller, younger animals, "the young of the year". This factor caused the average weight of the females to decrease when the main breeding peak was over. The weights reached their lowest levels during the winter when the whole population overwintered at about sixteen grammes per animal. As spring approached the weights of both males and females increased until, in late spring, they reached their full pre-breeding weights.

During the breeding season eight litters were born to females that were weighed both before and after parturition within one trapping session (i.e. within seven days). The average weight loss of the females, due to the birth of a litter,was 6.1gms. (range 10.0 - 3.5gms.). This weight represented over a quarter (27.7%) of the post-partum weight of the animal.

Fig. 2.8. Average weight of _A.sylvaticus_ during Trapping B. (1972/3). (excluding juveniles)
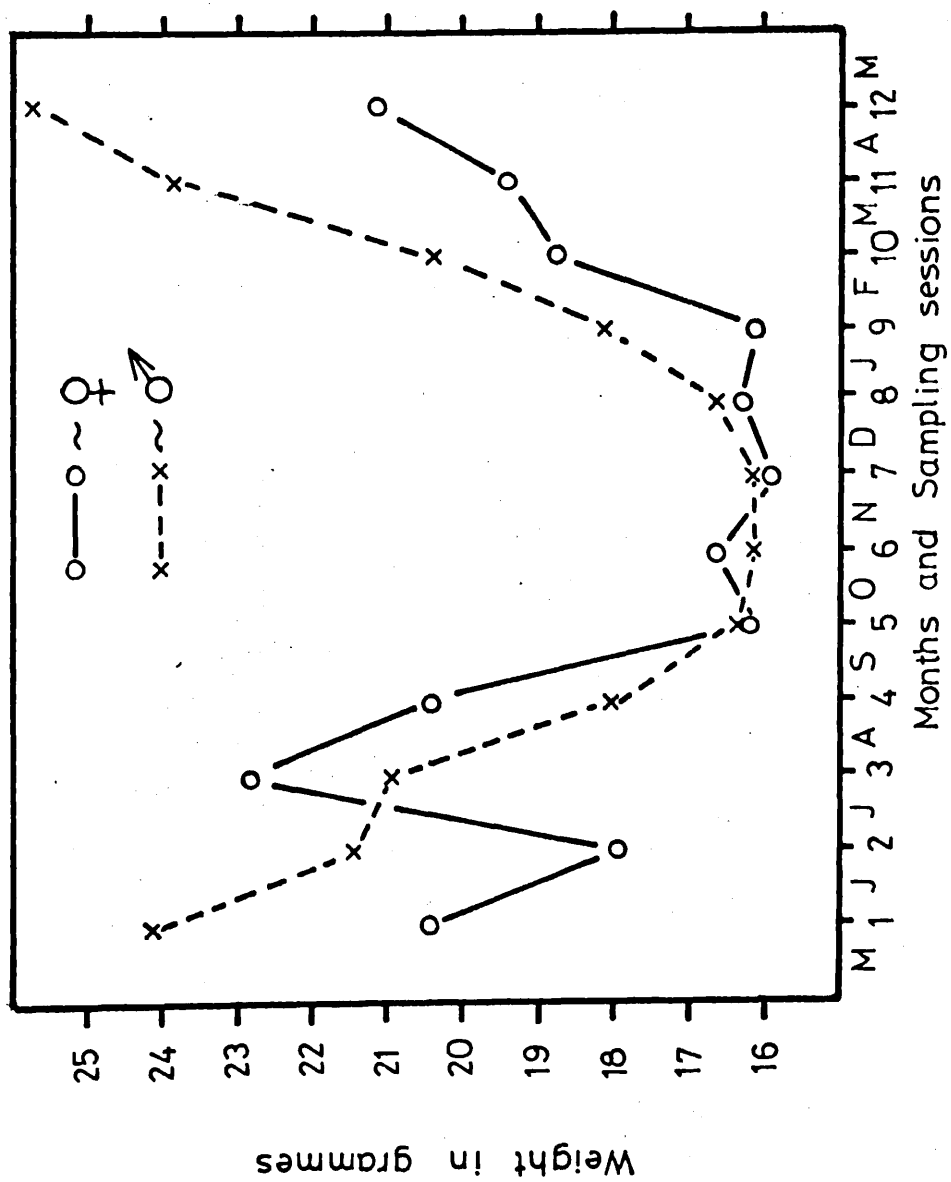
b) *Clethrionomys glareolus* and *Microtus agrestis*

In general the results obtained for the two vole species were similar to those of *A. sylvaticus*. However, the smaller number of animals captured meant that results were less comprehensive.

(iii) The distribution of rodent captures among the grid habitats

The grid area presented a number of different habitats for rodents. During Trap B 1260 separate rodent captures were made and the position of capture of each individual was carefully recorded. Examination of the frequency with which the different host species were captured in the three major habitats gave an indication of the intensity of utilisation of the different habitat types.

The vegetation of the area has been described in some detail in Section 3 of this chapter. The following remarks summarise the suitability, as cover, of the habitats for rodents:-

a) Bramble:- dense ground cover during spring and summer. After leaf-fall cover was limited to bramble cane tangles with variable cover afforded by leaf litter.

b) Woodland:- sparse ground cover during spring and summer, almost no ground cover during the remainder of the year.

c) Grassland:- dense cover throughout the year varying from 1½ - 2m. in spring and summer to ½m. in winter.

Each grid quadrat was allotted to one of the above habitat types depending on the dominant vegetation of the quadrat. Grassland dominated the grid area and quadrats with a preponderance of grass were three times more frequent than quadrats with brambles or woodland. Table 2.3. presents the distribution of rodent captures in the three major grid habitats. The actual numbers of captures in each of the three habitats gave a biased indication of habitat preference because grassland was much more common on the grid. The corrected numbers of captures, where the numbers of grassland captures were divided by three, gave a more realistic picture (Fig. 2.9.).

Both bank-voles and wood-mice seemed to prefer bramble covered quadrats in the corrected data. *C. glareolus* was captured more frequently in grassland than in wood, whereas in *A. sylvaticus*, no preference was clear between grassland and woodland. Grassland was preferred by *M. agrestis* and even where captures were made in quadrats dominated by wood or bramble some covering of grass was always present.

Southern (1964) adequately explains these observations in his discussion of the habitat and feeding preferences of the three rodent species and the results are not at variance with other studies.

(iv) Survival of animals during the Trapping Period

The length of the period spent on the grid by different individuals of *A. sylvaticus* varied greatly from animal to animal. A particular female individual (toe clip serial No. 4001) was captured and marked during the first sampling

Table 2.3 . The distribution of rodent captures in the three major habitats on Trap Grid B. (1972/3)

		Brambles	Woodland	Grassland
C.glareolus	number of captures	80	25	126
	% of total captures	34·63	10·82	54·54
	corrected number of captures	80	25	42
A.sylvaticus	number of captures	271	142	523
	% of total captures	28·95	15·10	55·87
	corrected number of captures	271	142	174
M.agrestis	number of captures	9	6	78
	% of total captures	9·67	6·45	84·87
	corrected number of captures	9	6	26

Fig. 2.9 The percentage of rodent captures in the three major grid habitats. (Data corrected to allow for dominance of grassland on grid.)
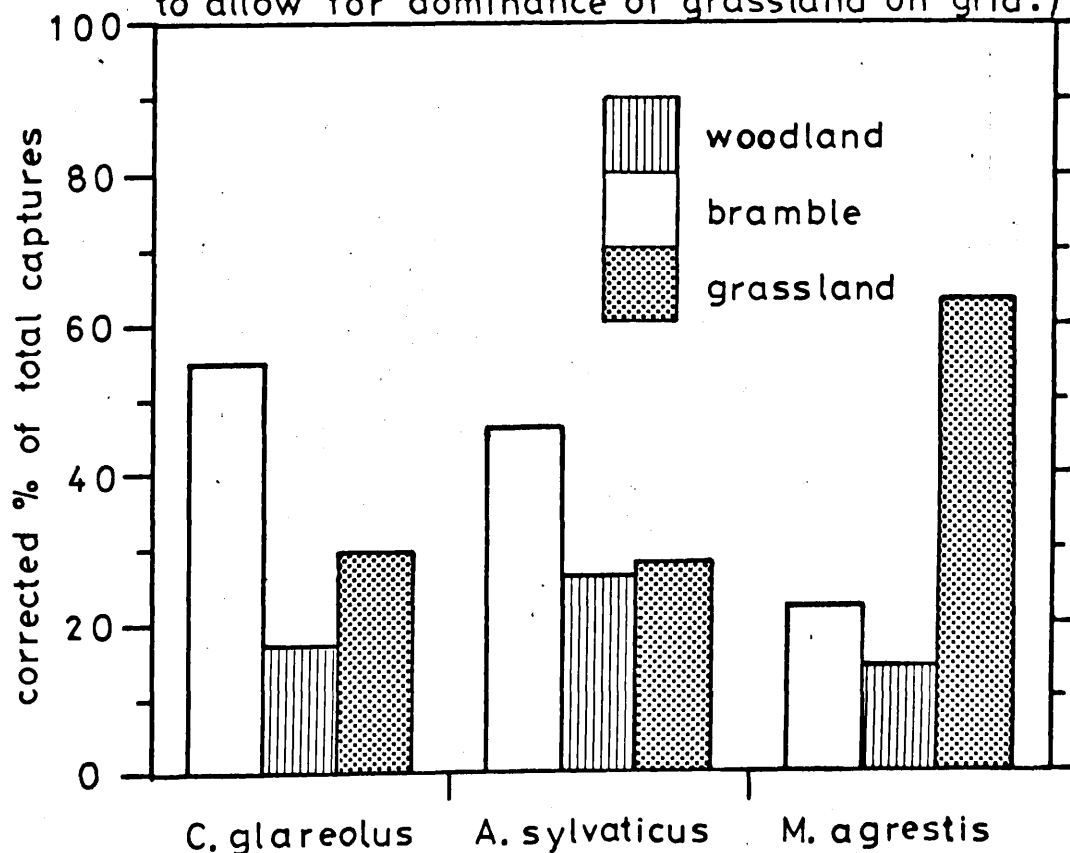
period and was still present on the grid twelve months later. Other individuals remained for eight and ten months. However, a majority of the animals were present for only a few trapping sessions.

Sampling was carried out on a monthly basis. Prior to its initial capture it was equally possible that an animal had been present on the grid for a month or that it had been present for only a few hours. Similarly, an animal may have died or left the grid only a few hours after its final capture or it may have remained until only a few hours before the beginning of the next sampling session. Consequently, the trapping of an animal during a sampling session was taken to indicate its presence on the grid for one month, i.e. it was assumed to have arrived half way between sessions and left half way between sessions.

Fig. 2.10. shows the frequency distribution of the estimated number of months in which animals were present on the grid. The frequency histogram does not indicate a "life-table" in its true sense. Arrival on the grid could have been due to birth or to immigration and similarly, death or emmigration could have been causes of the animals' absence from subsequent samplings. Formulae exist for establishing life-tables from mark-recapture data, standard methods have been discussed by Pucek, Ryszkowski and Zejda (1969), but such calculations were of little value to the present study.

Almost half of the animals captured disappeared after only one sampling period (46.3%). Progressively fewer

Fig.2.10 Frequency histogram of the number of months presence on the grid of A. sylvaticus individuals.
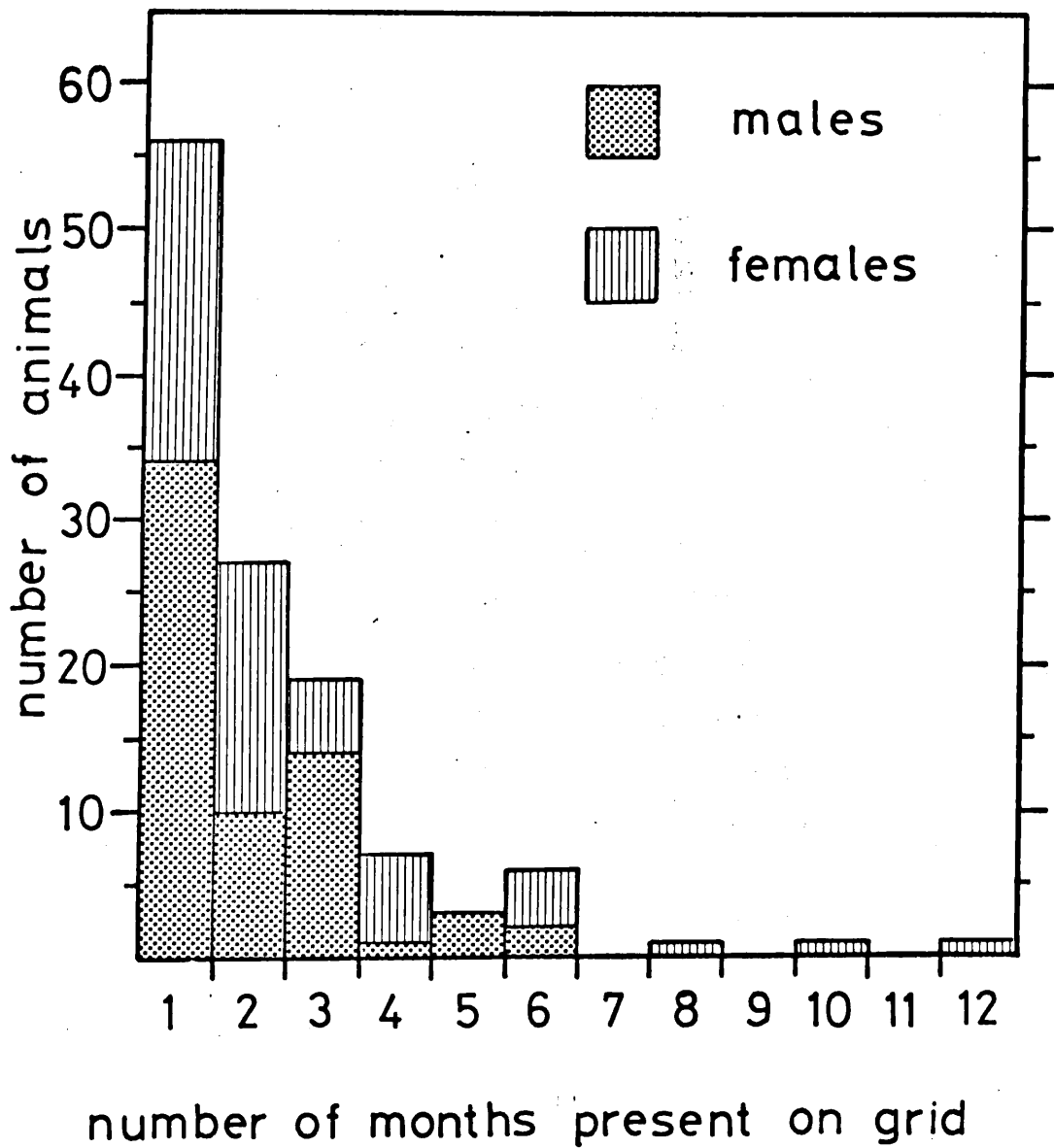
animals survived further samplings. There was no signifi-
cant difference between the numbers of males and females
leaving after one month (x^2 = 0.95, 0.20 > p > 0.50), after
two months (x^2 = 2.22, 0.10 > p > 0.20) or after three or
more months (x^2 = 0.02, 0.95 > p > 0.90).

In Fig. 2.11, solid lines represent male *A. sylvaticus*
and dashed lines represent females. Read horizontally the
figure shows the length of time a mouse was present on the
grid, as detected by trapping. Read vertically, for each
sampling session, it shows the total population size, the
composition of the population and the number of new animals
captured.

Comparative data for *C. glareolus* and *M. agrestis*
could not be assembled due to the smaller numbers of
captures and recaptures of those species.

(v) The definition and occurrence of migratory and
sedentary animals

The distinction between migratory and sedentary
animals is difficult to make on mark/recapture data alone.
It has been suggested that animals captured on only one
occasion during a trapping should be termed migratory,
while those captured more than once should be defined as
resident or sedentary animals (Janion, 1962). However,
traps introduce food material and refuge sites into the
area and, hence, its carrying capacity is temporarily
increased. Animals migrating through the area during
trapping may be induced to remain there because of the
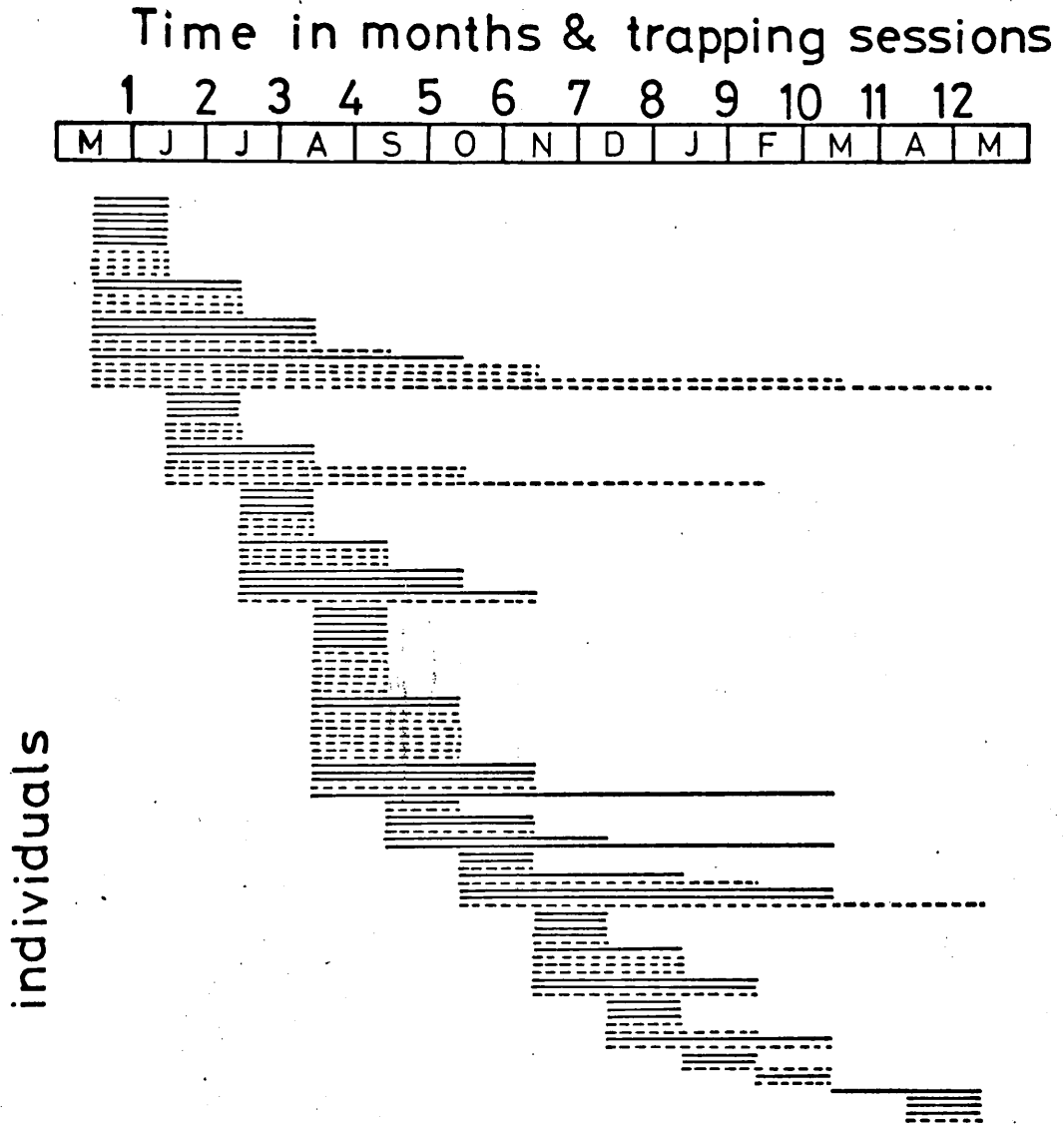
Fig. 2.11 Capture data for A.sylvaticus for 1972/3 on Trap Grid B.

---------- females

————— males

increased carrying capacity. In those circumstances migrant animals would be captured on more than one occasion and, therefore, be incorrectly defined as residents. To avoid this difficulty animals captured during only one sampling session were defined as migrants and those captured in two or more sampling sessions were termed residents. Thus, an animal could be captured on up to seven occasions in one session and be defined as a migrant. In contrast, an animal captured only twice would have been defined as resident if the two captures were in different sampling sessions.

Once again, only *A. sylvaticus* was studied with respect to the settlement of animals. Furthermore, individuals that were captured in the first or in the final sampling sessions could not be included in the analysis of results because it was not possible to identify migrants in those periods. This was due to the fact that, in the first session, their previous history could not be determined and, in the final session, it was not possible to postulate about their fate.

During the ten samplings for which the data was suitable for analysis there were 760 captures of animals classed as residents. A total of 193 resident animals were identified in the ten sampling periods. Thus, the average number of captures per session for sedentary animals was 3.94. Similarly, ninety-one captures of forty-six migrant animals gave an average of 1.98 captures per sampling session. The average number of captures per

sampling session for migratory and sedentary animals were highly significantly different when compared by means of a 2 x 2 contingency table (χ^2 = 12.42, p <0.001). When the data was separated into the sex categories and analysed the difference between the frequency of capture for sedentary and migratory animals was significant for both males (χ^2 = 4.93, p <0.05) and females (χ^2 = 7.62, p <0.01). The difference between the capture frequency of male and female sedentary animals was not significant (χ^2 = 0.12, 0.95>p>0.98). Similarly, the difference between male and female migratory animals was not significant (χ^2 = 0.20, 0.80>p>0.90).

Migratory animals were present in the grid population throughout the year. However, the population contained more migrants during the breeding season when 18.8% of all captures fell into the migratory category. During overwintering the population was more settled, only 7.3% of the captures being migrants. The position during pre-breeding could not be assessed due to the low population density and the need to exclude samplings one and twelve from the presented results.

(iv) Activity_areas_and_centres_of_activity

The position of each capture of individual animals was carefully noted. The observed area of activity was calculated for individuals of *A. sylvaticus* during both breeding and overwintering periods. Areas of activity, for animals during pre-breeding, were not estimated due to the very small numbers of animals concerned.

The Inclusive Boundary Strip method was used to compute areas of activity from the mark/recapture data (Stickel, 1954). The areas were plotted to scale on graph paper and measured by means of a planimeter. Only those animals that were captured on eight or more occasions during one of the periods were used in calculations. This, of necessity, ruled out any animals captured during only one trapping session. Thus, the areas of activity were computed only for "sedentary" animals, "migratory" individuals were ignored for the point of view of these estimations. Where animals were captured eight or more times, in both the periods under investigation, two separate areas of activity were calculated, one for each of the two periods.

In all, nineteen animals were used in activity area calculations for the breeding period and twenty were used for the calculations for overwintering animals.

Table 2.4. shows the results of the calculated areas of activity for male and female *A. sylvaticus* during the two periods. No significant difference was found between the mean activity areas of male and female animals during the breeding season ($t = 0.91$, $p > 0.1$, d.f. = 18) or during overwintering ($t = 1.70$, $p > 0.05$, d.f. = 19). The difference between the areas of activity of breeding and overwintering females was, once again, not significant ($t = 0.49$, $p > 0.1$, d.f. = 18). However, the areas of activity of breeding and overwintering males were very significantly different ($t = 2.81$, $p < 0.01$, d.f. = 19). When male and female results were pooled for each period this difference resulted in an overall reduction in the mean area of activity for the overwintering population

Table 2.4.

The areas of activity of male and female A. sylvaticus

during the breeding and overwintering periods

Trapping Period B

SEASON	SEX	n	Mean area of activity in hectares	S.E.	S.D.
BREEDING	♂	8	0.2164	+0.0500	0.0421
	♀	11	0.1619	+0.0316	0.1067
	BOTH	19	0.1846	+0.0264	0.1224
OVERWINTERING	♂	12	0.1000	+0.0000	0.0300
	♀	8	0.1413	+0.0223	0.0640
	BOTH	20	0.1165	+0.0100	0.0500

n   = no. of animals

S.E. = standard error of mean

S.D. = standard deviation

when compared with the breeding population, (t = 2.33, $p <$ 0.05, d.f. = 38).

The results obtained in this study were in close agreement with those of previous authors for *A. sylvaticus* (Miller, 1958; Brown, 1956; Kikkawa, 1964) with respect to "home range" sizes.

Centres of activity were calculated in specific cases depending on the needs of the study (see Chapter 3). They are not presented as separate results.

4.2. The Flea Populations

The analysis of large quantities of numerical data requires that some statistical evaluation of the results should be applied. However, the use of such evaluation is a somewhat neglected subject with respect to ectoparasite populations. Often techniques have been used where they are, in fact, inapplicable. Such a case is the 't' test used without transformation. Furthermore, in many studies, methods of analysis have been used which do not make full use of the information available within the data.

Rumreich and Wynn (1945) have shown that the skewness of the distribution of flea populations on their hosts, such as that shown in Fig. 2.12., makes statistical treatment difficult when average flea counts, for different host categories, are to be compared. Evans and Freeman (1950) commented on the marked skewness of the distribution of the data gathered during a study of *C. nobilis* on mice and voles at Oxford. In order to overcome this skewness they transformed the data using a new variable, Y, which they obtained from log 1 + X (where X is the number of fleas on a captured host). Williams (1964, pp. 193-254) observed that the data of Evans and Freeman (1950) gave a close fit to a logarithmic curve. In a later study Ulmanen and Myllymäki (1971) found the distribution of fleas on *M. agrestis* closely fitted a log-normal curve. They used the "square root of X plus one" transformation method to overcome skewness and to "stabilise variation". They noted that the fit to a log-normal curve was, probably,

Fig. 2.12

The frequency distribution of
C.nobilis on male (——) and
female (---) A.sylvaticus.

x ~ the calculated 'expected' values
in a log. series (see text)
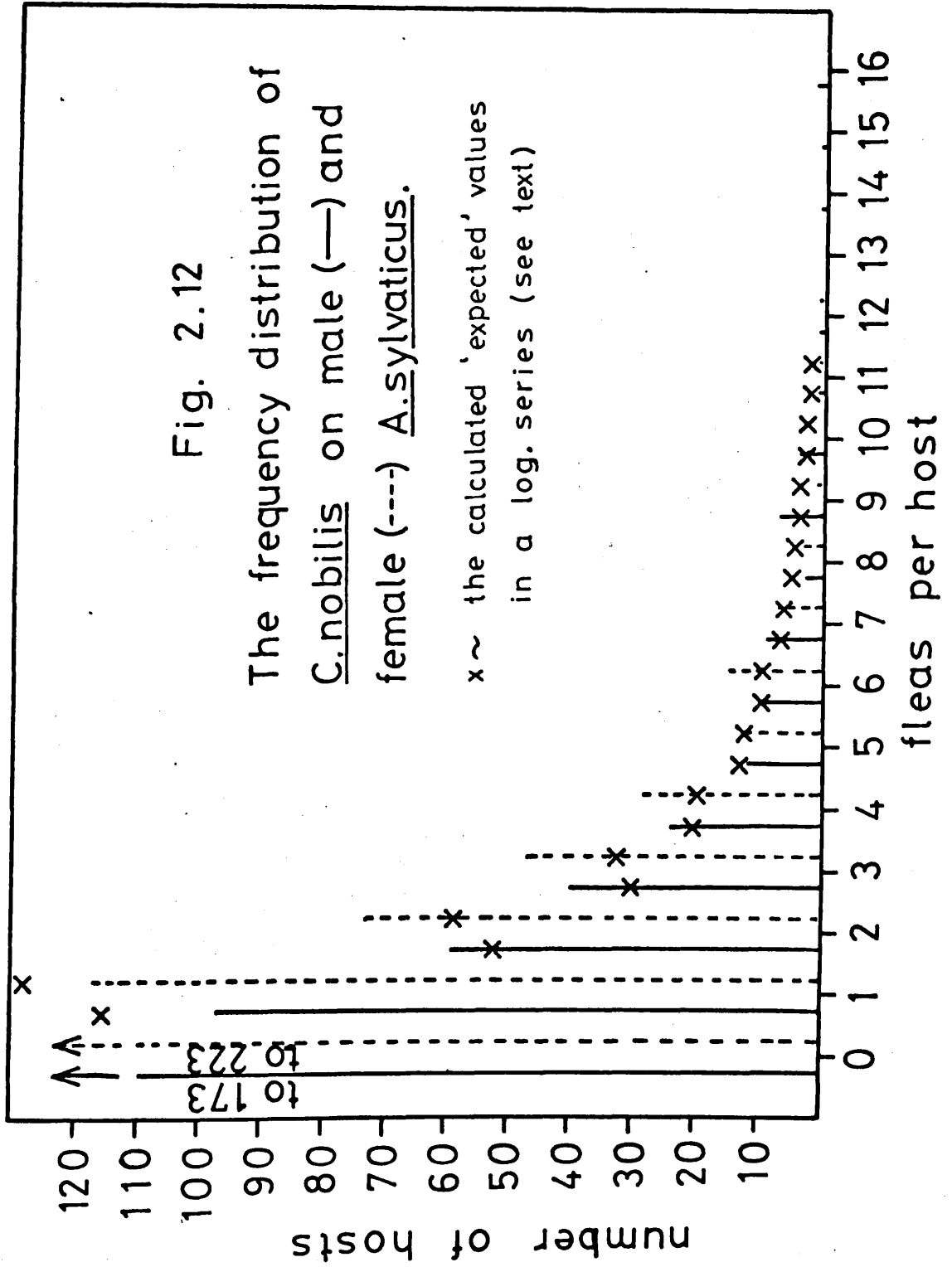
superficial but went on to use parametric tests on their
transformed data throughout their study.

In the present study the distribution of *C. nobilis*
on male and female *A. sylvaticus* closely fitted a logarith-
mic distribution ($X^2 = 19.15$, $p > 0.20$, d.f. = 15 for
males; $X^2 = 21.77$ $p > 0.10$, d.f. = 17 for females). However,
similar analysis of sub-samples indicated that the fit was
superficial because some sub-samples fitted negative
binomial or even Poisson distributions. If transformation
and parametric methods were to have been used in analysis
of data each sub-sample would have had to be tested for
goodness-of-fit to several distribution patterns. The
appropriate transformation would then have been applied
(see Elliot, 1971) and parametric tests, such as the "*t*",
test carried out. This method would have been very tedious
and extremely time consuming to apply.

An alternative was the use of "distribution-free" non-
parametric statistical methods; such techniques make no
assumption as to the parent distribution of the data. One
of the non-parametric equivalents to the "*t*" test is the
Mann-Whitney "U" test. The "U" test has a power efficiency
of not less than 86% and may be much more efficient than
parametric methods used on transformed data (Siegel, 1956;
Wilcoxon and Wilcox, 1964). However, a disadvantage of the
"U" test is that it is necessary to place the individual
recording values in ranks and, in studies where many hund-
reds of recordings are accumulated, the test becomes un-
wieldy. In the present study a compact tabular method of

applying the "U" test was developed and proved very quick and efficient. An example calculation is given in Appendix II. The "U" test was used throughout this study where flea indices of different host categories were to be compared.

4.2.1. The Flea Infestations of *A. sylvaticus*

(i) Variation in the level of *C. nobilis* infestations

(a) Yearly infestation cycles

Altogether a total of 1697 specimens of *C. nobilis* were taken from captures of *A. sylvaticus* during the twelve samplings of Trap Period B. The monthly infestation percentages and the average numbers of fleas per host (the flea index) for the pooled adult male, adult female and juvenile host categories are presented in Fig. 2. 13 . The monthly flea indices followed, quite closely, the curve of the infestation percentage. The relationship between the logarithms of these two parameters was linear (Fig. 2. 14). Thus, the more fleas infesting each captured animal the greater was the dispersal of fleas throughout the population. When 50% of hosts were infested the mean number of fleas per host was 1.4. At the 100% level of infestation among the population the number of fleas per host could be expected to be in the region of 5.0.

Infestation of *A. sylvaticus* with *C. nobilis* reached a well defined peak during spring and early summer and then gradually declined as the summer wore on, to reach a low by the early autumn. The infestation was maintained at a steady level throughout most of the hosts' overwintering period until, after a period of marked increase in flea numbers, the spring infestation peak was reached once more. Small differences between monthly samples were thought to be of minor consequence and, overall, the curves are remarkably smooth for this type of study.

Fig. 2.13 The relationship between infestation percentage and index of C.nobilis on A.sylvaticus. Trapping B.(1972/3)
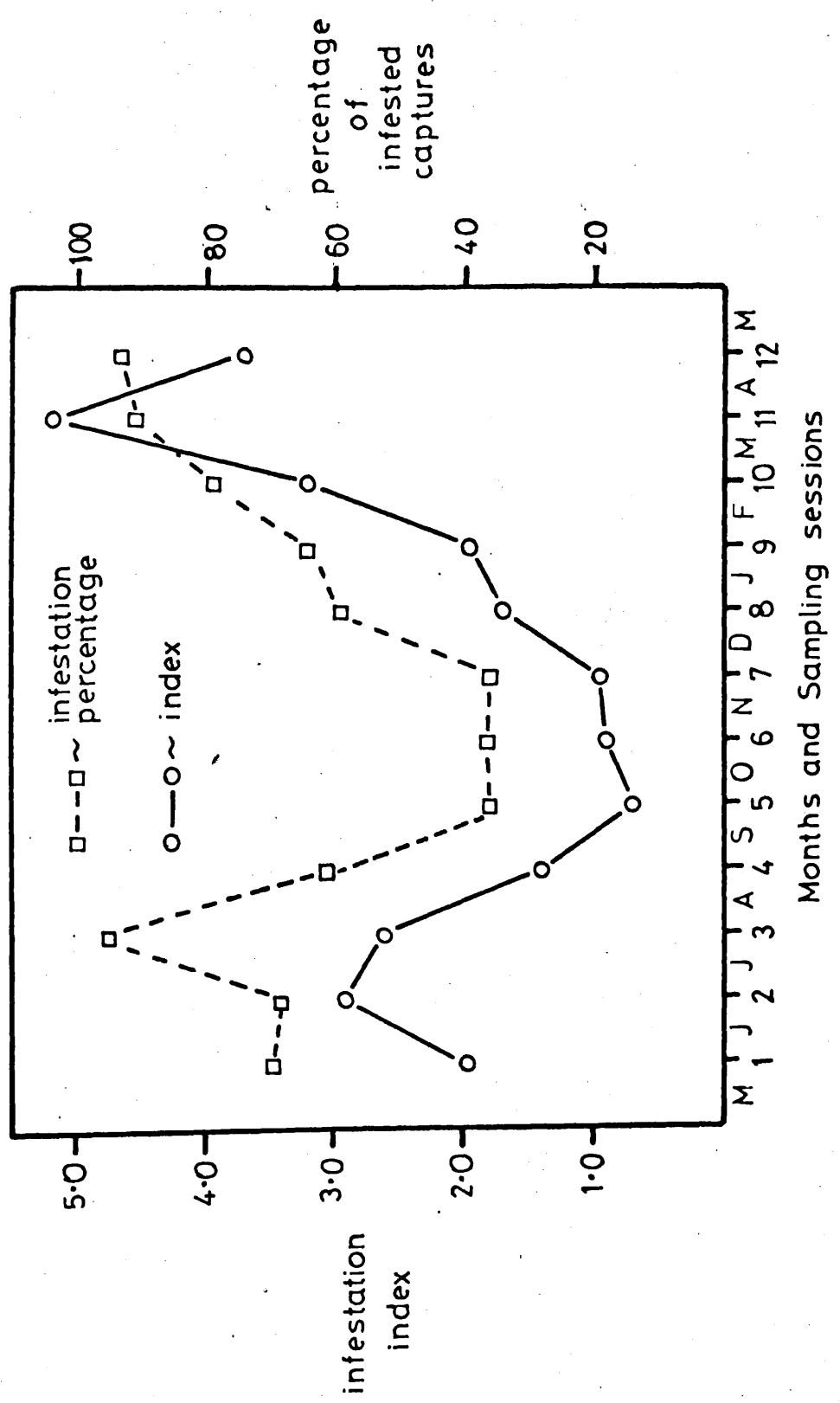
Fig. 2.14 Correlation of C.nobilis index and % infestation of A. sylvaticus. Trap Grid B (1972/3)

$r = 0.95$

$p < 0.001$

for y on x :-

$y + 3.00 = 1.67x + 0.29$

Log. C.nobilis index

Log. % A.sylvaticus infested
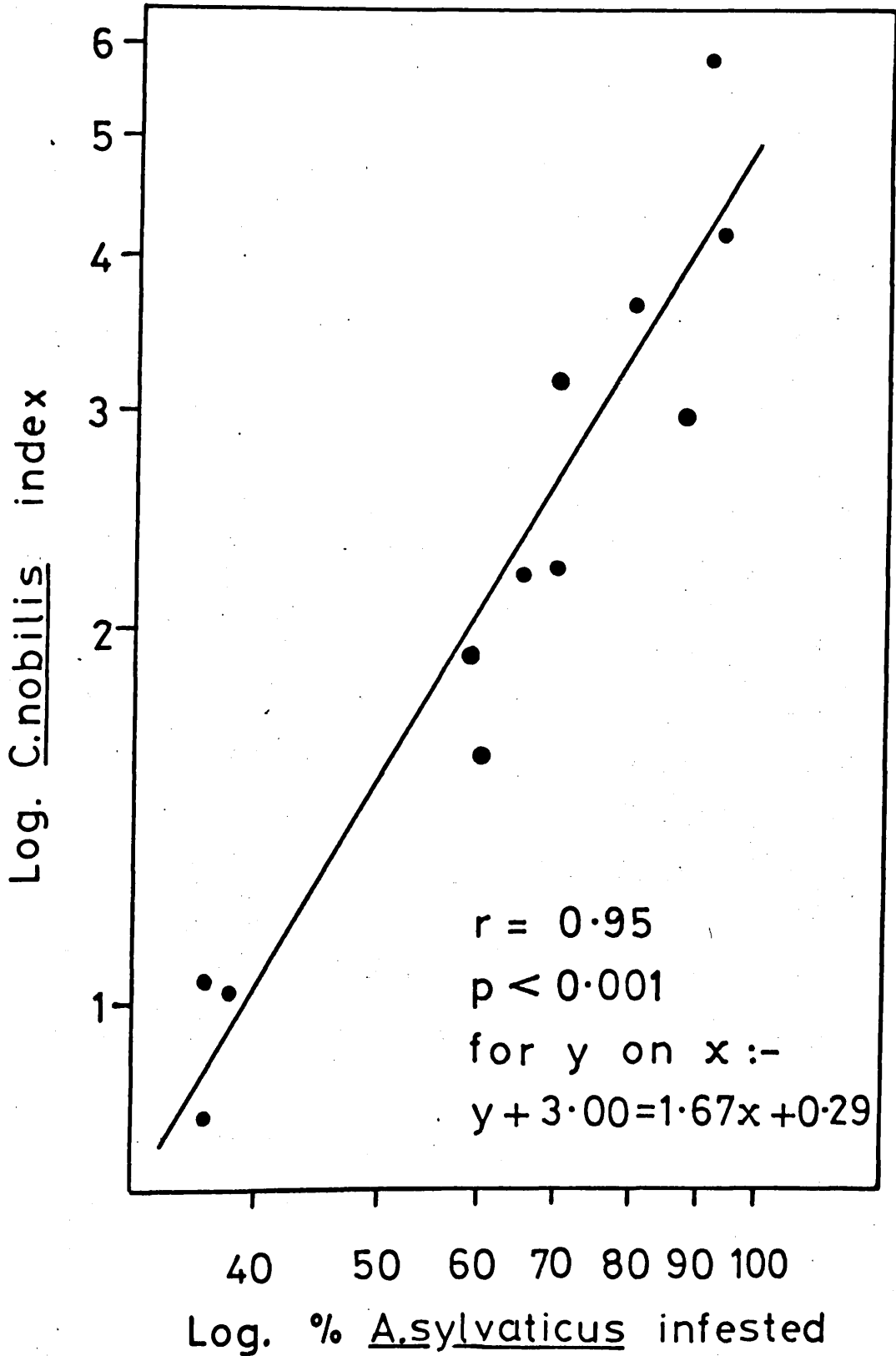
When the data from the samplings within the three major periods of the hosts' annual cycle were pooled and compared some interesting results emerged.

The flea index for *C. nobilis* on *A. sylvaticus* in the samples taken in the hosts' breeding season (sessions 2, 3, 4 and 5) was 1.87. During pre-breeding (sessions 10, 11, 12 and 1) the infestation index was 2.78. When Mann-Whitney "U" analysis was applied to compare these samples, pre-breeding mice were found to be highly significantly more heavily infested than breeding ones ($d = 3.42$, $p < 0.001$). Even fewer fleas infested overwintering animals (sessions 6, 7, 8 and 9), the flea index at that time was found to be 1.37. This was significantly lower than the index of both breeding ($d = 3.40$, $p < 0.001$) and pre-breeding animals ($d = 5.69$, $p < 0.001$).

(b) Infestation of the two sexes

The large sample size of *C. nobilis* taken from wood-mice allowed a detailed comparison of the distribution of the flea fauna of the hosts with respect to sex categories.

During the pre-breeding season sixty-nine female and eighty male captures of *A. sylvaticus* were made. The flea indices for the males and females were 3.67 and 2.02 respectively. Males were found to be very significantly more heavily infested than females at that time ($d = 2.72$, $p < 0.01$).

The higher level of male infestation was not maintained during the breeding season when the index for male wood-

mice was 2.13 and for females, 1.65. These indices were
not significantly different (d = 1.42, p>0.05).

The levels of infestation of the two sexes were very
similar during overwintering. The indices were 1.34 for
males and 1.29 for females. These values were, once again,
not significantly different (d = 0.14, p>0.05).

Just as the pooled data for infestations varied from
season to season so did the data for the individual male
and female populations. The index for male animals was
significantly different in each of the three periods of
the hosts' annual cycle. The results were similar to the
pooled data and showed that pre-breeding males were more
heavily infested with fleas than breeding males and that
breeding males were more heavily infested than overwinter-
ing animals. The results for female hosts were slightly
different from the males. Breeding females and pre-
breeding females harboured more fleas than overwintering
ones. However, pre-breeding and breeding females harboured
similar *C. nobilis* infestations. Thus, it seems, that the
significant difference in the infestations of pre-breeding
and breeding animals observed in the pooled data is due,
almost entirely, to the very high index of the pre-breeding
males.

Fig. 2.15 summarises the observations on the *C. nobilis*
index on *A. sylvaticus* during the three major periods of
the hosts' annual cycle and Table 2.5. gives a review of the
statistical analyses of these samples based on the Mann-
Whitney "U" test.

Fig. 2.15 The levels of infestation of C.nobilis on A.sylvaticus for the three periods of the host's annual cycle. Trapping B. (1972/3)
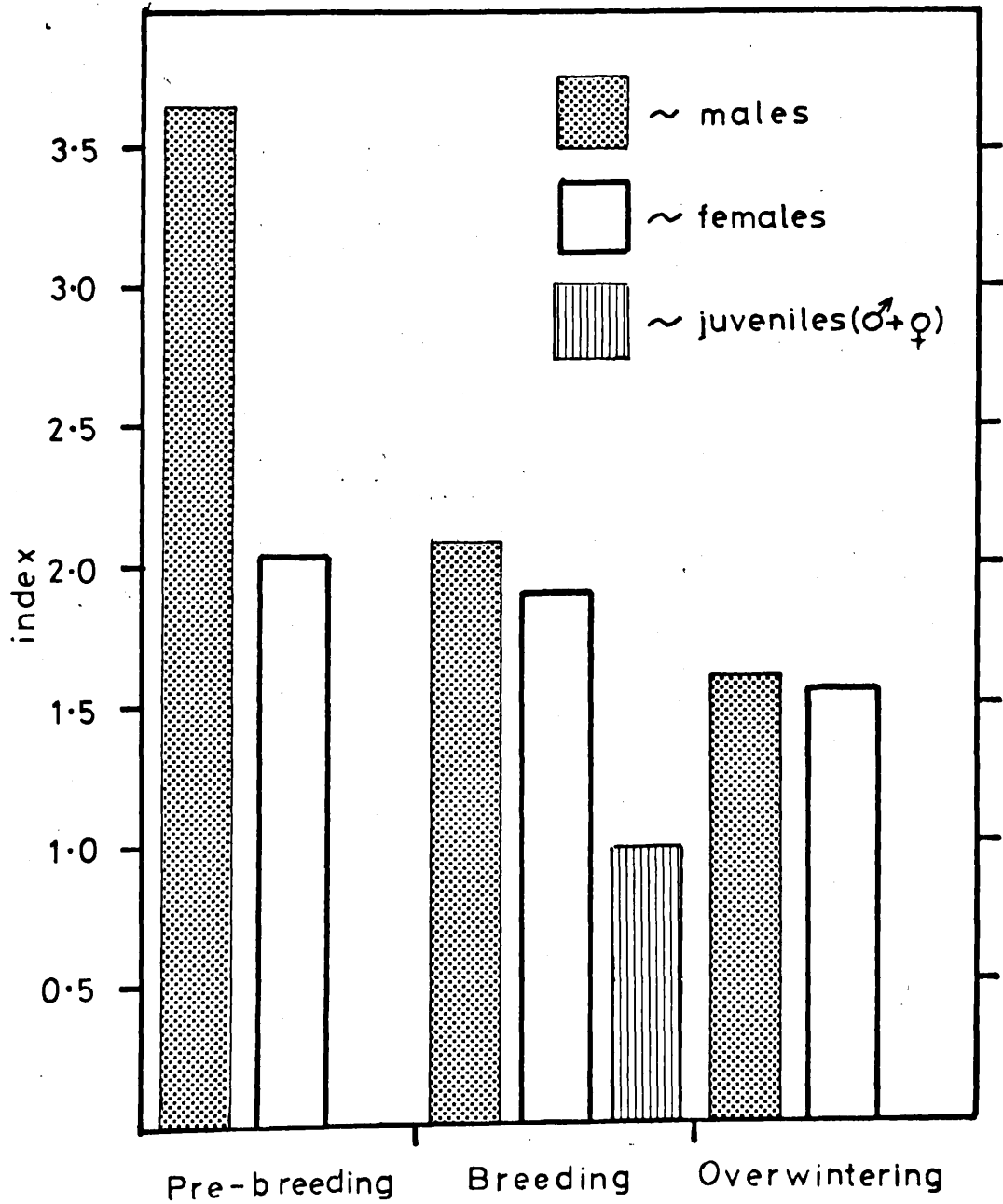
Table 2.5.

A summary of the statistical analysis of sub-samples of
C. nobilis on *A. sylvaticus* during the three periods of the
hosts' annual cycle.

N.S.   =   not significant

*   =   significant

**   =   very significant

***   =   highly significant

$\bar{x}$ =   flea index of sub-sample

n   =   number of captures in sub-sample.

Table 2.5.

	Pre-breeding		Breeding		Overwintering
	male $n = 69$ $\bar{x} = 3.67$	female $n = 80$ $\bar{x} = 2.02$	female $n = 211$ $\bar{x} = 1.65$	juvenile $n = 56$ $\bar{x} = 0.98$	male $n = 172$ $\bar{x} = 1.34$
Pre-breeding female $n=205$ $\bar{x}=2.02$	—	—	$d=1.26,$ $p>0.05.$ N.S.	—	—
Pre-breeding male $n=172$ $\bar{x}=3.67$	—	$d=2.72,$ $p<0.01$ **	$d=3.29,$ $p<0.001$ ***	—	$d=5.42,$ $p<0.001$ ***
Breeding male $n=178$ $\bar{x}=2.13$	—	—	$d=1.42,$ $p>0.05$ N.S.	$d=4.38,$ $p<0.001$ ***	$d=3.47,$ $p<0.001$ ***
Breeding juvenile $n=56$ $\bar{x}=0.98$	—	—	$d=2.86,$ $p<0.01$ **	—	—
Overwintering female $n=80$ $\bar{x}=1.29$	$d=2.92,$ $p<0.01$ **	—	$d=2.15,$ $p<0.05$ *	—	$d=0.14,$ $p>0.05$ N.S.

(c) Infestation of the different age groups

During the breeding season the grid population included a proportion of animals categorised as juveniles. These animals exhibited a low level of *C. nobilis* infestation. The index was 0.98 and was found to be highly significantly different to the more heavily infested adult animals (d = 3.50, $p < 0.001$). Juvenile males and females exhibited similar levels of infestation at that time (d = 1.01, $p >$ 0.05). The indices were 0.59 for males and 1.31 for females.

(d) The flea infestations of migratory and sedentary *A. sylvaticus*

It has been shown that, based on certain criteria, it was possible to categorise the grid populations of *A. sylvaticus* into sedentary or resident animals and migratory or non-resident animals. It is interesting to compare the flea infestations of these categories.

The flea index for sedentary animals was found to be 1.98 and the index for migrants was 1.78. When compared by means of the Mann-Whitney "U" test these indices were found not to be significantly different (d = 1.25, $p > 0.05$). However, when male and female animals were analysed separately an important difference was noted. The flea indices for sedentary and migratory male *A. sylvaticus*, 2.09 and 1.91 respectively, were not significantly different (d = 0.54, $p > 0.05$). Whereas, the indices for sedentary and migratory females, 1.88 and 1.55 respectively, were significantly different (d = 2.25, $p < 0.05$). Thus, there was a basic difference between the infestations of the sexes of migratory animals. Migratory males had the same number of

fleas as residents but female migrants had fewer than
residents.

(ii) Rates of Re-infestation of A. sylvaticus with
fleas (all species)

Many of the mice that were captured on the trapping
grid, during Trap Period B, were taken on several occasions
within each sampling period. Often mice were captured and
defleaed as many as five or six times within the week.
This gave an opportunity to study the rates of re-infest-
ation of the host animals. The efficient methods of
defleaing ensured that animals were released, into their
environment, without fleas and that any subsequent infesta-
tion had developed exclusively since the last capture.
Since the total pick-up of fleas, over a period, was to be
measured the results of re-infestation for all flea species
were pooled.

Table 2.6. shows the numbers of captures, the numb-
ers of fleas and the flea index for A. sylvaticus, during
the three periods of the host's annual cycle, depending on
whether the capture was the first, second, third and so on
of that particular animal within the sampling period. For
example, during the pre-breeding period, nineteen animals
were captured on five separate occasions during the seven
day sampling periods. On the occasion of their fifth
capture the animals carried fifty-one fleas between them,
giving an index of 2.68 fleas per animal. The value of
the normal deviate (d) for a comparison, by Mann-Whitney
"U" analysis, between the flea indices of consecutive days

Table 2.6
Rates of re-infestion of <u>A.sylvaticus</u> during the three periods of the host's annual cycle.

		capture frequency						
		1	2	3	4	5	6	7
Pre-breeding	captures	45	29	26	21	19	9	–
	fleas	174	95	54	36	51	14	–
	index	3·87	3·28	2·08	1·71	2·68	1·56	–
	d		1·32	1·21	0·10	0·88	1·36	–
Breeding	captures	114	84	61	52	35	19	4
	fleas	215	232	161	87	72	42	3
	index	1·89	2·76	2·64	1·67	2·06	2·21	0·75
	d		1·03	0·31	0·66	0·14	1·05	1·54
Over-wintering	captures	94	81	65	53	43	29	14
	fleas	158	141	77	82	44	28	19
	index	1·68	1·74	1·18	1·54	1·02	0·97	1·36
	d		0·54	0·27	0·35	0·38	0·47	0·14

Fig. 2.16 The flea indices of the first three and last four captures in sampling sessions with statistical comparison. A.sylvaticus, (1972/3).
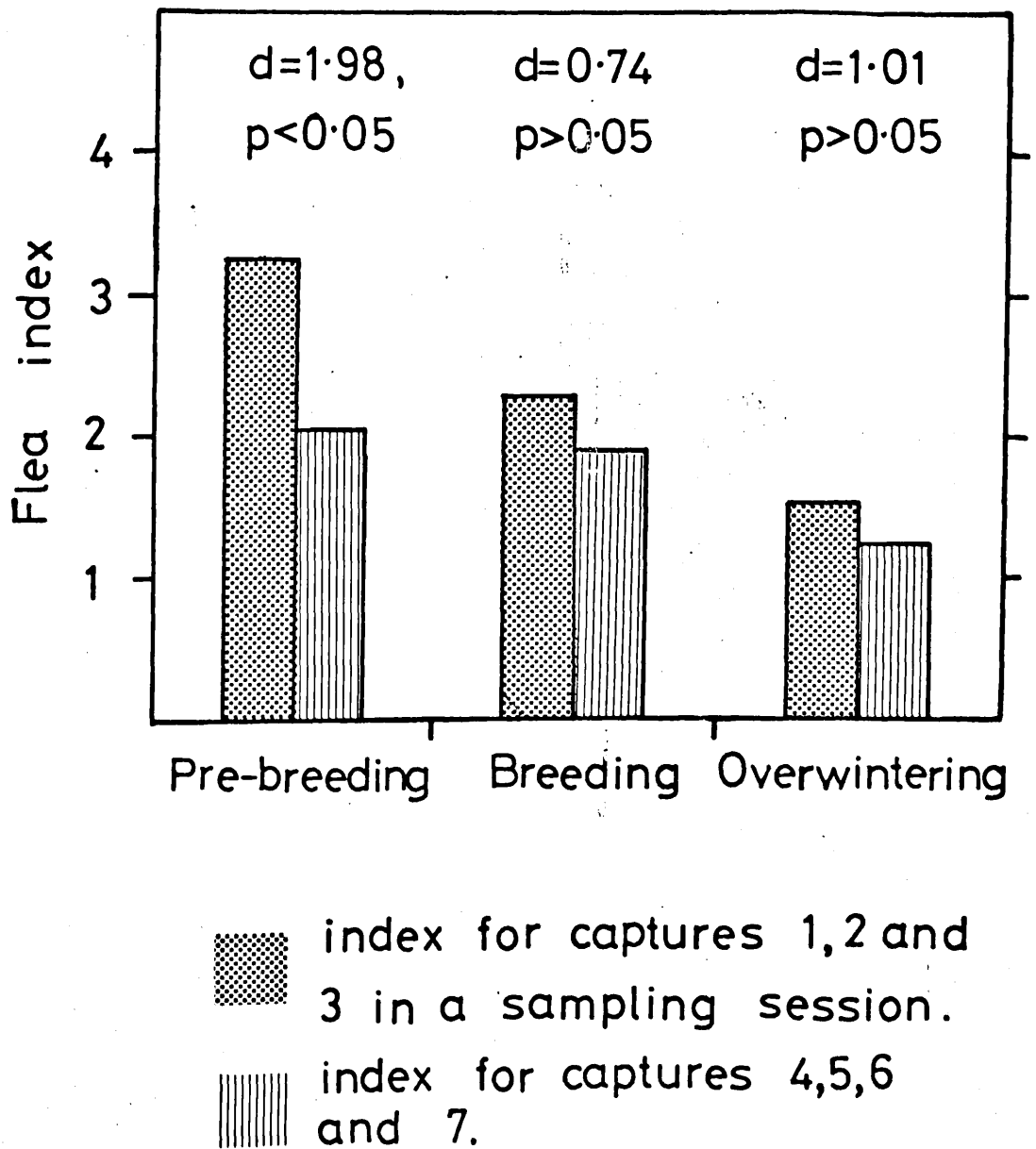
Table 2.7   Rates of re-infestion of _A.sylvaticus_ with fleas.

Trap Period B		capture frequency						
		1	2	3	4	5	6	7
daily analysis	captures	253	194	152	126	97	57	18
	fleas	547	468	292	205	167	84	22
	index	2·16	2·41	1·92	1·63	1·72	1·47	1·22
	d	0·16	1·02	0·39	0·07	0·43	0·86	
days 1,2,3 and 4,5,6,7 grouped	captures	600			302			
	fleas	1308			477			
	index	2·18			1·58			
	d	2·11 , $p < 0.05$						

is given in the table. Thus, when the index of 2.68 was compared with 1.56, obtained for animals captured on six occasions, the normal deviate was 1.36.

Flea indices were significantly different, at the 95 % level, only in cases where d exceeded 1.96. Hence, it can be seen from the table that, where separate indices were taken for each capture frequency, and consecutive frequencies were compared, no significant differences were observable in the data.

However, Fig. 2.16. shows the values of d when average indices of the first, second and third times of capture were compared with the average of the fourth and subsequent captures for the three periods of the hosts' annual cycle. During pre-breeding the index of the fourth and subsequent captures was significantly less than for the average of the first three captures. This situation was not repeated for the breeding and overwintering populations, where the lower d values were not significant.

When the data was pooled for the whole year, the flea index for the first three days of a sampling period was found to be significantly higher than the index for the final four days ($d = 2.11$, $p < 0.05$). Nevertheless, consecutive days did not vary significantly from one another (Table 2.7.).

(iii) Changes in the species composition of the infestation

The flea collections from *A. sylvaticus* contained ten different flea species which showed different patterns of occurrence on the host animals (Table 2.8). The monthly

Table 2.8.

The percentages of different flea species in monthly samples of *A. sylvaticus*. Trapping Period B. (actual numbers in parenthesis)

Flea species	M/J	J/J	J/A	A/S	S/O	O/N	N/D	D/J	J/F	F/M	M/A	A/M	TOTALS
C.nobilis	95.08 (174)	93.31 (265)	88.26 (233)	90.74 (196)	80.73 (88)	89.81 (97)	87.91 (80)	92.22 (166)	97.02 (163)	98.39 (122)	100.00 (57)	100.00 (56)	92.23 (1697)
M. turbidus	4.37 (8)	4.58 (13)	9.85 (26)	7.41 (16)	9.20 (10)	1.85 (2)	5.50 (5)	1.67 (3)	1.19 (2)	-	-	-	4.62 (85)
P. silvatica spectabilis	-	0.35 (1)	0.76 (2)	0.46 (1)	7.34 (8)	3.70 (4)	2.20 (2)	1.11 (2)	0.60 (1)	-	-	-	1.14 (21)
N. fasciatus	-	-	0.76 (2)	0.46 (1)	-	0.93 (1)	1.10 (1)	3.33 (6)	-	-	-	-	0.60 (11)
R. pentacantha	-	-	-	-	0.92 (1)	0.93 (1)	3.30 (3)	1.67 (3)	-	0.81 (1)	-	-	0.49 (9)
H.t. talpae	0.55 (1)	-	-	0.46 (1)	0.92 (1)	1.85 (2)	-	-	-	0.81 (1)	-	-	0.33 (6)
M. penicilliger mustelae	-	0.70 (2)	0.38 (1)	-	0.92 (1)	-	-	-	1.19 (2)	-	-	-	0.33 (6)
D.d. dasycnema	-	0.70 (2)	-	-	-	-	-	-	-	-	-	-	0.11 (2)
M. walkeri	-	-	-	0.46 (1)	-	0.93 (1)	-	-	-	-	-	-	0.11 (2)
O.h. howardi	-	0.35 (1)	-	-	-	-	-	-	-	-	-	-	0.05 (1)
TOTALS	183	284	264	216	109	108	91	180	168	124	57	56	1840

percentages of the species which made up the hosts' flea
burden showed that, of the ten species captured, *C. nobilis*
completely dominated the sample throughout the year.
During spring, on the pre-breeding animals, the species
constituted the entire flea population of the animals. In
only two periods did the *C. nobilis* contribution to the
flea fauna of *A. sylvaticus* fall below ninety percent of
the total.

   During the summer *M. turbidus* became common and
constituted almost ten percent of the total number of fleas
during some samplings. In the winter period, peaks of
P. silvatica spectabilis and *R. pentacantha*, together with the
remnants of the *M. turbidus* population from the summer,
combined to give a total exceeding ten percent of the flea
sample.

   All the other captured flea species occurred in no
distinct yearly pattern, they were probably stragglers from
other host species. For example, in the late summer a
small colony of Norway rats, *Rattus norvegicus* Berkenhout,
established themselves close to the north-western corner
of the grid. They brought with them an infestation of the
rat flea *Nosopsyllus fasciatus* (Bosc.). A few of these
fleas found their way onto individuals of *A. sylvaticus*,
especially the animals with home ranges close to the rat
colony. During the early winter the rat population was
eradicated, by gassing, for hygiene and public health
reasons. The rat fleas continued to infest a few of the
wood-mouse population although none were found after the
February/March sampling period.

Because of the dominance of *C. nobilis* in the sample the graph of the total flea infestation index during the twelve samplings will not be presented separately (for *C. nobilis* see Fig. 2.13.). However, the relationship between the flea index and the actual numbers of insects captured was quite interesting. There was a very marked decrease in the overall flea index during August although only fo rty-eight fewer fleas were captured. This decrease was almost certainly due to the dilution effect of the sudden influx of juvenile animals into the population. During mid-winter there was a marked increase in the numbers of fleas captured, the numbers more than doubled during December. Because the numbers of animals captured stayed about the same there was an increase in the flea index which continued throughout the rest of the winter and spring. This sequence of events is probably very important in the annual cycle of the ectoparasite populations. The actual numbers of fleas captured during spring declined. However, the numbers of host captures declined even more rapidly and the result was a constant increase in the flea index.

(iv) Sex ratio of_the_flea populations parasitising

A. *sylvaticus*

There was an unequal distribution of male and female fleas among the 1697 specimens of *C. nobilis* taken from wood-mice during Trapping Period B. Overall, 41.54% of the flea population was male, there being 705 male fleas capt- ured and 992 female fleas in the twelve samplings. The observed deviation from a normal one to one sex ratio for

Fig. 2.17 The percentage of male C.nobilis on A.sylvaticus. Trapping B.(1972/3)
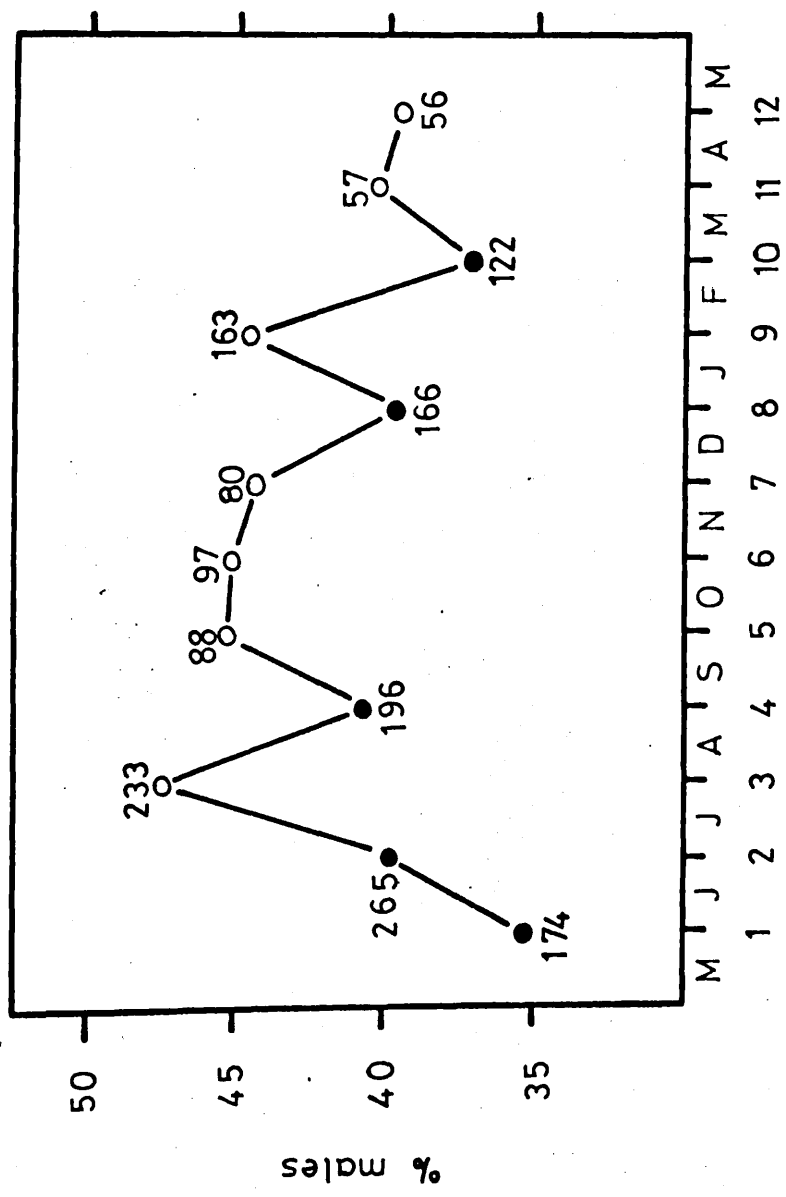
Results of χ^2 analysis :-

• ~ significant (P<0·05)

o ~ not significant(P>0·05)

numerals represent

total numbers of

fleas captured.

the insects was highly significant (x^2 = 45.87, p<0.001).

The ratio of male to female fleas was not constant during the trapping period and considerable fluctuations in the proportion of male fleas between samples was observed (Fig. 2.17.). There was no clear-cut seasonal variation in the sex ratio of males to females although four of the five individually significant variations from a one to one ratio occurred during the winter/spring period. At that time males made up only 39.38% of the 1003 fleas taken from *A. sylvaticus* and the pooled data for the winter/ spring samplings showed a highly significant variation from one to one (x^2 = 45.23, p<0.001, d.f. = 6). During the summer/autumn period (samples 3,4,5,6 and 7) only a single, individually significant, variation from a one to one ratio was observed and the pooled data for the five summer/autumn samplings showed that males comprised 44.67% of the 694 fleas taken. These samples, when pooled, showed no significant variation from a one to one sex ratio (x^2 = 7.89, p>0.05, d.f. = 4).

The validity of this system of data grouping may be debated. However, tests for homogeneity within the above groups of samples showed no significant deviations within the groups. Thus, for the five samples comprising the summer/autumn group, when tested for homogeneity by means of a 5 x 2 contingency table, a x^2 of 1.62 was obtained (p > 0.80, d.f. = 4). Similarly, for the winter/spring samples a 7 x 2 contingency test gave a x^2 value of 3.41 (p > 0.50, d.f. = 6).

The above data showed that two homogeneous groups of data existed and that the winter/spring period was the

Table 2.9.

The sex ratio of flea species from *A. sylvaticus,* other than *C. nobilis,* with results of Chi-square analysis for significant variation from a one to one sex ratio. Trapping B (1972/3).

FLEA SPECIES	No. OF FLEAS ♀	No. OF FLEAS ♂	TOTAL No. OF FLEAS	% MALE	χ^2	p
M. turbidus	47	38	85	44.71	0.95	>0.20
P. silvatica spectabilis	11	10	21	47.62	0.05	>0.80
N. fasciatus	6	5	11	45.45	0.09	>0.50
R. pentacantha	6	3	9	33.33	-	
H.t. talpae	3	3	6	50.00	-	
M. penicilliger mustelae	5	1	6	16.67	-	
M. walkeri	2	0	2	-	-	
O.h. howardi	0	1	1	100.00	-	
D.d. dasycnema	1	1	2	50.00	-	

source of the deviations from the one to one sex ratio that
was observed within the year's pooled sample. When the
summer/autumn and the winter/spring groups were compared
difference between the variations in sex ratio was found
to be significant $(\chi^2 = 4.72, p < 0.05)$. Hence, it
seemed that males were most common in the samples during
summer and autumn and decreased during winter and spring
although individual variations between samplings were of
little significance.

The sex ratios of the fleas taken from *A. sylvaticus*,
other than *C. nobilis*, are shown in Table 2.9 . The samples
are quite small and only the collections of *M. turbidus*,
P. silvatica spectabilis and *N. fasciatus* were suitable for
statistical analysis. None of the sex ratios of these
samples showed significant variation from one to one.

(v) The flea infestations and areas of activity of
hosts

For certain individuals of the species *A. sylvaticus*,
during the breeding and overwintering periods, it was
possible to compute areas of activity from the mark and
recapture data. It must be carefully noted that these
areas did not represent the "home-ranges" of animals as
defined by Burt (1943) and Jewell (1966). The areas of
activity were, almost certainly, underestimates of the
actual home range dimensions. They did, however, bear
some relationship to the amount of ground habitually
covered by the animals during the period of the study and
they were, probably, directly proportional to the actual
home range areas. They compare favourably with the size of

the home-range areas offered by other authors (see Brown, 1966 for review).

The total number of fleas taken from the animal for the captures that were used to define the area of activity were divided by the number of captures to arrive at an index for that particular host animal for the period. For example, during the breeding period animal 0300 (toe clip serial number) was captured twenty-five times and the distribution of those captures was used to estimate the area of activity which was then measured, by means of a planimeter, and found to be 0.1643 hectares. Thirty-six fleas, of various species, were taken from the animal during the twenty-five captures, thus giving an index for flea infestation at each capture of 1.64.

The indices were plotted against the area of activity for each animal and are presented as scatter diagrams (Fig. 2.18(i) and Fig. 2.18(ii)). During breeding both indices and areas were quite widely scattered. Regression analysis showed that the number of fleas on each capture and the area of activity were significantly positively correlated ($r = 0.503$, $p < 0.05$, d.f. $= 18$). That is not to say that the flea index is dependant on activity area; other factors acting on both parameters may have resulted in the observed correlation. These factors will be more fully discussed at a later stage. During overwintering the relationship was found to be negatively correlated, although the correlation was not significant ($r = -0.270$, $p > 0.05$, d.f. $= 19$). Thus, it has been shown that factors causing the observed correlation during breeding did not occur in the overwintering period. The lack of correlation, during

Fig. 2.18

(i) Breeding.

r = 0·50, d.f.=18
p<0·05

flea index

activity area in hectares

(ii)Overwintering.
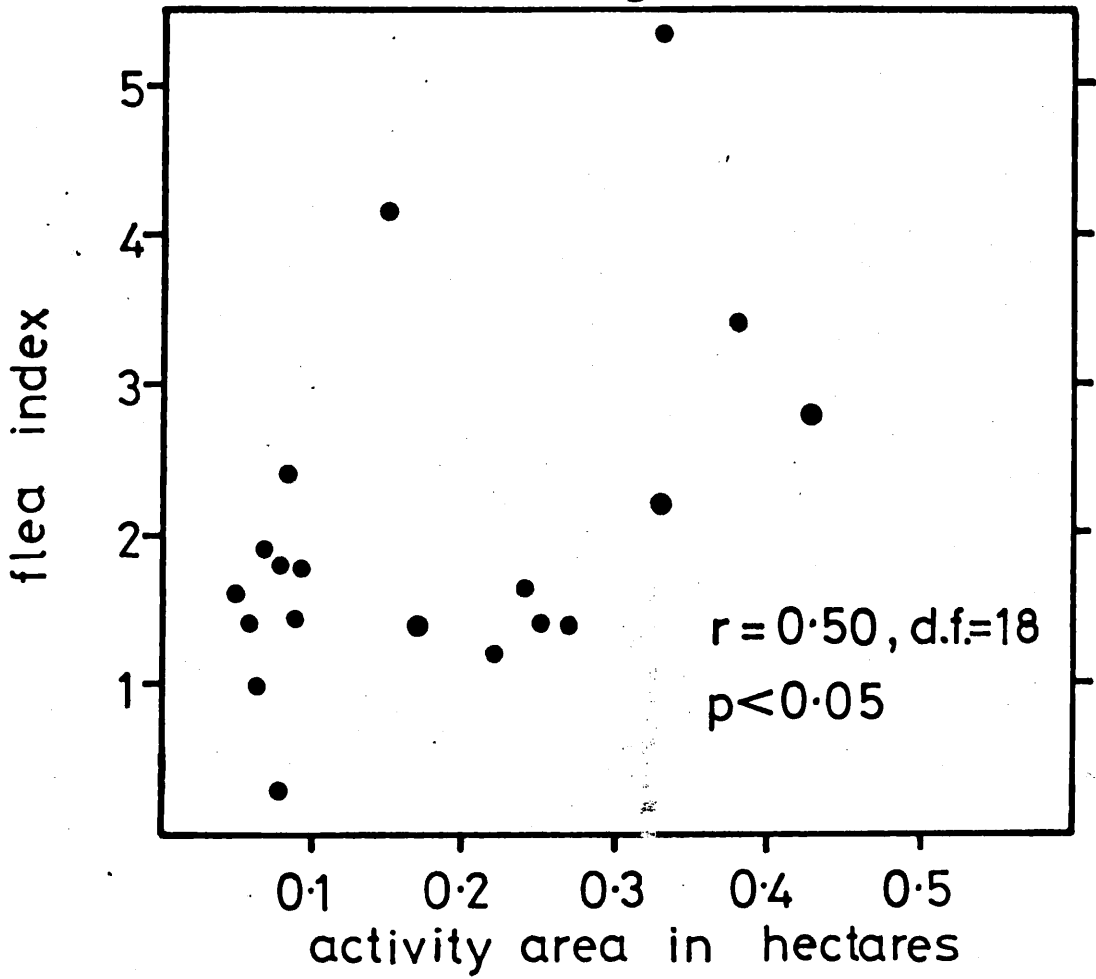
r= -0·27,d.f=19
p>0·10 (not sig.)
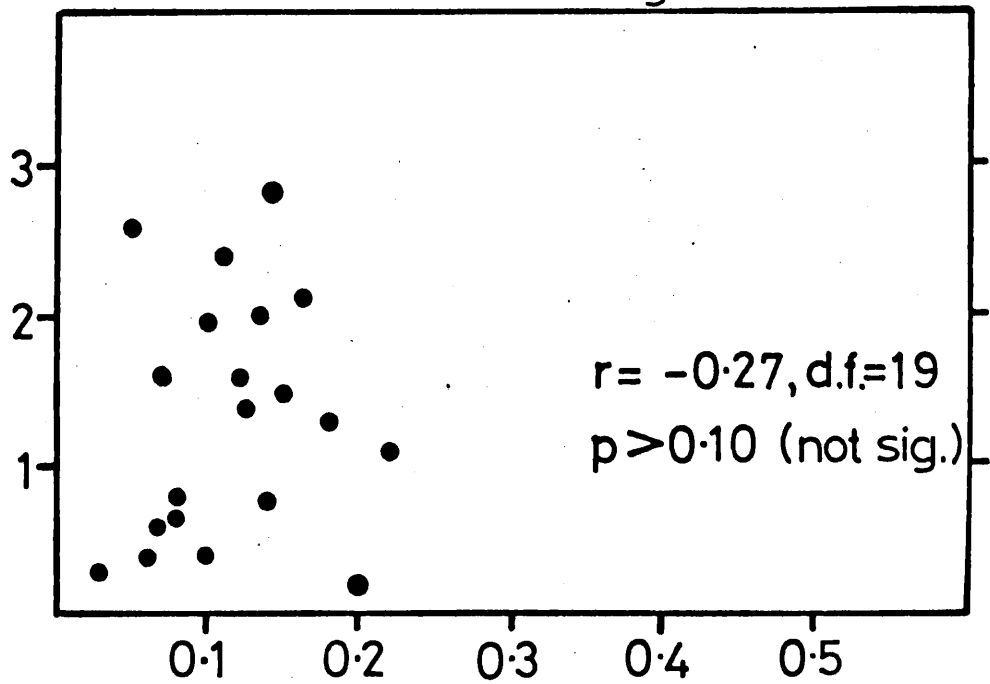
overwintering, was probably caused by the comparative homogeneity of the sample with respect to size of activity area.

4.2.2. The flea infestations of *C. glareolus*

(i) Variation in_the_level_of _C._nobilis _infestations

A number of captures of *C. glareolus* was made during sampling of the small mammal communities on Trapping Grid B. Although the number of captures was not large some analysis of results was thought to be worthwhile. A total of 235 captures of the bank-vole, *C. glareolus*, yielded 470 specimens of *C. nobilis* during the twelve sampling periods of Trapping Period B. The small numbers of captures for some of the sampling periods meant that flea indices for a few of the individual sampling periods were rather meaning-less. However, when the sampling periods were, once again, grouped with respect to the different phases of the host's annual cycle appreciable numbers of fleas allowed some analysis of results and comparison with the results from *A. sylvaticus* already described.

The flea index, for *C. nobilis* on *C. glareolus*, for the samples taken during the breeding season was 2.30. During the overwintering period the infestation index fell to 1.45. When Mann Whitney "U" analysis was applied to compare these two indices the breeding animals were found to be very significantly more heavily infested ($d = 2.51$, $p < 0.001$). In the prebreeding period the infestation rose and the flea index was 2.35. When compared the prebreeding animals were highly significantly more heavily infested with fleas than the overwintering animals ($d = 2.71$, $p < 0.001$). There was no significant difference between the infestations of prebreeding and breeding animals ($d = 0.08$,

p > 0.05).

The small size of the sample from *C. glareolus* did not allow detailed analysis of the sex and age categories within the phases of the hosts' annual cycle. However, comparison of the gross male and female samples was possible. The overall *C. nobilis* index for male *C. glareolus* was 2.01, when this was compared with the infestation index of female bank-voles, which was 1.88, no significant difference was detected (d = 0.76, p > 0.05).

Some of the above results are interesting when compared with similar results from *A. sylvaticus*. Both bank-vole and wood-mouse populations had peak infestations in the prebreeding season and the flea index, at that time, was similar for both species (d = 0.10, p > 0.05). However, in *A. sylvaticus* the infestation showed a marked decrease in the breeding season whereas, in *C. glareolus*, the infestation was maintained at a high level. The bank-voles were more heavily infested than the mice at that time (d = 2.56, p < 0.01). Both rodent populations had lowered infestation indices in the overwintering period, but, *C. glareolus* was still more heavily infested (d = 2.16, p < 0.05).

(ii) Changes in the species composition of the infestation

Nine different flea species were taken from the captured bank-voles during Trapping Period B (Table 2.10). *C. glareolus* is thought to be a primary host of six of those species while three were accidental infestations from other

Table 2.10

The percentages of different flea species in monthly samples of *C. glareolus*. Trapping Period B
(actual numbers in parentheses)

Flea Species	M/J	J/J	J/A	A/S	S/O	O/N	N/D	D/J	J/F	F/M	M/A	A/M	TOTALS
C. nobilis	80.95 (68)	66.50 (137)	76.09 (35)	75.00 (12)	40.00 (6)	32.14 (9)	48.89 (44)	55.06 (49)	85.11 (40)	87.50 (35)	82.86 (29)	54.55 (6)	66.68 (470)
M. penicilliger mustelae	1.19 (1)	6.70 (14)	2.17 (1)	-	6.67 (1)	14.28 (4)	28.89 (26)	29.21 (26)	2.13 (1)	12.50 (5)	14.29 (5)	9.09 (1)	12.02 (85)
P. silvatica spectabilis	-	12.13 (25)	8.70 (4)	6.25 (1)	40.00 (6)	50.00 (14)	6.67 (6)	7.87 (7)	6.38 (3)	-	-	-	9.33 (66)
M. turbidus	14.28 (12)	12.62 (26)	8.70 (4)	18.75 (3)	13.33 (2)	3.57 (1)	8.89 (8)	4.49 (4)	-	-	2.86 (1)	36.36 (4)	9.19 (65)
R. pentacantha	1.19 (1)	1.45 (3)	-	-	-	-	4.44 (4)	3.37 (3)	4.26 (2)	-	-	-	1.84 (13)
H.t. talpae	1.19 (1)	0.48 (1)	2.17 (1)	-	-	-	-	-	2.13 (1)	-	-	-	0.56 (4)
M. walkeri	-	-	2.17 (1)	-	-	-	1.11 (1)	-	-	-	-	-	0.28 (2)
T. poppei	1.19 (1)	-	-	-	-	-	-	-	-	-	-	-	0.14 (1)
P.s. soriscis	-	-	-	-	-	-	1.11 (1)	-	-	-	-	-	0.14 (1)
TOTALS	84	206	46	16	15	28	90	89	47	40	35	11	707

animals.

The monthly occurrence of the species showed some interesting seasonal variations. *C. nobilis* was the most frequently captured flea species and comprised 66.29% of the total number of fleas from the voles. During spring and summer *C. nobilis* was the dominant flea in the samples. However, in autumn the proportion of that species fell and other, less common, flea species began to contribute a significant percentage in the samples.

Two of the Ceratophyllid flea species, *M. penicilliger mustelae* and *M. turbidus,* were quite common in the samples, together they made up more than 21.00% of the total flea captures. *M. turbidus* reached peak numbers during summer and autumn and then declined with the onset of winter, while *M.p. mustelae* although present in most of the summer samples, reached a peak in its population in mid-winter.

The seasonal occurrence of *P. silvatica spectabilis* was particularly well defined. They entered the population in the second sampling period (June/July) and reach a peak in their proportion of the population in late autumn and early winter. They finally left the population in early spring.

H. t. talpae and *R. pentacantha* are both flea species which are thought to be typical of Cricetid rodents although they were quite infrequent in the samples. Of the other species *P. s. soriscis* is typical of small insectivores, *T. poppei* is most common on *A. sylvaticus,* when it is present, and *M. walkeri* has *M. agrestis* as its primary host.

(iii) Sex ratio of the flea populations parasitising

C. glareolus

A total of 470 specimens of C. nobilis were taken from the C. glareolus captures during Trapping B. The overall percentage of males in the sample was 47.23 (222 male: 248 female). The ratio of males to females did not vary significantly from one to one (X^2 = 1.44, 0.20 > p > 0.50).

Fig. 2.19. shows the percentage of male C. nobilis and the overall numbers of that species taken during the twelve sampling periods. Where the samples were large enough for analysis, there was no significant variation from a one to one sex ratio. The difference between these results and those obtained from A. sylvaticus was quite interesting. In the samples from the wood-mouse the preponderance of females was highly significant. When the results from wood-mice and from bank-voles were compared, by 2 x 2 contingency tables, the difference was found to be significant (X^2 = 4.86, p < 0.05).

Sex ratios for the other flea species captured on C. glareolus are shown in Table 2.11.

Fig. 2.19 The percentage of male C.nobilis on C. glareolus.

Trapping B. (1972/3)
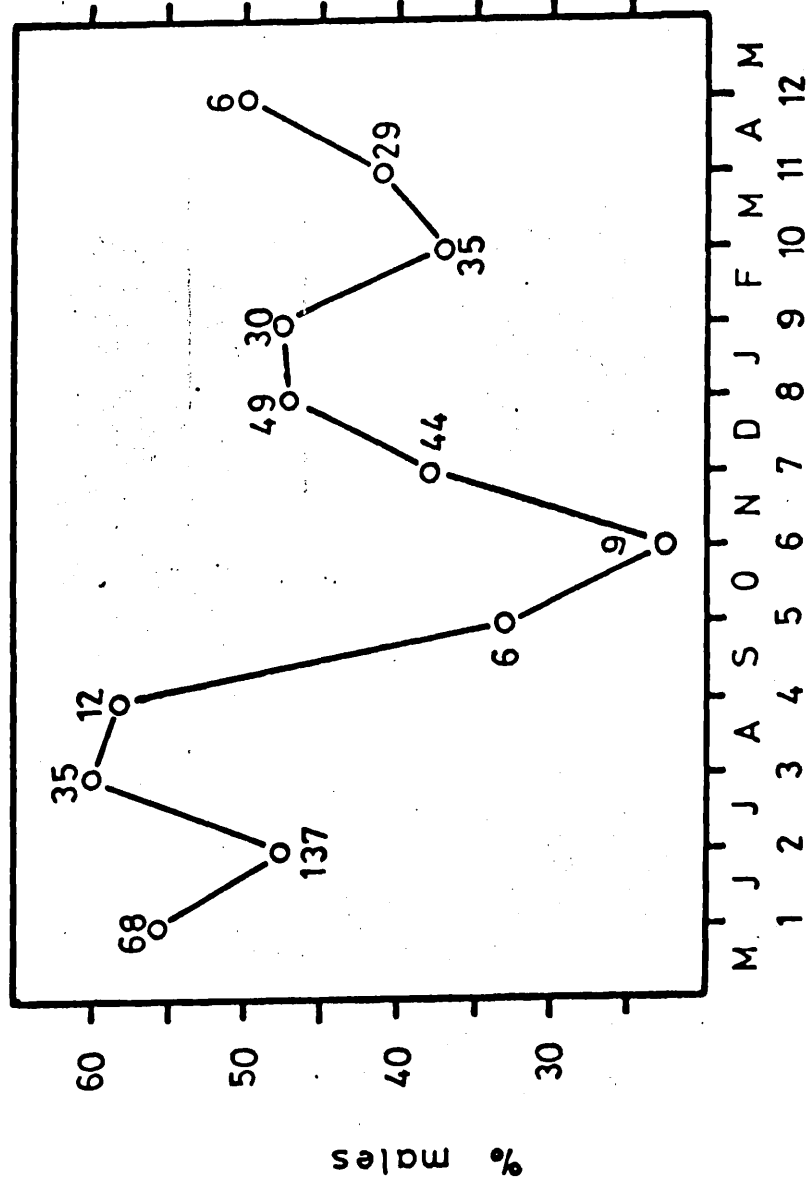
Results of χ^2 analysis :-

no significant deviations from 1:1 sex ratios. (samples 5,6 and 12 too small for analysis).

numerals represent total numbers of fleas captured.

Table 2.11.

The sex ratio of flea species from *C. glareolus*, other
than *C. nobilis*, with results of Chi-square analysis for
significant variation from a one to one sex ratio.
Trapping B (1972/3)

FLEA SPECIES	No. OF FLEAS ♀	No. OF FLEAS ♂	TOTAL No. OF FLEAS	% MALE	χ^2	P
M. turbidus	34	33	67	49.25	0.02	>0.05
M. penicilliger mustelae	53	32	85	37.65	5.19	<0.05
P. silvatica spectabilis	30	36	66	54.55	0.55	>0.05
R. pentacantha	11	2	13	15.38	-	-
H.t. talpae	3	1	4	25.00	-	-
T. poppei	1	0	1	0	-	-
M. walkeri	1	1	2	50.00	-	-
P.s.soriscis	0	1	1	100.00	-	-

4.2.3. The flea infestations of *M. agrestis*

During the twelve monthly samplings of Trapping Period
B only ninety-five captures of the field-vole, *M. agrestis*,
were made. A total of 680 fleas were taken from the captur-
ed animals, comprised of specimens of ten different species.
Undue emphasis should not be placed upon results where the
number of individuals captured was quite small. However,
the data was interesting in some respects. It offered a
comparative viewpoint as to the differences in the composi-
tion of the flea fauna of the rodent species and, to a
degree, completed the overall study of all three rodent
species inhabiting the study area.

The level of infestation with fleas was very high
among the voles. During the study the average number of
fleas on each captured vole was more than seven. Fig. 2.20
shows the average number of fleas on each *Microtus* captured
for the eleven samplings in which voles were detected on
the grid (no captures in sampling 3). The number of captu-
res for some of the samplings was very small, only samplings
one, two, six, eleven and twelve gave significant numbers
of field-voles. The average of eleven to fourteen fleas
per capture was very high and it is interesting that it
came at a time when there appeared to be a sudden increase
in the numbers of voles present after a period of very low
field-vole density. These results cannot be directly
compared with the levels of infestation in *A. sylvaticus*
and *C. glareolus* for two main reasons. Firstly, a great
majority of the captures of *M. agrestis* were made during

Fig. 2.20 The flea index of M.agrestis

Trapping B. (1972/3)

no captures in sampling 3.

Months & Samplings

Total flea index
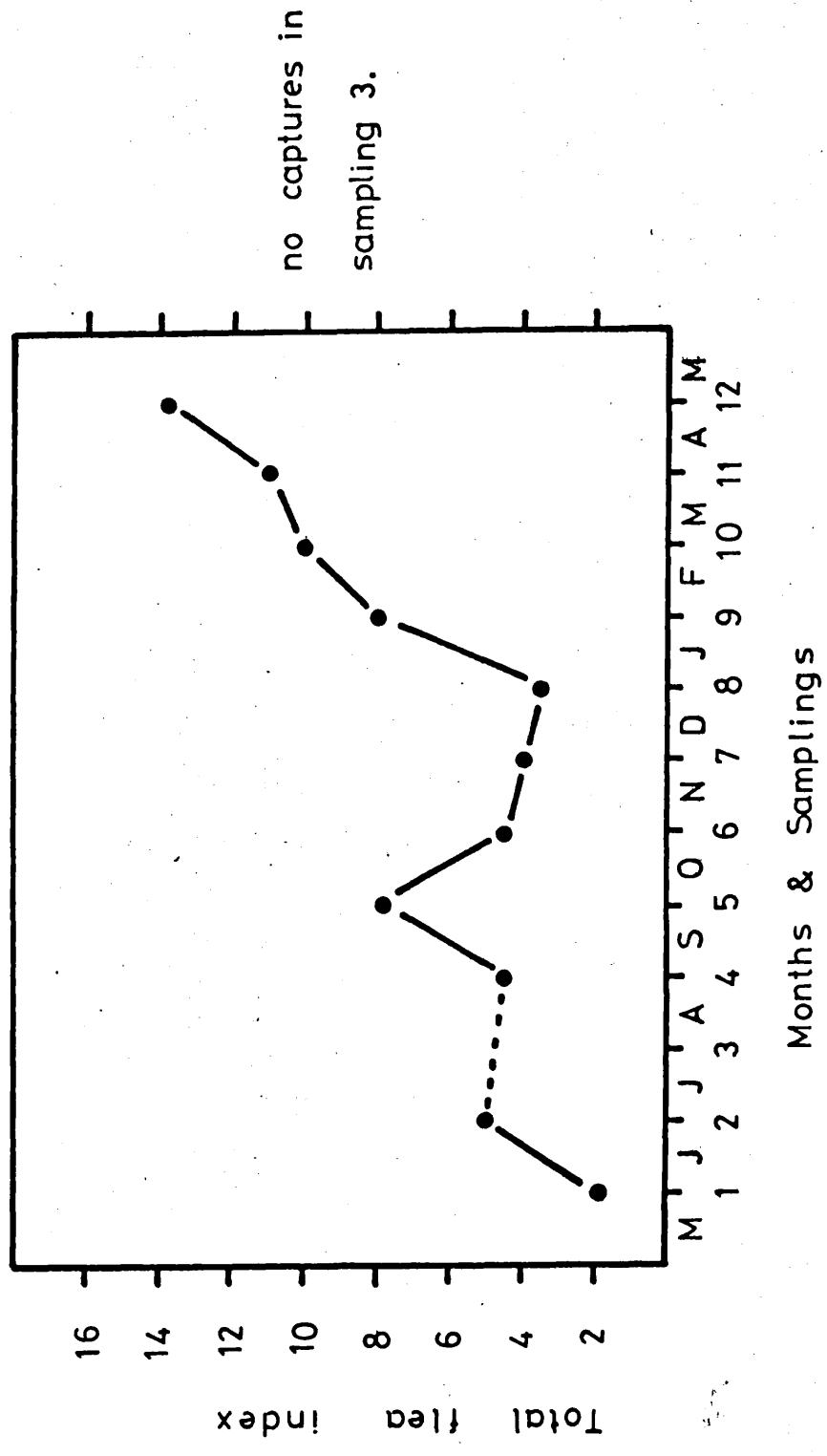
the pre-breeding season and, as has been already shown, this was the period of peak infestation in all species. Secondly, the sampling of a majority of the field-vole captures took place during a time of marked population increase. The grid population density of the species was very low during the first ten samplings, despite the fact that environmental conditions were quite favourable and large numbers of voles had been detected in the area two years previously. A sudden increase in animals was observed in spring 1973 possibly due to breeding or migration or both. This influx would have resulted in old nests and runways being re-opened and much exploration. Large numbers of dormant fleas would have been stimulated to emerge from abandoned nests.

Certain changes took place in the contribution that the various flea species made to the total infestation during the year. Once more, small sample size limits the validity of the results although some general trends were evident. *C. nobilis* and *P. silvatica spectabilis* were the primary species parasitising field voles and they shared the position as most abundant species in the flea fauna. *C. nobilis* tended to predominate in summer whereas, in autumn and winter *P. silvatica spectabilis* tended to be the most abundant species. *M. walkeri,* which has *M. agrestis* as its primary host, reached significant numbers during spring and early summer. The other "vole-fleas", *M. turbidus, R. pentacantha* and *M. penicilliger mustelae,* did not contribute significantly to the *Microtus* flea fauna at any stage during the year. Table 2.12. summarises the percentages of the different flea species on the monthly field-

Table 2.12.

The percentages of different flea species in monthly samples of *M. agrestis*. Trapping Period B. (actual numbers in parentheses)

FLEA SPECIES	M/J	J/J	J/A	A/S	S/O	O/N	N/D	D/J	J/F	F/M	M/A	A/M	TOTALS
C. nobilis	60.98 (25)	45.00 (18)	-	100.00 (9)	10.91 (6)	20.75 (11)	50.00 (2)	57.14 (8)	78.13 (25)	10.00 (1)	73.25 (178)	81.56 (146)	63.09 (429)
P. silvatica spectabilis	7.32 (3)	35.00 (14)	-	-	89.09 (49)	73.58 (39)	50.00 (2)	28.57 (4)	9.38 (3)	90.00 (9)	5.35 (13)	-	20.00 (136)
M. walkeri	31.71 (13)	12.50 (5)	-	-	-	5.56 (3)	-	-	-	-	11.52 (28)	5.59 (10)	8.68 (59)
M. turbidus	-	7.50 (3)	-	-	-	-	-	-	3.13 (1)	-	1.23 (3)	6.70 (12)	2.79 (19)
M. penicilliger mustelae	-	-	-	-	-	-	-	7.14 (1)	-	-	4.12 (10)	1.12 (2)	1.91 (13)
R. pentacantha	-	-	-	-	-	-	-	7.14 (1)	6.26 (2)	-	1.23 (3)	2.23 (4)	1.47 (10)
H.t. talpae	-	-	-	-	-	-	-	-	3.13 (1)	-	1.65 (4)	2.23 (4)	1.32 (9)
D.d. dasycnema	-	-	-	-	-	-	-	-	-	-	1.23 (3)	-	0.44 (3)
P.s. soriscis	-	-	-	-	-	-	-	-	-	-	0.41 (1)	-	0.15 (1)
N. fasciatus	-	-	-	-	-	-	-	-	-	-	-	0.56 (1)	0.15 (1)
TOTALS	41	40	0	9	55	53	4	14	32	10	243	179	680

vole samples.

Only five of the flea species, that were taken from the voles, occurred in numbers large enough to allow analysis of the sex ratio. Table 2.13. shows that only *C. nobilis* varied significantly from a one to one sex ratio (χ^2 = 8.11, p<0.01). The sex ratio of *C. nobilis* on *M. agrestis* did not vary significantly from the sex ratio of that flea species on *A. sylvaticus* (χ^2 = 0.35, p<0.05) or on *C. glareolus* (χ^2 = 1.51, p<0.05).

Table 2.13.

The sex ratios of fleas from *M. agrestis* with the results of Chi-square analysis for significant variation from a one to one sex ratio.

Trapping B (1972/3)

| FLEA SPECIES	No. OF FLEAS		TOTAL No. OF FLEAS	% MALE	X^2	P
	♀	♂				
C. nobilis	244	185	429	43.12	8.11	<0.01
M. walkeri	31	25	56	44.64	0.64	>0.05
M. turbidus	16	3	19	15.79	-	-
P. silvatica spectabilis	71	65	136	47.79	0.26	>0.05
M. penicilliger mustelae	8	5	13	38.46	0.69	>0.05
R. pentacantha	5	5	10	50.00	0.00	>0.05
H.t. talpae	7	2	9	22.22	-	-
D.d. dasycnema	1	2	3	66.67	-	-
P.s. soriscis	1	0	1	0	-	-
N. fasciatus	0	1	1	100.00	-	-

4.3. The *L. testaceus* populations

During Trapping Period B a total of 292 specimens of the beetle *L. testaceus* were removed from the small mammal captures. Table 2.14. summarises the rodent capture results and indicates the numbers of beetles recovered from the various host species and sex categories.

The comparatively large numbers of rodents and insects obtained in the study allowed statistical analysis of gross samples to be undertaken and, in certain cases, sub-sample analysis was possible.

The Chi-square test was applied for comparison of infestations of the different host categories. The extremely large proportion of animals with one or no beetles (94.37% in *A. sylvaticus*) meant that analytical methods taking into account the frequency distributions of the data were not worthwhile. Furthermore, the clear-cut differences between the gross samples meant that the method was sufficiently fine for the data under comparison.

The host preferences of the beetle were suggested by comparison of the levels of infestation of captures of the three different host species. Table 2.15. summarises the analysis of the results. Values of χ^2 are tabulated for the compared results from pairs of host species, obtained by 2 x 2 contingency tests. From the table it is clear that the wood-mice harboured many more beetles than the vole species. This suggests a marked host preference for *A. sylvaticus*. There was no significant difference in the level of infestation of *C. glareolus* and *M. agrestis* with

Table 2.14.

The numbers of male and female rodent captures and
individuals of *L. testaceus* taken from them (1972/3)

HOST SPECIES	HOST SEX	HOST CAPTURES	No. OF BEETLES
Apodemus	♂	436	124
sylvaticus	♀	526	151
(wood-mouse)	BOTH	962	275
Clethrionomys	♂	174	6
glareolus	♀	61	5
(bank-vole)	BOTH	235	11
Microtus	♂	56	4
agrestis	♀	39	2
(field-vole)	BOTH	95	6

Table 2.15 Statistical comparison of
the infestation of rodents with
L. testaceus. Trapping B. (1972/3)

			M.agrestis		A.sylvaticus	
			95 caps	6 beetles	962 caps	275 beetles
C.glareolus	11 beetles		$\chi^2 = 0.33$		$\chi^2 = 41.49$	
	235 caps		$0.50 > p > 0.80$		$p < 0.001$	
A.sylvaticus	275 beetles		$\chi^2 = 12.93$			
	962 caps		$p < 0.001$			

L. testaceus.

Only the samples from *A. sylvaticus* and *C. glareolus* were large enough to allow statistical comparison of the numbers of beetles infesting male and female hosts, within a species. In both cases the level of infestation of male and female animals was similar ($X^2 = 0.005$, $0.90 > p > 0.95$ for *A. sylvaticus*; $X^2 = 2.03$, $0.10 > p > 0.20$ for *C. glareolus*).

The sample of *L. testaceus* from wood-mice was large enough to allow investigation of the annual variations in abundance of the beetle. The beetle index on captures of *A. sylvaticus*, on a monthly basis for Trapping B, is given in Fig. 2.21. . Two periods of comparatively high infestation were observed during the late spring of both years in which sampling took place.

Throughout the year the infestation of *A. sylvaticus* with *L. testaceus* was quite light when compared with the levels of infestation of the flea species. Fig. 2.22. shows the frequency distribution of captures with various numbers of beetles. Most animals harboured one or no beetles and animals with more than two beetles were very rare.

Fig. 2. 23. shows that the beetle index and the percentage of *A. sylvaticus* infested were highly significantly positively correlated. When plotted on a logarithmic scale the relationship was close to a straight line. From

Fig. 2.21 The level of infestation of captures of _A.sylvaticus_ with _L.testaceus_. Trapping B. (1972/3).
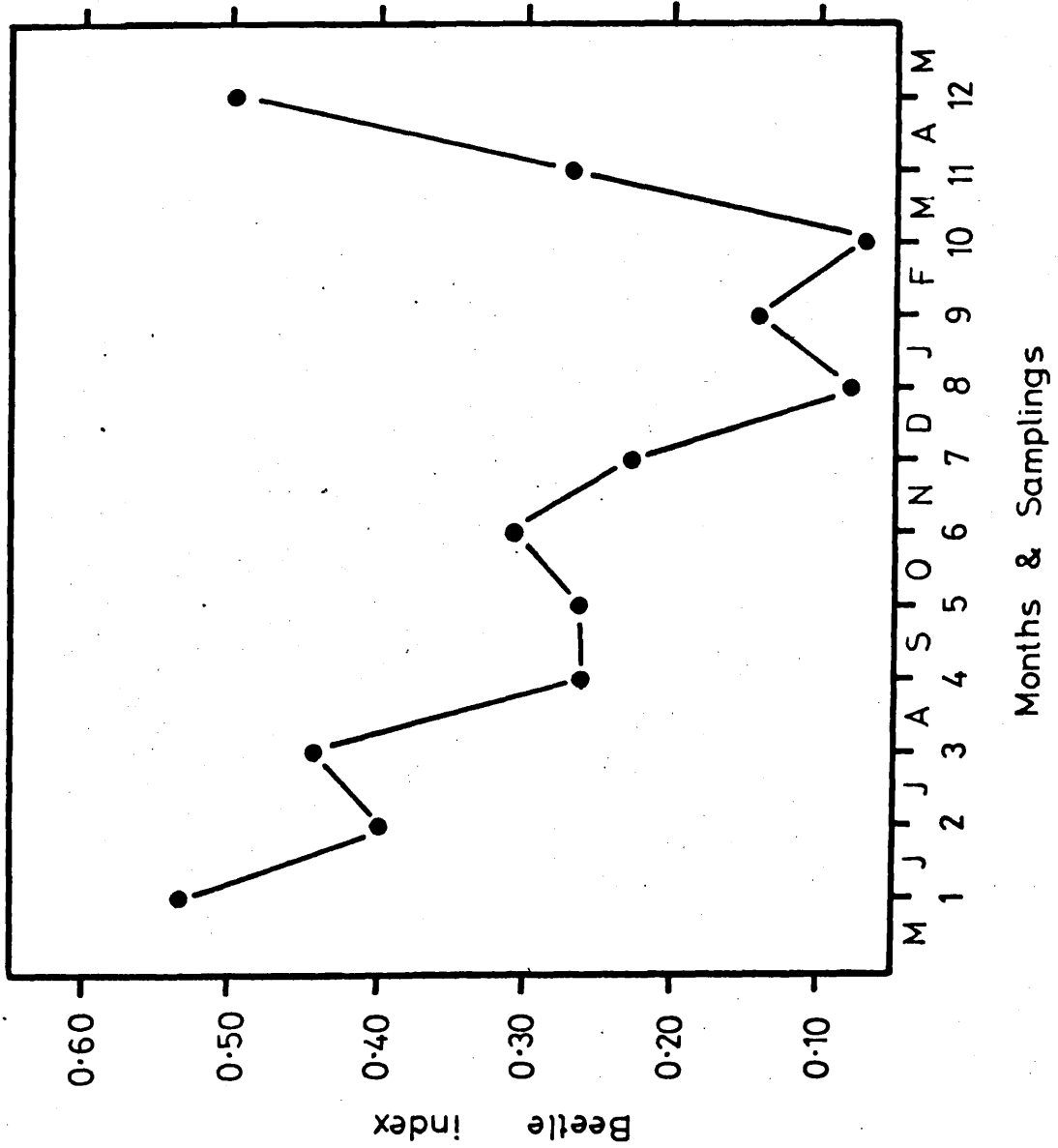
Fig. 2.22 Frequency distribution histogram of <u>L.testaceus</u> on captures of <u>A.sylvaticus</u>.Trapping B.(1972/3)
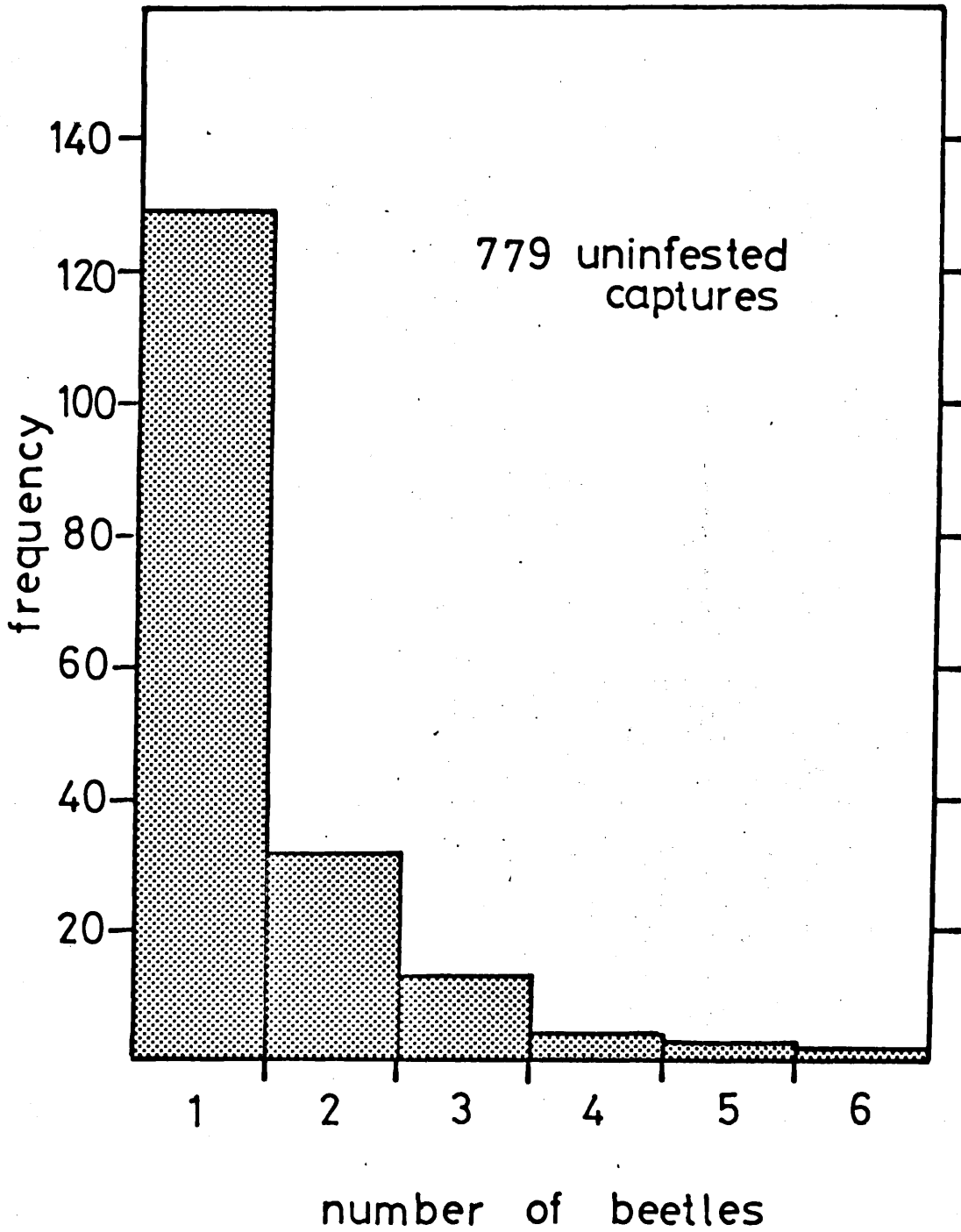
this relationship it may be noted that at low indices relatively few mice harbour all the beetles whereas, at higher indices, comparatively more mice carry the insects. This occurrence is similar to the relationship between index and infestation in fleas and shows an interesting parallel.

Fig. 223 Correlation of _L. testaceus_ index and % infestation of _A. sylvaticus_. Trapping B. (1972/3)

r = 0·95
p < 0·001
for y on x :-
y = 1·00x + 1·89

Log. _L.testaceus_ index

Log. % _A.sylvaticus_ infested
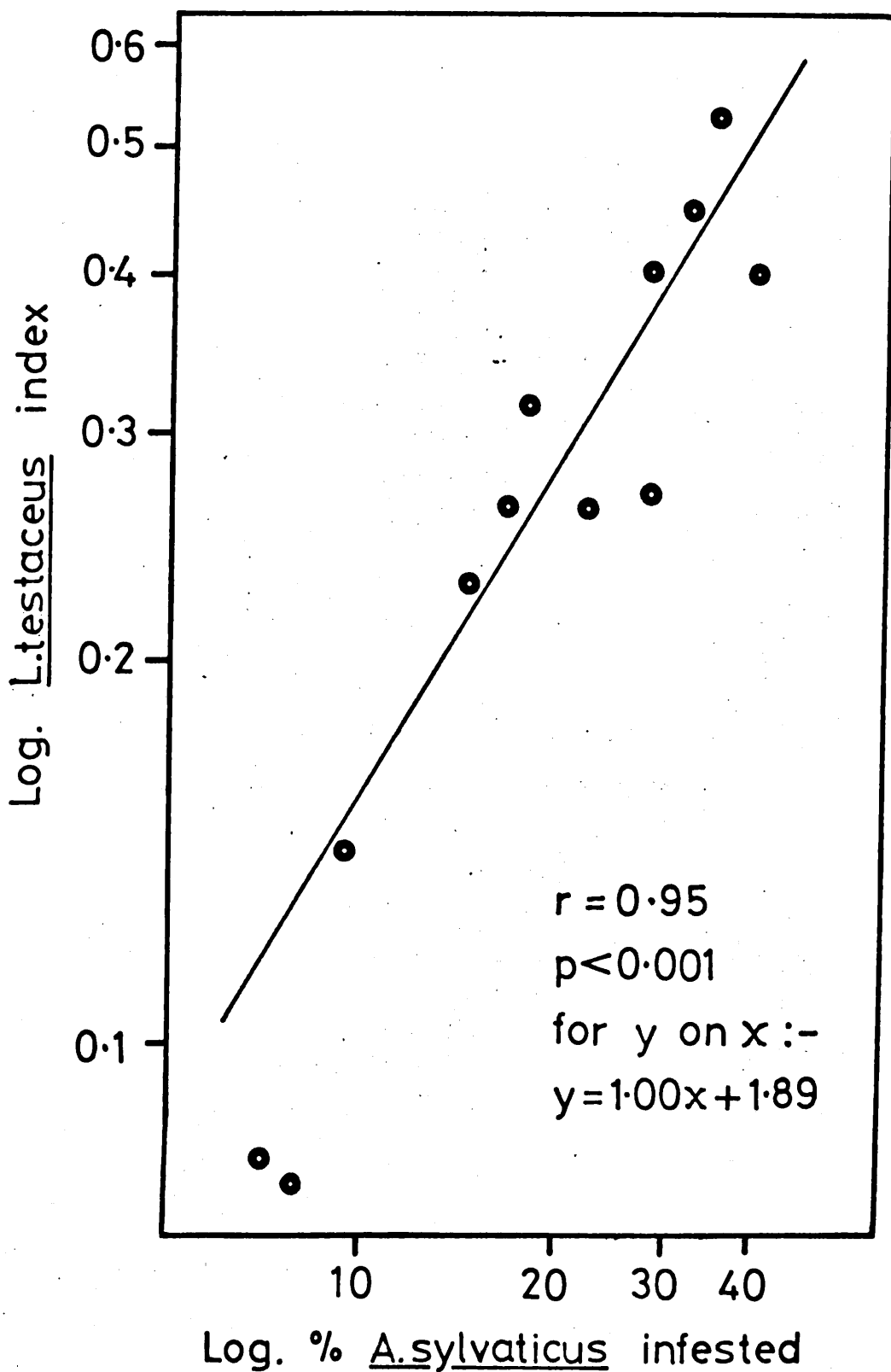
5. Discussion

5.1. Techniques

Observed changes in the level of infestation of epi-
fauna on host animals may be brought about by both natural
and artificial phenomena. Methods of trapping and handling
of mammals have a marked effect of the degree of accuracy
with which infestations are collected. It has been obser-
ved (Ulmanen and Myllymäki, 1971) that the numbers of fleas
recorded on hosts (and, therefore, certain other members of
the epifauna) are probably always underestimates. This
observation is, almost certainly, true for most studies of
ectoparasitic arthropods of mammalian species. Only in
investigations such as those of Buxton (1936-1941) and Beer
and Cook (1968), where hosts were shaved or skinned and the
hair dissolved to leave only the chitinous bodies of the
parasites, can complete accuracy be assured.

Where the average number of parasites per host capture
is low, as is the case in most flea studies of small
mammals, it is self-evident that discrepancies, introduced
by technique deficiencies, may become quite important in
their effect on the observed infestation index. Live-
trapped animals undoubtedly, give more reliable results
than those that have been snap-trapped (Cole and Keopke,
1947; Gross and Bonnet, 1949; Brinck, 1966; Ulmanen and
Myllymäki, 1971). However, Stark and Kinney (1962) have
observed large scale emigration of fleas from disturbed
hosts. This disturbance may occur during capture and
subsequent handling even when animals are live trapped and

it is important to note that some escape of fleas is possible, from live traps of the "Longworth" design, through quite large gaps between the nest-box and tunnel sections. In the present study egress of fleas was limited to the actual door opening, which, in most traps was quite tight fitting, and the various small apertures which were necessary for correct functioning of the mechanism. The major openings between the nest and tunnel sections were sealed by means of a polythene bag which was introduced during trap setting. Thus, losses of fleas, after capture of the host, were reduced.

Ulmanen and Myllymäki (1971) have shown that the number of fleas taken from captured *M. agrestis* may vary depending on the means of removal from the host's pelage. They showed that spraying with pyrethrum and examination of live hosts was only 79% effective when compared with a method where host animals were killed and then searched for fleas. Short-term anaesthesia, as used in the present study, results in a high degree of accuracy when collecting fleas from the host's body, and is similar in efficiency to methods utilising sacrifice of the host animal.

The observed flea indices for some of the more recent studies of ectoparasites of *A. sylvaticus, C. glareolus* and *M. agrestis* are summarised in Table 2.16. It is evident from the table that, in all three host species, the highest levels of flea infestation were observed in the present study. It should be noted, however, that variations in age structure of host populations; differences in habitat and trapping season; naturally occurring fluctuations in the actual levels of infestation and geographical position

Table 2.16.

A comparison of the flea indices and techniques of the

present study and some previous investigations.

_____

all animals live trapped unless stated.

* figures in parentheses represent number of hosts

captured.

Table 2.16.

HOST	AUTHORITY	INDEX*	FLEA SPECIES	METHOD OF DEFLEAING	STUDY SEASON	LOCALITY
A. sylvaticus	Evans & Freeman (1950)	0.890(730)	all species	"blowing"	all year	Oxford, England
	George & Corbet (1959)	0.880(124)	"	dead animals searched (snap trapped)	"	Scotland
	PRESENT STUDY	1.913(962)	"	anaesthetisation	"	Egham, S. England
C. glareolus	Evans & Freeman (1950)	1.710(325)	all species	"blowing"	all year	Oxford, England
	George & Corbet (1959)	1.470(232)	"	dead animals searched (snap trapped)	"	Scotland
	PRESENT STUDY	3.017(235)	"	anaesthetisation	"	Egham, S. England
M. agrestis	George & Corbet (1959)	1.610(512)	all species	dead animals searched (snap trapped)	all year	Scotland
	Varma & Page (1966)	2.200(110)	"	anaesthetisation	"	Scotland
	Cowx (1967)	1.830(513)	"	not specified	"	Keighley, N. England
	Cotton (1970)	1.310(1655)	C. nobilis only	"blowing"	"	Oxford, England
	Ulmanen & Myllymäki(1971)	4.200(501)	all species	dead animals searched	"	S. Finland
	PRESENT STUDY	7.158(95)	"	anaesthetisation	"	Egham, S. England

may have been, wholly or in part, responsible for the observed differences between the results of this and the preceeding studies. Nevertheless, it is suggested that the methods used in this work are the most effective so far described for the continual monitoring of infestation levels of the epifauna of small mammals.

5.2. The Mammals

The annual cycle of small mammal populations is a continuous process and, strictly speaking, no two days within a cycle are totally similar. However, during certain periods of the cycle it is possible to make some general statements concerning the behavioural state of the members of the community and the effects of that behaviour on their epifauna. Thus, the rodent's annual cycle may be divided into the following three broad periods of approximately similar duration:-

(i) Overwintering

In the present study the onset of the overwintering period was not well defined. During autumn young, sexually immature animals became an increasingly important section of the population (Fig. 2.6.). Finally, these animals, together with a portion of the population which had undergone breeding but with regressed sexual organs, contributed more than 56% of the population. At that point overwintering was said to have begun. During the subsequent three sampling periods the animals in the grid population were in an asexual, sub-adult condition. The population was remarkably stable with few animals disappearing and few immigrants (Fig. 2.5.).

(ii) Prebreeding

The transition into the prebreeding period was dramatic. In early March all the male animals captured were in breeding condition. However, the females remained as

sub-adults in the February/March sample and mature female animals did not appear in the population until the following month. These results are in agreement with the observations of Southern (1964). There was a sudden decrease in the number of animals trapped on the grid. The overwintering population was stable at about twenty to twenty-five animals. However, with the onset of pre-breeding the population was reduced by half. This occurrence has been observed by several authors (Miller, 1958; Kikkawa, 1964; Tanton, 1965).

(iii) Breeding

In the present study the onset of breeding was noted in late June, this was when juveniles began to enter the population. Gestation and weaning probably take about six weeks, and therefore, it may be argued that breeding had begun sometime prior to the appearance of juveniles in the trappable population. However, in the previous trapping (May/June) almost 50% of the females remained imperforate and it was clear that, taking the population as a whole, significant breeding did not begin until late June. Maximum numbers of animals were observed on the grid during August and September when breeding reached a peak. The breeding of all three rodent species has been reviewed by Southern (1964). He stated that, as in the present study, the breeding seasons of mice and vole species are approximately synchronous although variations may occur depending on weather conditions and food availability.

In the light of the detailed knowledge of the biology of the host species it is now possible to discuss the observations reported in previous sections with respect to the epifauna of the host animals.

5.3. The Fleas

During these investigations a total of twelve differ-
ent flea species were recovered from the small mammal
hosts. As in preceeding studies of small mammal fleas in
this country only *C. nobilis* was captured in large numbers.
This flea species represented almost 78% of the total
number of fleas taken (2596 out of 3329). Thus, it is only
possible to discuss, in detail, the relationships of this
species and its hosts. Other authors have overcome this
difficulty by pooling the data for all flea species (e.g.
Ulmanen and Myllymäki, 1971). However, the variable biology
of the different species makes this advisable only where
the total flea infestation is to be discussed as a whole.
In the present study data has been presented, almost
exclusively, for *C. nobilis*; only where pooling of all flea
data is applicable or desirable for comparative purposes
has this been done. It seems unlikely that any field
study will be so extensive as to allow detailed investig-
ations of any of the other species. This is certainly the
case for *A. sylvaticus*, where the populations of other flea
species are very small.

(i) Flea_Index_and_Percentage Infestation Phenomena

The very close relationships between the *C. nobilis*
index and the proportion of infested *A. sylvaticus* within
the population has been shown in Fig. 2.13.   This occur-
rence has been observed by Olson (1969) for infestations of
X. cheopis on *R. rattus* and by Ulmanen and Myllymäki (1971)
for the pooled flea infestations of *M. agrestis*.

Extrapolation of the plots led to those authors to predict
flea indices of 6.8 and 8.0, for *R. rattus* and *M. agrestis*
respectively at 100% infestation of the rodent population.
These figures are in good agreement with the predicted
100% infestation index of 4.5 for the smaller and less
heavily infested *A. sylvaticus* (Fig. 2.14). Olson (1969)
demonstrated that at an index of below 0.05 the relation-
ship is complex with fleas concentrated on fewer hosts
than might be expected. Such extremely low indices were
not encountered in the present study.

It is apparent that peaks of the infestation percent-
age lagged behind peaks of the index. This might be
expected if, as has been suggested, certain hosts or their
nest sites were more attractive to the fleas than others.
The infestation would build up on these animals, probably
due to a higher reproductive rate in nests with favourable
micro-environment. The index, merely the total number of
fleas captured divided by the number of host captures
would not detect this. Dispersal of fleas, when conditions
were favourable; would lead to increase in percentage
infestation although the index might remain constant or
even fall. During unfavourable conditions the index and
infestation percentage fell in synchrony.

Ulmanen and Myllymäki (1971) have stated that numerous
causes apparently contribute to observed differences in the
level of infestation of small mammals with fleas. However,
the annual variations in the *C. nobilis* index on the wood-
mouse population, as a whole, may be better understood
with reference to the actual numbers of hosts observed to

Fig. 2.24 Correlation between monthly indices of C.nobilis on A.sylvaticus and size of grid host population.

r = - 0·79
p < 0·01
for y on x :-
y = 38·37 - 6·88x
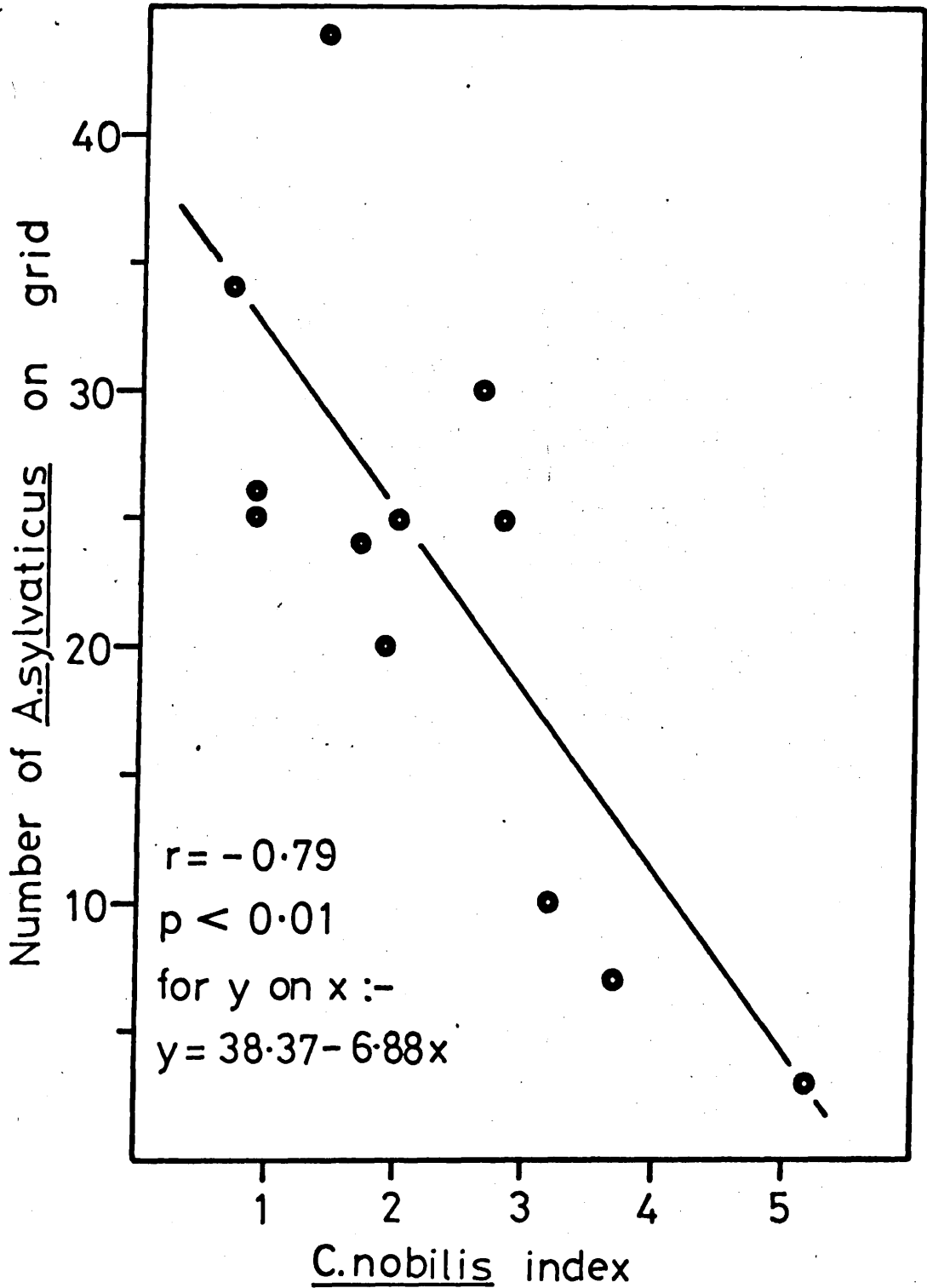
be present on the grid. There was very significant negative
correlation between the *C. nobilis* index and the detected
numbers of wood-mice present in the study area (Fig. 2. 24).
It may be postulated that these two parameters, although
correlated, are governed by other, common factors. However,
Cotton (1970) has suggested that, on *M. agrestis, C. nobilis*
breeds throughout the year, the constantly high nest temp-
eratures affording a degree of insulation from the low
winter temperatures which would otherwise curtail reprod-
uction. Small mammals do not have this advantage and some
die-off occurs while flea numbers are partially maintained
by winter breeding. Thus, at times of low host population
density, the fleas become "concentrated" on the remaining
hosts. During the dramatic reproductive peak of the hosts
the fleas do not keep pace with the rise in host numbers,
they become "diluted" among the large number of potential
hosts. This, at first sight, seems a failure in the
ability of fleas to take advantage of the host's annual
cycle of abundance. However, survival is poor amongst the
host animals during population peaks (Brown, 1966) and it
may be that the expenditure of "resources" in infesting
hosts at that time is not worthwhile. Eskey (1930) showed
infestations of *R. rattus* with *X. cheopis* to be dependant
on the numbers of hosts within the study area.

(ii) The Flea Indices During the Periods of the Hosts'
Annual Cycle.

The *C. nobilis* infestations of *A. sylvaticus* and *C.*
glareolus were statistically analysed with respect to the
three major periods of the hosts' annual cycle. In both

species infestation reached a peak during the pre-breeding
period. Thus, the highest indices were obtained during
times of very low host population density. Janion (1962)
obtained similar results for the flea infestations of *A.*
agrarius, A. flavicollis and *C. glareolus*. The "concentration"
of fleas on hosts, at that time, has been discussed.
However, there are other important factors which must be
considered when attempting to explain the infestation peaks.
During the previous autumn, and throughout the whole of the
breeding season, large numbers of "breeding" nests were
left abandoned. These neglected nests would contain numbers
of coccooned imagines which were the results of flea breed-
ing during the nests' brief occupation. Development of
fleas is very slow in these nests due to the low temperatures
and the coccooned imagines lay dormant until stimulated to
emerge. Cotton (1970) has suggested that disturbance due
to the activity of the small mammal or sudden temperature
rises cause emergence and the subsequent infestation of
hosts results in the very high spring flea indices. This
is probably true for *A. sylvaticus* and *C. glareolus* as well
as for *M. agrestis*. Similarly, during late winter and early
spring, a decline in the density of the small mammal
community results in the abandonment of many "permanent"
nests. Fleas from these nests would play a further part in
increasing the infestations of the hosts during pre-breeding.

In the pre-breeding period animals show a marked
increase in activity. Home range sizes increase because
of the very low level of interaction between individuals at
a time of low rodent density. Miller (1958) has demonstr-
ated that the home ranges of *A. sylvaticus* during March to

May, precisely the period of maximum flea indices, were
four times as large as the September to November ranges,
the period of lowest infestation. Brown (1966) stated
that animals often wander quite long distances in search
of a mate. Thus, during pre-breeding there exists a large
population of fleas "free" in the environment and certain
of the hosts behavioural mechanisms bring about the neces-
sary contact between the parasites and the host animals
which will found the new small mammal populations for the
coming year.

The *C. nobilis* index on *A. sylvaticus* during breeding
was significantly lower than the pre-breeding index. It
is interesting to compare this result with the corresponding
data for *C. glareolus* where no decline was apparent. Indeed,
when compared, individuals of *C. glareolus* were more heavily
infested than *A. sylvaticus* during breeding. It appears
that the heavy *C. nobilis* infestations of *A. sylvaticus*
during pre-breeding cannot be maintained at the same high
level when the host's breeding begins. A reduction in the
activity of hosts or a lowering in the number of "free"
fleas in the environment, or a combination of both, means
that recruitment into the adult flea population is depend-
ant on replacement, by breeding, in "permanent" or "breed-
ing" nests of the host. This replacement is more efficient
in *C. glareolus* where summer flea populations are maint-
ained at their pre-breeding levels. Smit (1957) suggested
that *C. nobilis*, as well as its closely related continental
counterpart *C. agyrtes* Heller 1896, were originally paras-
ites of *Apodemus* or its ancestors. However, in the present

study the results indicated that breeding may have been more successful on *C. glareolus*. Extensive, controlled laboratory experiments would be required in order to confirm this view.

At the peak of breeding large numbers of juvenile host animals are recruited into the population. Before weaning fleas have access to the young through the mother of the litter but these animals are very lightly infested when they enter the population and result in a "dilution" of the fleas and, hence, a lowering of the index.

At the onset of overwintering the index of *C. nobilis* on both *A. sylvaticus* and *C. glareolus* reached their lowest levels. As the community settled down for overwintering the highly stable populations gave the fleas a good opportunity for breeding throughout the winter because the rodents' bodies maintain, for long periods, the high nest temperatures that are required for speedy development. Flowerdew (1973) has shown that a specimen of *M. agrestis* spent only about one and a quarter hours out of its nest in the seven hours from midnight to 07.00 hours. In such cases nest temperatures would remain quite high for long periods of time. Thus, well before the end of the overwintering period, the *C. nobilis* index on both host animals began to rise.

When the results of overwintering was taken as a whole the indices of *A. sylvaticus* and *C. glareolus* were significantly lower than both the pre-breeding and breeding indices. However, the bank-vole was observed to maintain a significantly higher overwintering infestation than *A. sylvaticus*.

The observations added further evidence to the theory that
C. nobilis may breed more readily on the bank-vole.

(iii) The Flea Indices of the Host Sex and Age
Categories.

Only the results from *A. sylvaticus* were sufficiently
comprehensive to allow analysis of the infestation data on
the different host age and sex classes with respect to the
three stages of the hosts' reproductive cycle. Evans and
Freeman (1950), the only previous workers who have presented
comprehensive data on the flea infestations of *A. sylvaticus*,
did not analyse their results with respect to host sex and
age categories. Ulmanen and Myllymäki (1971) reviewed the
literature on the subject but, of the authors that they
mentioned, only George and Corbet (1959) include results
from *A. sylvaticus* and some doubt exists as to the validity
of their results due to the quite small numbers of *A.
sylvaticus* that were taken and the fact that snap traps were
used in sampling the populations.

In the present study males were very significantly
more heavily infested than females during the pre-breeding
period. Many authors have observed higher levels of infest-
ation in male small mammals and various explanations have
been put forward. Buxton (1948) mentioned that it was
probable that a mammalian sex hormone is necessary for full
reproductive development of fleas. This is most certainly
true for the rabbit flea, *S.c. cuniculi*. However, the high
infestation rate of small mammals could only be explained
if the hormone required was an androgen. In rabbit fleas

an oestrogen is required. Rothschild, Ford and Hughes
(1970) failed to show any effect of mammalian hormones on
male *X. cheopis*. Differences in size between male and female
A. sylvaticus (Figs. 2.3. and 2.4.) were too small to be the
only explanation, although the possible effects of weight,
used as a measurement of size, have been discussed by
several authors (Yeh and Davis, 1950; Mohr, 1961; Phillips,
1966). Smit (1962), Brinck-Lindroth (1968) and Ulmanen
and Myllymäki (1971) have suggested that differences in
activity may account for the higher infestations of males
and there can be little doubt that such differences in
activity exist.

During the breeding period the observed differences
in the levels of *C. nobilis* infestation of male and female
A. sylvaticus were much less marked. Indeed, when the indices
were compared the difference was below the level required
for 5% significance ($d = 1.42$). These similar levels of
infestation are difficult to explain considering the
different behavioural characteristics of breeding male and
female animals. However, there are two main reasons for
similarity of any two infestations of sympatric animals:-
(i) Intense interchange of fleas may result in an almost
common flea population among the two host categories.
This would result in similar levels of infestation.
(ii) A variety of factors may affect the male and female
indices, quite separately, although resulting in a
superficial similarity.

George and Corbet (1959) attempted to explain the higher infestation of adult voles by considering that adult animals live in old nests with established, breeding flea faunas, while juveniles occupy recently made nests with a small flea fauna which has not yet begun to reproduce itself. These observations are, almost certainly, valid and would explain the highly significant difference between the flea infestations of adult *A. sylvaticus* and juveniles during breeding. However, differences in activity may also contribute to the observed variations in the adult and juvenile infestation levels. Brown (1966) has shown that immature animals have very small home ranges soon after weaning or are driven away by dominant animals, in which case they would become members of the migrant population.

Both structurally and behaviourally juvenile male and female animals are quite similar and the observed similarities in the infestation of these host classes is to be expected, this has been shown to be the case for the flea infestations of *M. agrestis* by Ulmanen and Myllymäki (1971).

Smit (1962), Brink-Lindroth (1968) and Ulmanen and Myllymäki (1971) have observed a decreasing difference in the infestation index of male and female animals during late autumn and winter. The latter authors attribute this change to the occurrence of sub-adults in the overwintering population. In the present study the *C. nobilis* infestation indices of male and female *A. sylvaticus* were almost identical. The undeveloped or regressed sexual organs of overwintering animals result in a reduction in the social strife within the small mammal population (Brown, 1966).

As in the case of the breeding population similarities in flea indices may be attributed to external factors operating on the male and female sections of the small mammal community or to a close physical association between individuals resulting in an almost common flea infestation.

Further study to investigate the occurrence of similarity of the levels of *C. nobilis* infestation of male and female *A. sylvaticus* during the breeding and overwintering period of the host annual cycle is reported in Chapter 3.

(vi) The Species Composition of the Flea Infestations

Table 2.17 summarises the total percentages of the various flea species over the whole year from the small mammal infestations. It indicates the primary or prefered host animals together with the most frequent accidental or secondary hosts taken from papers by Smit (1957, 1957a). It can be seen that the results were in quite close agreement with current opinions upon the host preferences and host specificity of the flea species. Comparison of the importance of different flea species as components of the infestations of sympatric small mammal species are very rare in the literature.

Several interesting individual points arose from the data. Smit (1957a) stated that *M. turbidus* is a parasite of all of the three host species that were present. At Alderhurst *M. turbidus* appeared to show a preference for *C. glareolus*. Similarly *M.p. mustelae* prefered the bank-vole although it has been thought to be a flea species with no particular host preferences between the two vole species.

Table 2.17

The occurrence and host preferences of the flea species captured

FLEA SPECIES	Percentage of total infestation			Preferred Host*	Accidental Hosts*
	A. sylvaticus	C. glareolus	M. agrestis		
C. nobilis	92.23	66.29	63.09	A. sylvaticus ?	Microtinae
P.s. spectabilis	1.14	9.31	20.00	C.glareolus; M.agrestis	A. sylvaticus
M. turbidus	4.62	9.45	2.79	C.glareolus; A.sylvaticus M.agrestis.	-
M. walkeri	0.11	0.28	8.68	C.glareolus; M.agrestis	A. sylvaticus
M.p. mustelae	0.33	7.76	1.91	"	"
R. pentacantha	0.49	1.83	1.47	C.glareolus; A.sylvaticus M.agrestis.	-
N. fasciatus	0.60	-	0.15	R. rattus	voles and mice
T. poppei	-	0.14	-	A. sylvaticus	M. agrestis
P.s. soriscis	-	0.14	0.15	shrews	voles and mice
D.d. dasycnema	0.11	-	0.44	"	"
O.h. howardi	0.05	-	-	Sciurus carolirensis	A.sylvaticus; C.glareolus.
H.t. talpae	0.33	0.56	1.32	C.glareolus; A.sylvaticus M. agrestis.	-

* from Smit (1957,1957a)

M. walkeri and *P.s. spectabilis* have been stated to have both
the field-vole and the bank-vole as preferred hosts.
However, these fleas were more important contributors to
the epifauna of *M. agrestis* than *C. glareolus*. *T. poppei*, a
monoxenous flea of the wood-mouse, was completely absent
from its preferred host but a single specimen was taken
from a bank-vole. The specimen may have been imported
from another small mammal population.

The appearance of *N. fasciatus* corresponded to the
influx of a small colony of *R. rattus*. There was no
evidence of successful colonisation of the indigenous small
mammals although some limited breeding success may have been
achieved as indicated by the sudden appearance of eleven
specimens of the flea on a small group of *A. sylvaticus* some
time after the destruction of the rat colony. However,
this observation may have been due to the wood-mice opening
and exploring deserted rat burrows and nest-sites.

(v) The Sex Ratios of the Flea Infestations

Table 2.1. summarises some recent estimations of the
sex ratios of flea species infesting small mammals. The
results of this study concerning *C. nobilis* are quite
similar to those of previous investigations. However, work-
ers have tended to pool sex ratio data from the various
host species (e.g. Evans and Freeman, 1950; George and
Corbet, 1959; Varma and Page, 1966). A separation of
results from the present study into individual host species
groupings has shown some interesting points.

When compared by means of 2 x 2 contingency tables the

sex ratio of male to female *C. nobilis,* on *A. sylvaticus,* was significantly different to the sex ratio of the fleas infesting *C. glareolus.* On wood-mice female fleas outnumbered males whereas no significant variation from a one to one sex ratio could be detected in the sample from *C. glareolus.* The infestation of *M. agrestis* was intermediate in this respect, there was a significant variation from a one to one ratio but the proportion of males to females did not significantly vary from either the wood-mouse or bank-vole samples.

Without knowledge of the primary sex ratio on emergence and the sex ratio within the population as a whole it is difficult to draw conclusions from sex ratio data.

It has been reported that the nests of voles have a higher relative humidity than nests of the wood-mouse although no absolute measurements have been produced. It is well recognised that high relative humidity increases reproductive success in many flea species. The high infestation rates of voles when compared to mice may, in part, be due to differences in nest humidity. Furthermore, the preference of *M. walkeri* for nests of high humidity has been noted by Smit (1957) and *C. glareolus* and *M. agrestis* are the primary hosts of that flea species.

Humidity may effect the actual sex ratios in a variety of ways. Excessive desiccation causes death of adult fleas and death is accelerated as humidity is reduced (Edney, 1945 for *X. cheopis* and *X. brasiliensis*). Male fleas, being much smaller than females and having a greater surface area to volume ratio, would tend to be more vulnerable to desiccation. Furthermore, Leeson(1936) showed that, when taken

from wild populations, male fleas die more quickly than females as a result of starvation. These factors may account for the larger numbers of male *C. nobilis* on voles. However, the observed sex ratio may not always indicate the actual sex ratio of the entire flea population and Buxton(1938) has shown that, under some circumstances, female *X. cheopis* show an increased affinity for the host. Nevertheless, Cotton(1970) was unable to detect a significant difference between the sex ratios of *C. nobilis* infesting the bodies of *M. agrestis* and those inhabiting the nests during a full year's sampling.

Evans and Freeman (1950) and Cotton (1970) were unable to demonstrate any correlation between sex ratio and the season of the year. However, in the present study the sex ratio of *C. nobilis* during the summer and autumn months was found to differ significantly from the ratio during winter and spring. In the winter/spring samples females were more abundant but during summer/autumn there was no significant difference between the numbers of males and females. Cotton (1970) felt that late winter and spring was the period of emergence of *C. nobilis* on *M. agrestis* and he observed that the sex ratio of fleas on emergence from laboratory cultures was 36% males. This figure is in close agreement with the observed sex ratio on *A. sylaticus* during Cotton's "period of emergence".

(vi) Flea_Infestations and the Activity_Areas_of the
Hosts

Mohr (1961), Mohr and Stumpf (1962, 1964 a and b) and
Phillips (1966) have discussed the relationship between
host home-range size and the ectoparasite load in small
mammals. They have shown that, in general, animals with
larger home ranges tend to carry more ectoparasites than
those with smaller ranges. In the present study this was
shown to be the case during breeding although the relation-
ship could not be demonstrated in the overwintering
population (Fig. 2. 18.).

It is very unlikely that the relationship between
ectoparasite burden and home range size is a simple one.
It is usual that larger animals become dominant and possess
large home ranges (Brown, 1966) and Mohr and Stumpf (1962)
have suggested that body size, or a function of it such as
surface area, may play an important part in the intensity
of pick-up. Furthermore, animals with home ranges that
are very large might be expected to be the older, more
mature animals. These animals would have well developed
nest populations of fleas which would also tend to increase
flea infestation. Thus, several factors may lie below the
superficial correlation between home range size and flea
index.

During overwintering the home range sizes of small
mammals tend to become less well defined and the actual
size tends to be reduced. This probably explains the
observed lack of correlation between activity area and flea
index during that period.

(vii) The Re-infestation of _A. sylvaticus_ with Fleas

Meyer (1938) has shown that rodents, from which the flea population has been removed, may regain many fleas in a very short time. Evans and Freeman (1950) found that uninfested animals regained as many fleas after only twenty-four hours as they did after one month, they further noted no marked decline in the number of fleas taken from animals which had been captured and had their fleas removed on four successive days. They commented, however, that if captures had been repeated over longer periods the number of fleas per capture might well have declined.

The work of these authors has suggested that the rodent's nest site is an almost unending source of fleas and the suggestion has been strengthened by the observation of Davis (1934) who recorded a maximum of ninety-two fleas in one of thirty-eight nests of _Microtus_. The over-all results of the present study indicate that this is not the case for _A. sylvaticus_. When animals were captured, and their total flea infestations removed, on three days during a sampling session their infestation on subsequent captures was significantly smaller. Thus, the removal of, on average, less than six fleas from each animal resulted in lowered infestations. Had the nest infestations been more than about twenty-five fleas such a decline in numbers could not have been detected. These results support the finding of Cotton (1970) who found very many fewer _C. nobilis_ in nests of _M. agrestis_ than did Davis (1934).

When the data was analysed with respect to the three major periods of the hosts' annual cycle only the results from the pre-breeding period showed a significant decrease

in the infestations of the fourth and subsequent captures.
Thus, the removal of the large numbers of fleas from the
body of animals has an important impact on the nest popul-
ation, which is reduced.   This observation gives an indic-
ation that the increase in observed flea numbers on animals
during pre-breeding is not backed-up by increased numbers
in the nest, and furthermore, pick-up from the environment
does not replace the lost fleas.   Thus, it would appear,
that a higher proportion of fleas may infest the body of
the animal during the yearly period of high activity and
movement that preceeds breeding.

(viii)   The Infestation of Migratory and Sedentary
A. sylvaticus

Janion (1960) has shown that the average number of
fleas on settled rodents is higher than on migrating indiv-
iduals.   However, during a period of "mass occurrence",
probably corresponding to a peak in the increase-peak-crash-
low long-term cycle, these differences did not exist
(Janion, 1962).   The author suggested that the generally
"unsettled" nature of the population had disrupted the
normal situation.

In the present study no significant difference was
found to exist between the levels of infestation of sedent-
ary and migratory A. sylvaticus.   The results from all flea
species were pooled in order to measure general "pick-up"
from the environment, which might be expected to include
fleas from other host species, as well as infestation from
nest-sites of the host.   However, when male and female
animals were considered separately it was observed that

while male animals conformed with the results of the popul-
ation as a whole female migrants carried fewer fleas than
residents.

It is probable that resident animals obtain many of
their fleas from mature nests while migrants are more
susceptible to accumulation of infestation from the general
environment. Where these two sources are of equal import-
ance the infestation will be similar among migrants and
residents. It would appear that migratory females are less
likely to pick up fleas than migratory males. This may be
due to behavioural differences in the host or it may be
due to parasite preferences.

5.4. The Beetles

Very little is known concerning the biology of the interesting beetle *Leptinus testaceus*. One of the most important points which remains unanswered is the nature of its relationship with the multitude of its postulated "hosts". Most investigations to date have been restricted to records of host species (Claassens and O'Rourke, 1964; Claassens, 1965; Maser and Hooven, 1971) and taxonomic morphological or distributional studies (Parks and Barnes, 1955; Fairley, 1963 and 1965; Jeannel, 1922).

A. sylvaticus has been shown to be a frequent host for *L. testaceus* in Britain and Ireland (Reid, 1942; Fairley, 1963 and 1965), although Elton, Ford and Baker (1931) noted its occurrence on the bank-vole, *C. glareolus*. However, eighteen bank voles collected in Ireland harboured no beetles (Claassens and O'Gorman, 1965). Claassens (1965) suggested that the woodmouse/beetle association may be accidental and that knowledge of its presence on other small mammals, such as voles, may help to clarify its ethology.

In the present study the occurrence of *L. testaceus* on the two vole species was rare. The high infestation rate of *A. sylvaticus* appears to indicate that the beetle has a definite preference for that small mammal species as host. It seems, therefore, at first sight, that in the community under investigation there are three rodent species of which one, *A. sylvaticus*, is the prefered host for the beetle and that accidental encounters of *M. agrestis* and *C. glareolus*

by the beetle, which occur with approximately equal regularity, account for their similar, lower levels of infestation. This explanation assumes that the beetles can distinguish between *A. sylvaticus* and the vole species.

Brown (1966) has shown that the home ranges of individuals of *A. sylvaticus* are much larger than those of *C. glareolus* and *M. agrestis*. These larger home ranges would subject *A. sylvaticus* to an increased probability of accumulating infestations of the beetle by chance encounters alone. Thus, the beetles would need to show no host selectivity. However, if home range size is the major factor affecting infestation level then male wood-mice might be expected to harbour more beetles than females as they have the larger home ranges (Miller, 1958; Kikkawa, 1964; Brown, 1966; Randolph, 1973). This was not found to be the case. It is possible that a combination of these two factors, the beetles preference for *A. sylvaticus* and the larger home ranges of these animals, result in the observed higher infestations in wood-mice.

Both Fairley (1963) and Claassens (1965) have sought to estimate infestation indices for *L. testaceus* on *A. sylvaticus*. In his study Fairley found that of 138 *A. sylvaticus* 15% of males and 4% of females were infested with *L. testaceus* and the average number of beetles was 1.2 for each infested male and 1.0 for infested females. He deduced, from this evidence, that beetles show a preference for male hosts. Claassens (1965) examined 109 wood-mice and observed that 12% of males and 13% of females carried the beetle. Male wood-mice, on average, carried one beetle and females two. The results of these two Irish authors

are conflicting, although it is possible that these repor-
ted "preferences" may not be statistically valid. During
the present study no significant differences in the
infestation of male and female *A. sylvaticus* or *C. glareolus*
were demonstrated.

Reid (1942) studied material collected earlier by
Elton, Ford and Baker (1931) and from the monthly distrib-
ution of the capture of ninety-three specimens of the beetle
he suggested that there may be three generations of *L.
testaceus* each year, having peaks of emergence in May,
September and December. Reid noted that more data would
be required to confirm his view. In the present study no
infestation peaks were discovered in September or December.
The majority of the beetles were collected during the late
spring and early summer months of April, May and June.
Reid (1942) observed that some larvae taken from the nest
of *A. sylvaticus* on April 23rd 1939 emerged as imagos on
May 12th, after a period of pupation. Emergence of beetles
in late spring and early summer would ensure that beetles
were able to take advantage of the large hosts home ranges
at that time, ensuring good dispersal. After dispersal
the late summer breeding period of the hosts would result
in large numbers of potential hosts. However, it is
important to exercise care when assuming that peaks of
observed infestation are equivalent to peaks of emergence.
It is possible that infestation peaks merely indicate
periods of increased affinity for the host. More observat-
ions of the emergence of imagos from pupae must be made
before emergence periodicity can be decided.

Having established that individuals of *A. sylvaticus*
are more heavily infested with beetles than the other
members of a mixed rodent community it is difficult to
suggest why this should be so. Ruschkamp (1922) has
suggested that *L. testaceus* feeds on mites and there is
little doubt that *A. sylvaticus* is often heavily infested
with those small acarines. Fairley (1963) discovered an
average of 455 mites of five different species per 100
specimens of *A. sylvaticus* and many more mites must exist
in the rodents' nests. Elton *et al.* (1931) identified twelve
different species of mites from wood-mice and eleven from
bank voles but the two host animals share only five species.

To summarise the literature and some of the results
of the present study the following are, perhaps, the most
important points when considering the ethology of *L. testaceus*
in this country:-

(a) The beetle is blind and dull brown in colour.

(b) Despite its blindness *L. testaceus* is extremely
agile and quick moving, although disturbance often
elicits immobility.

(c) The beetle is morphologically highly adapted to
spend a portion of its life in mammalian fur being
markedly flattened dorso-ventrally and covered with
short spines.

(d) *A. sylvaticus* is most frequently infested, in a
mixed population including *C. glareolus* and *M. agrestis,*
possibly because of its high mite burden or the disti-
nctive species it carries.

By combining an understanding of these points we may gain a better insight into the beetle's mode of life. *L. testaceus* is probably a nidicole, living much of its life in areas where visual stimuli are unimportant. Its agility, colouration and immobility behaviour may allow it to escape predation by its suggested commensal associate, *A. sylvaticus*. However, regarding the assertions of Ruschamp (1922) it may be noted that its agility may also help it to capture its prey, the mites inhabiting the nests and infesting the pelage of small mammals. Small mammal nests are transient structures, they often are abandoned as a result of death, movement or migration of their occupant. The life of a nest must be, in many cases, considerably less than the life of the wood-mouse, which itself is only a few months (Brown, 1966). Adequate dispersal before periods of peak host abundance is essential to a species which is dependant on a host for food and shelter. The morphological adaptations, described in some detail by Jeannel (1922), may only indicate important phoretic dispersal phases in the beetle's life history rather than true ectoparasitism.

C H A P T E R 3

EXPERIMENTS WITH THE RELEASE OF

MARKED FLEAS

1. Introduction

The extent of flea interchange between hosts, under field conditions, is unknown for most species infesting small mammals. Williams and Parer (1971) carried out experiments in a 550 acre enclosure and observed the dispersal of the European rabbit flea, *Spilopsyllus cuniculi* Dale, through the previously uninfested rabbit population. The infestation, consisting of 100 male and 100 female fleas, was originally established on a single pregnant doe rabbit. All rabbits in the enclosure, about 100 in each of four warren complexes, were infested within eighteen months, despite the fact that individuals of this flea species may remain attached to the same host for long periods. Mead-Briggs (1964) also demonstrated a high intensity of transfer of the rabbit flea within his enclosed rabbit populations.

Direct observations of flea interchange within a host population require some fleas to be marked. Several different marking techniques have been described. Radioactive isotopes have been used in America and Russia (Hartwell, Quan *et al.*, 1957; Soldatkin, Novokreshchenova *et al.*, 1961; Shura-Bura and Kharlamov, 1961; Sviriodov, 1963). Marking of fleas by the removal of the terminal sub-segment of the tarsus was described by Mead-Briggs (1964) and used in further experiments (Vaughan and Mead-Briggs, 1970). Kosminsky and Soloviova (1959) suspended dyes with 10-15% rosin in ethyl alcohol solution and deposited small droplets on the integument of fleas. Acetone soluble dye dusts have been puffed onto Calliphorine flies to produce a temporary mark (MacLeod and Donelly, 1957)

and this technique was successfully used for marking fleas
by Humphries (1969).

Experiments on flea interchange have been performed
in enclosures (Hartwell, Quan *et al.*, 1957; Mead-Briggs,
1964), but despite attempted simulations of field conditions
the enclosure of experimental animals probably enhances
the likelihood of flea transfer. Only experiments involving
wild populations can give a true impression of flea move-
ments but the nature of the habitat often makes mark and
recapture of fleas under field conditions very difficult,
especially among small mammal populations.

A high degree of flea transference between or among
different host categories would ensure that flea indices of
the classes involved remained similar. In effect, the
animals would share a common flea infestation. Conversely,
low incidence of flea transfer would result in the isolation
of the flea populations possibly resulting in variations
in the levels of flea infestation of different host sex,
age or social classes depending on the behaviour of the
category and the nature of the host/parasite relationship
at that time.

Similarities and differences in the levels of infest-
ation of host categories with *C. nobilis* were demonstrated
in Chapter 2. For example, during breeding male and female
A. sylvaticus harboured similar numbers of fleas, as deter-
mined by *C. nobilis* indices. This observation, at first
sight, is rather difficult to explain considering the vastly
different behavioural characteristics of the two sexes
during breeding. The similarity may have been due to high

degrees of social and/or spatial interaction between the
sexes, resulting in a common flea infestation, or it might
have been due to independant factors operating on both
sections of the small mammal community but with similar
outward results. Further equalities in infestation were
observed during overwintering and, here also, the same two
explanations could be put forward.

In order to decide between these explanations the
occurence of flea interchange between individuals of the
grid population of A. sylvaticus was investigated during
two trial periods. Despite the fact that trial 1. was
performed at the first sampling classed within the over-
wintering period, juvenile animals made up part of the
population and some adults remained in breeding condition.
This trial was, out of necessity, rather late for experi-
ments on breeding animals because the equality of levels
of infestation of male and female breeding A. sylvaticus
had only just been recognised. Most of the animals used
in trial 1. were in breeding condition (Table 3.1). Trial
2. was carried out during the final overwintering sampling
when the A. sylvaticus population was stable and function-
ally asexual. About three months separated the trials.

The experiments gave an opportunity to test, in
conjunction, flea marking techniques which had already been
proven successful separately (tarsus clipping - Mead-Briggs
1964; dye dusts - Humphries, 1969).

The release of a number of marked individuals into a
wild population and the eventual capture of a proportion

of the marked fleas together with unmarked ones suggested

that Lincoln Index techniques might be applied to the data.

In this way the total nidicolous infestation of the animals

concerned could be estimated. The application of this

technique (Lincoln, 1930) requires certain assumptions to

be made about the population and its sampling, these will

be discussed later in the chapter.

All experiments on the release of marked fleas were

performed using *C. nobilis*, none of the other flea species

were used at any stage during the investigation. Similarly,

A. sylvaticus was the only host species used.

2. Materials and Methods

The immediate collection of large numbers of fleas for mark and recapture experiments cannot be ensured from field sources; the fleas must be bred. Cotton(1965) found that the short-tailed vole, *M. agrestis*, was the most suitable host for cultures of small mammal fleas. In the present study voles were infested with forty adult *C. nobilis* (about 15 male and 25 female) and kept in "observation cages" (Jewell, 1964). These cages were easily adapted for use as flea culture vessels. Sliding glass panels ensured that the fleas could not escape. The cages were constructed in two partially separated compartments, the feeding and exercise area and the nest area (Plate 2). The nest area was a perforated platform with a tray beneath it containing powdered dried ox blood and "Bemax". The vole's body helped to maintain a constantly high temperature and humidity within the culture cage. Eggs from the fleas fell into the nest where the larvae emerged and fed on the culture medium until they pupated. Adult fleas were extracted from the cultures by sieving the medium and by searching the body ofthe culture host animal.

Waxoline Blue (Microme dye number 536) and Rhodomine Red (Microme dye number 208) dye dusts were applied to the fleas to give temporary marks (MacLeod and Donelly, 1957), and one of the terminal tarsal sub-segments from the legs of fleas was removed as a permanent mark. Mead-Briggs (1964) found that this method of marking did not affect the activity or survival of rabbit fleas. Rothschild, Schlein *et al.* (1972) have shown that only the metathoracic

PLATE 2

THE FLEA BREEDING CULTURE VESSEL

(Jewell, 1964)

(i) The cage dismantled
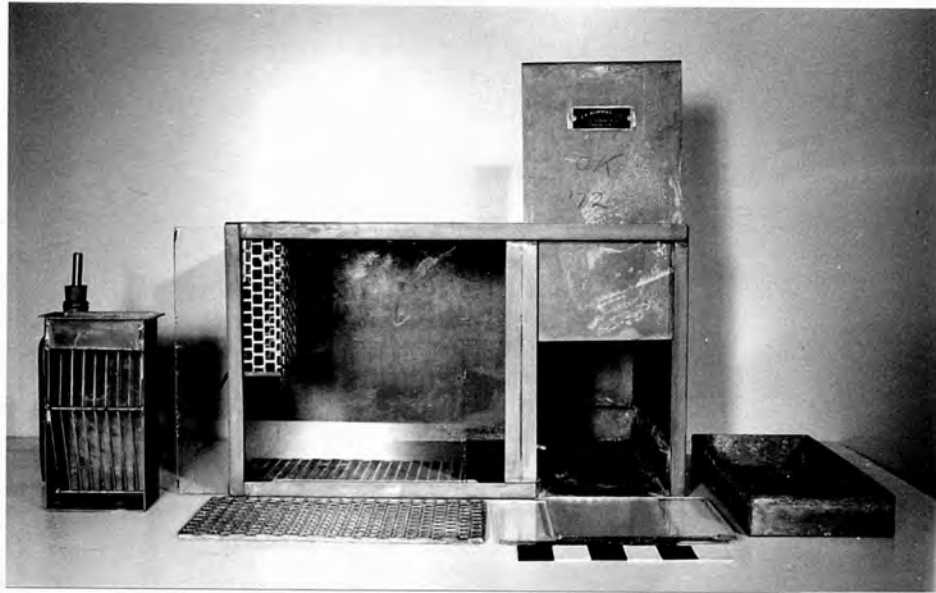
(ii) The nest-box set up ready for occupation

legs play an important part in jump propulsion in fleas
and that the tarsus is not involved. When marking fleas
a combination of clipping one of the six tarsi and applying
one of the dye dust colours offered twelve possible mark
combinations.

The majority of the members of the *A. sylvaticus* popul-
ation used in these experiments had been marked, by toe
clipping, during the previous sampling periods. Any new
animals were marked in that way on being captured for the
first time. During the two trial periods the normal
trapping regime on Trip Grid B was used except that the
traps were set on the final night of prebaiting. That
night's catch was examined and the animals identified by
their toe clip marks in the field. Certain mice were then
taken into the field laboratory to be used as hosts for
marked fleas, and the remainder were released immediately
at their site of capture.

The chosen mice were held in small containers and
specimen tubes with seven to fifteen marked fleas were
inverted on the dorsal region of the mouse and held in
place for about one minute. By the end of this time the
majority of the fleas had disappeared into the pelage;
any that failed to do so were removed and not used in the
experiments. The infested animals were then released at
their point of capture at 1400 to 1500 hours.

Trapping then continued for the usual seven consecutive
nights and all captured mice were removed from the grid
and taken to the field laboratory to be searched for fleas

in the normal way. In this manner the flea infestation
of the animal and any marked fleas were collected. Routine
microscope identification of the fleas was carried out,
using external characteristics (Smit, 1957) and fleas with
a last tarsal sub-segment missing were isolated. These
marked fleas were placed on a filter paper and a small drop
of acetone was applied to them to dissolve the dye dust
present and so reveal the colour of the mark. The dye dust
was found to remain on the body of the fleas, in detectable
quantities, for about one week, this was adequate for the
purpose of the study. Humphries (1969) reported similar
findings.

Careful notes were made of the mark combination and
the identity of the host animal. All captured animals were
returned to their site of capture by about 10.00 hours.
Table 3.1. shows the details of released, marked fleas and
their hosts for the two experimental trials.

Table 3.1.

Host data and details of the fleas released and their

marks for the two trails

TRIAL 1 (28.10 - 3.11.72)

	HOST				FLEAS RELEASED		
Toe Clip No.	Sexual Condition	Average wt. during trial in gms.	No. of subsequent recaptures	Mark*	♀	♂
0032	♀ perf.	20.2	5	RF.R.	9	5
1400	♀ imperf.	13.8	6	RF.B.	9	3
0300	♀ perf.	19.8	5	LF.R.	10	3
4100	♂ abdom.	10.7	5	LF.B.	8	4
1020	♂ scrotal	17.2	7	RM.R.	7	5
0034	♀ perf.	21.9	6	RM.B.	9	4
4001	♀ perf.	19.3	7	LM.R.	5	2
				TOTAL	57	26

TRIAL 2 (24.1. - 30.1.73)

4040	♀ imperf.	12.7	6	LH.R.	4	5
0100	♀ imperf.	13.6	7	LM.R.	5	5
4001	♀ imperf.	18.6	7	RH.R.	5	5
0020	♂ abdom.	18.9	3	RF.R.	5	4
0300	♀ imperf.	21.1	7	LH.B.	4	5
0001	♂ abdom.	17.9	7	LF.B.	4	5
0250	♂ abdom.	17.4	7	LF.R.	4	5
0010	♀ imperf.	19.3	5	RM.B.	5	5
2400	♀ imperf.	17.5	6	RF.B.	5	5
				TOTAL	41	44

* The tarsus clip symbol is given first, e.g. RF.= right fore leg, LM. = left middle leg, RH. = right hind leg, and then R. = Rhodomine Red and B. = Waxoline Blue.

3. Results

Of the 168 specimens of *C. nobilis* marked and released on *A. sylvaticus*, during the two trials, forty-four fleas (26.2%) were recaptured. Thirty-two of these (72.7%) were recaptured on their original hosts and twelve (27.3%) had transferred to different host animals.

Eighty-three fleas were released during the first trial period (October 28th to November 3rd). Only four instances of flea interchange were observed among the twenty-eight recaptured fleas. The total grid population of mice was twenty-six. The flea transfers were observed within a group of animals thought to represent a mother and her offspring. Trapping results showed that during the previous sampling period (September 30th to October 6th) a perforate female (toe clipping serial number 4001) was observed to be lactating and the ten to twelve gramme weight range of the three sexually immature animals (4100, 4030 and 4040) which were caught during the first trial period, was consistent with the theory that they were members of the litter that was being suckled during the September/October sampling. Furthermore, during the trial period, animals 4001 and 4100 were found occupying the same trap and later 4030 and 4040 also entered a trap together. Marked fleas were released on 4001 and 4100 and, in all, four instances of flea transference were observed within this group (Fig. 3.1.). No flea transference occurred during the nights when the animals shared traps. The calculated positions of the centres of activity of these animals added further

Figure 3.1.

The animals involved in flea transfers in Trial 1.
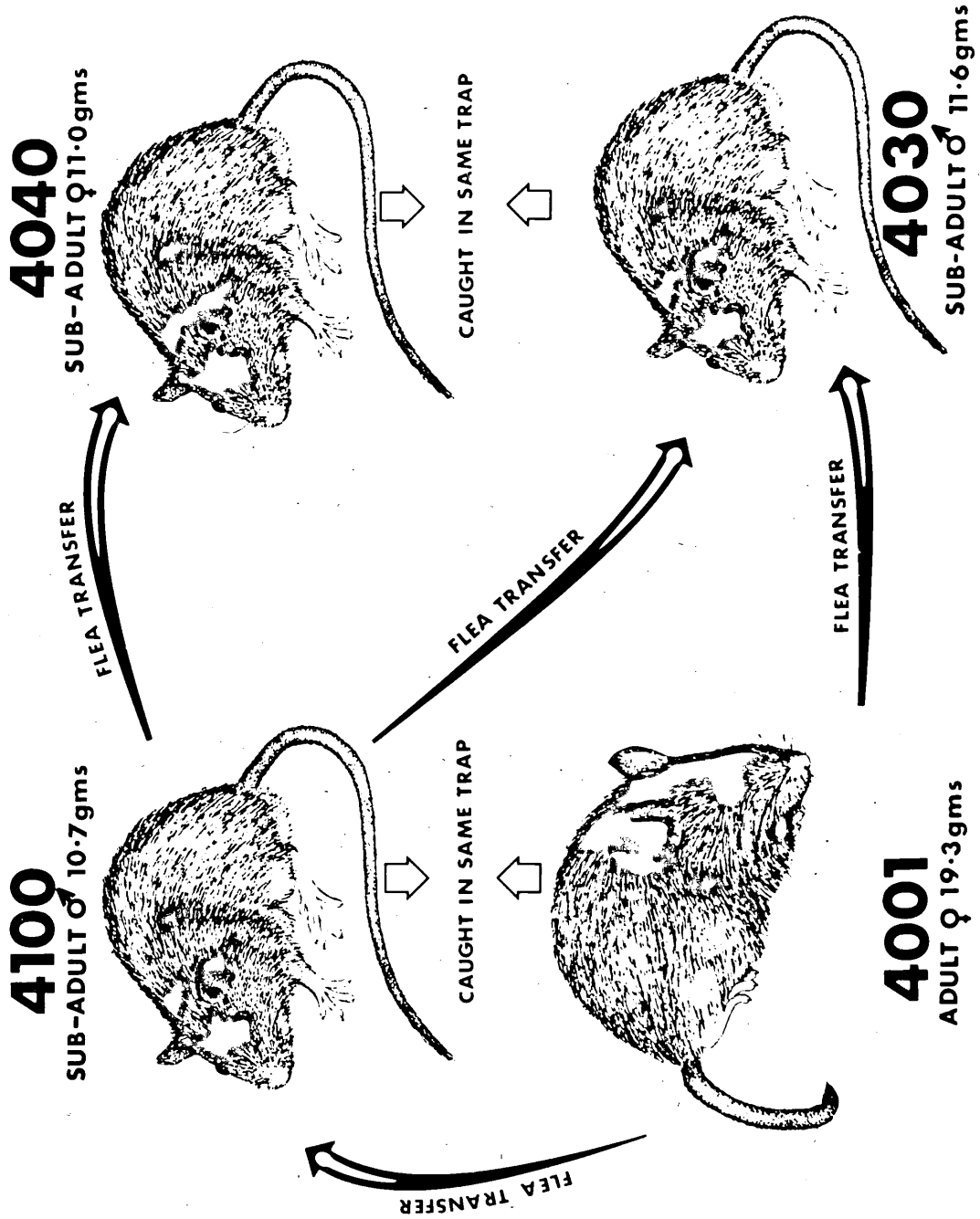
evidence to this theory (Fig. 3.2.). These results show
that the four animals had close social and spatial relation-
ships, probably sharing a nest-site and therefore having
a common flea population. Fleas were released on five
other adult animals during the first trial period. No
interchange of fleas was demonstrated between these animals
or the other seventeen animals which made up the grid
population at that time. Flea interchange was demonstrated
only between the breeding female and her litter.

During the second trial period all the mice detected
on the grid were in a non-breeding or asexual condition.
Twenty mice were trapped and nine were used for the release of
eighty-five marked fleas (Table 3.1.). Only two of the
mice with marked fleas were not, subsequently, involved in
flea transfer. Furthermore, four of the other mice were
recipients of marked fleas and hence, in all, eleven of the
twenty mice that were present were involved in interchange
of fleas. This indicates that a close relationship existed
between some of the animals of the host population at that
time. Table 3.2. shows the data for the animals involved
in flea transfers during the second trial period.

Sixteen fleas were recaptured during the second trial
and, of these, eight had been involved in flea interchange.
That is, it was as likely that a flea would be recaptured
from a host other than the one on which it was released as
from its original host. This was in marked contrast to
trial 1., where only four of the twenty-eight recaptured
fleas changed hosts and these were among a postulated
family group.

Table 3.2.

Data for the animals involved in flea transferences during Trial 2

DONOR				RECIPIENT				Number of fleas transferred	Number of instances of flea transfer
Toe clip Serial No.	Sexual Condition	Weight in grammes	Used for the release of marked fleas	Toe clip Serial No.	Sexual Condition	Weight in grammes	Used for the release of marked fleas		
2400	♀ imperforate	17.5	YES	0055	♂ abdominal	20.4	NO	1	1
0100	♀ imperforate	13.6	YES	0021	♂ abdominal	18.8	NO	1	1
0300	♀ imperforate	21.1	YES	0001	♂ abdominal	17.9	YES	1	1
4040	♀ imperforate	12.7	YES	4001	♀ imperforate	18.6	YES	1	2*
0300	♀ imperforate	21.1	YES	0041	♀ imperforate	18.3	NO	1	1
0020	♂ abdominal	18.9	YES	1200	♂ abdominal	17.0	NO	2*	1

* Usually flea transfers, from donor to recipient, involved a single flea transferring on one occasion. However, 4040 and 4001 were twice involved in instances with a single flea transferring on each occasion and in one instance 0020 donated two fleas to 1200.

The centres of activity (Hayne, 1949) were calculated for all the animals involved in the two trials (Fig. 3.2. for trial 1; Fig. 3.3. for trial 2). The average distance between the centres of activity was 26.3m. in the first trial, whereas the distance between the centres of activity of animals that exchanged fleas was, on average, 10.6m. The difference between these distances was very significant ($d = 2.60$, $p < 0.01$). Similar results were obtained for the second experiment. The average distance between animals' centres of activity was 39.9m. but it was only 14.4m. between those that exchanged fleas. In this case the results are highly significantly different ($d = 4.26$; $p < 0.001$).

The observed areas of activity of the animals were not always mutually exclusive, some overlap occurred. The amount of overlap of activity area is a measure of the spatial association between animals. The amount can be calculated by dividing the total number of different grid squares in which the two animals under investigation were captured by the number of squares in which both were captured. The average overlap of the observed areas of activity of animals not involved in flea transfer was 17.9% and 12.1% for trial one and trial two respectively. The overlap of animals that exchanged fleas was 53.2% and 56.9% for the two trials. The difference between overlap of exchanging and non-exchanging animals was significant in both cases ($d = 2.21$, $p < 0.05$ for trial 1; $d = 3.50$, $p < 0.001$ for trial 2).

By comparison of the proximities of the centres of activity and the amounts of overlap of the observed activity

Figs 3.2 and 3.3

The centres of activity

and toe clip numbers

of A.sylvaticus used

for release of marked

fleas or involved in

flea transfer, (arrows

indicate flea transfers).

0   10   20   30

metres
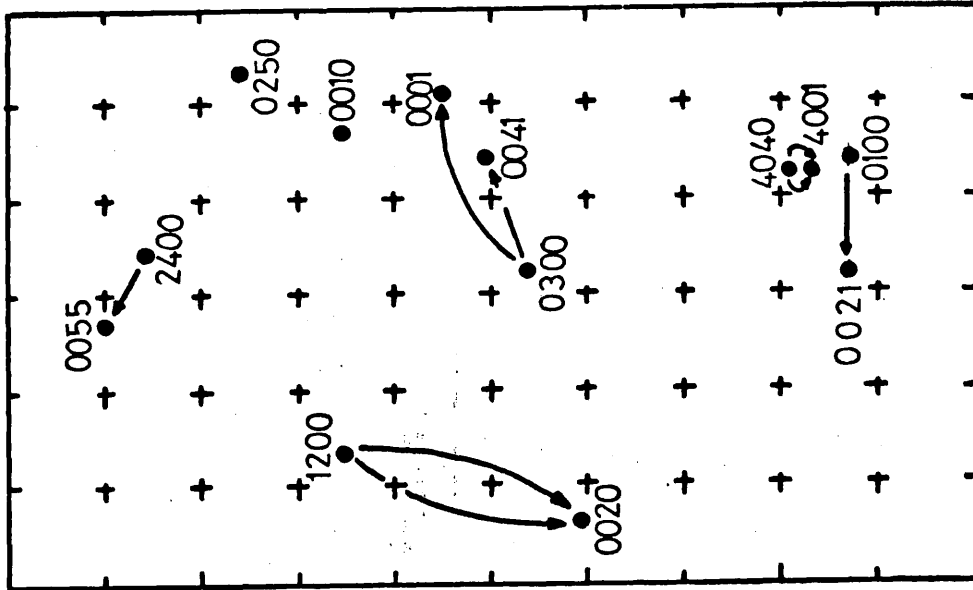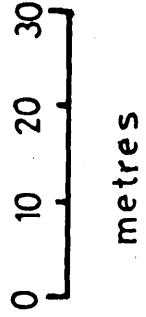
Fig.3.3 Trial 2.
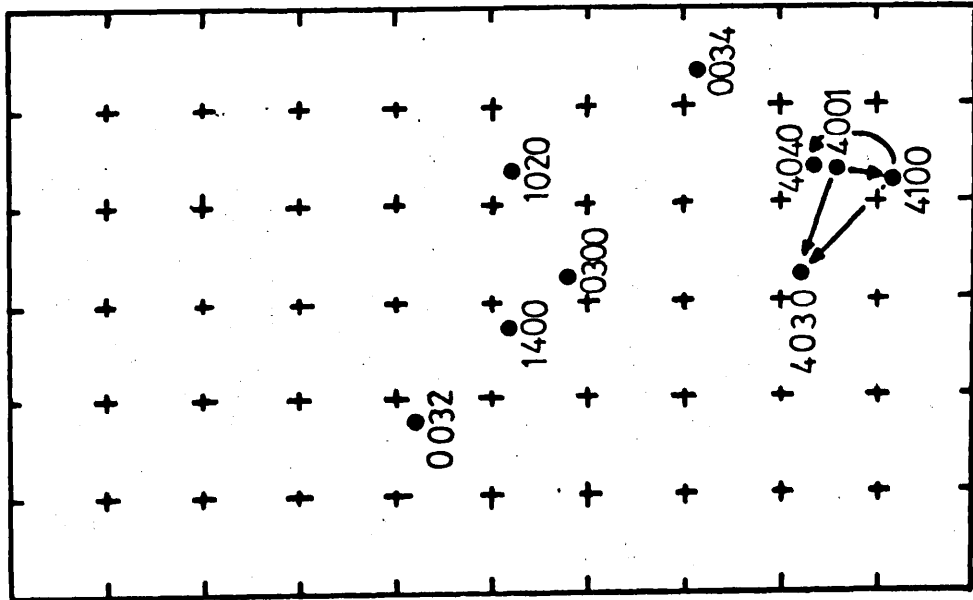
Fig.3.2 Trial 1.

areas it has been shown that the animals which exchanged
fleas had a close spatial relationship with one another.
This relationship existed, in the first trial, between a
mother and her offspring. Flea interchange was not demon-
strated between the other animals on the grid. During the
second trial the relationship existed between the remnants
of the family group that had maintained their relationship
during the overwintering period as well as between other,
adult animals present on the grid at that time.

Most of the fleas that were recaptured on their
original hosts were found on the day immediately after
release. Fig. 3.4. shows the distribution of the recaptured
fleas over the time of the two trials. The recaptures for
both experiments are combined. Twenty of the thirty-two
fleas were taken on day one, indicating that fleas frequently
remain on the host for a number of hours or that they get
on to the host for more than one feed in twenty-four hours.
The first explanation seems more likely.

For the purposes of population estimates based on the
Lincoln Index fleas taken from hosts on day one of the
trial samplings, the day immediately subsequent to the
release of marked fleas, were not included in the calcula-
tions. Perhaps the most important assumption which must be
made about populations under analysis by Lincoln Index
methods is that the marked and unmarked individuals must be
randomly mixed and equally trappable. Clearly, fleas which
could not be proven to have left the body of the host at
some stage after marking and release and before recapture

Fig.3.4. The distribution of recaptures of marked fleas during the trial periods (results pooled).
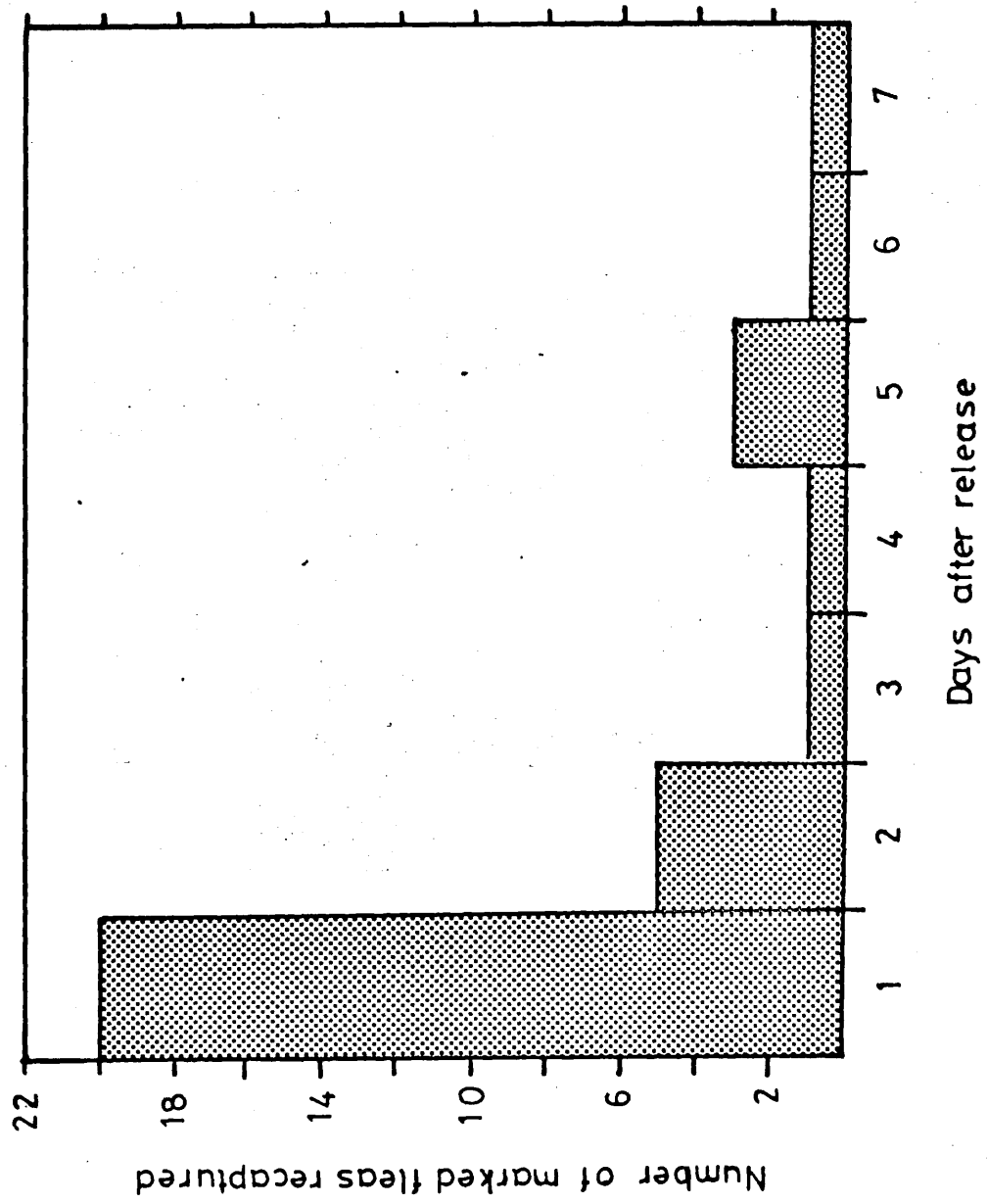
did not satisfy this condition. Furthermore, fleas ·
exchanging hosts and entering the parasite populations of
mice which had not been infested with marked fleas could
not be included with the recaptures because all of the
marked fleas did not have access to those hosts. Fleas of
species other than *C. nobilis* were ignored.

Hence, using the formula:-

$$\frac{T \times m}{g}$$

where:- T = total number of fleas captured on days

2 - 7.

m = total number of marked fleas released

minus those captured on day 1.

g = total number of marked fleas recaptured

from hosts used for release of marked

fleas.

N.B.   data for two trials pooled.

the total estimated number of fleas in the populations
infesting the sixteen animals in the trials was 1184. The
number of fleas infesting each animal was, therefore,
seventy-four. It must be noted that this is an estimate
of the numbers of *C. nobilis* only.

4. Discussion

Russian workers have used the technique of mark and recapture of fleas with assessment of the extent of flea interchange as a measurement of social "contact" of the hosts (Sviridov, Morozova *et al.*, 1963; Sviridov, 1963). This concept is based on the assumption that interchange of fleas between hosts by the independent movement of the parasites is minimal and that a great proportion of the observed exchange of fleas between hosts occurs when the animals are in very close contact, sharing intimate areas of home range. There is some evidence in support of this theory. Vaughan and Mead-Briggs (1970) have shown that rabbit fleas can move only very small distances under their own power, even in short grass enclosures. The conditions that made movement difficult for the fleas in those experiments almost certainly apply to small mammal fleas in field conditions. Furthermore, Vysotzkaja (1964), Haas (1966), Cotton (1970) and many other authors have demonstrated that a great proportion of the life of most fleas is spent within the host's nest. It is not unreasonable to assume, therefore, that instances of flea transfer are indicative of close spatial relationships between the animals involved and probably, consequently, quite close social relationships also. There is, however, some evidence that certain flea species may be quite mobile. Bates (1962) has shown that the sand-martin flea *Ceratophyllus styx* Roths. could move 33.8m. in four days. These movements were made by walking over a sandy cliff-face which would have allowed almost constant sensory sampling of the environment,

resulting in a direct line of progression. Movement by jumping or walking in a grassy undergrowth or in a maze of subterranean tunnels would result in very much slower progress.

The technique for marking fleas used in this study was quite successful. The limitations imposed by the study techniques now at our disposal restrict increase in our knowledge of the field ecology of small mammals and their ectoparasite populations. The development of new techniques is important for an improved understanding of the interactions within the communities. The use of marked fleas seems to offer some advantages as a study tool in this respect and it has been used by several authors. Sviridov (1963) injected P[32], in the form of sodium phosphate solution, into specimens of the great gerbil, *Rhombomys opimus*, and then allowed fleas of the genus *Xenopsylla* to feed on them. After feeding on the blood of radioactive gerbils the fleas themselves became tagged. He went on to make various ecological observations on the fleas and the "contact" of the hosts. The use of radioactivity for flea marking has two disadvantages when compared with methods utilising tarsus clipping and dye dust combinations. Firstly, all fleas are identically marked so that no information concerning the exact identity of the donor animal is available. The large number of possible mark combinations in the technique described above allowed many different animals to be given uniquely marked populations and the fate of these fleas was determined on recapture. Also, the feeding activity and mobility of fleas

may be affected by radioactivity (Kharlamov, 1965) so that the extent of flea transfer may be altered by changes in the behaviour of fleas due to the radioactivity. Mead-Briggs (1964) was unable to demonstrate that fleas with a terminal tarsal sub-segment missing were at any disadvantage when compared with unmarked specimens. However, the use of dye dusts, as a marking technique, is only suitable for short term studies lasting not longer than about one week.

The numbers of marked fleas that were recovered when they were released on hosts from wild populations was quite high. More than a quarter of the released fleas were recaptured and this figure compares quite favourably with experiments involving the release of fleas onto enclosed vole populations (Hartwell, Quan *et al.*, 1958).

The extent of interaction between individuals of a small mammal population is determined by seasonal changes in behaviour governed by environmental conditions. Brown (1966) investigated the occurrence of dominance hierarchies and "clanning" in *A. sylvaticus* and cast doubt upon the widely accepted idea of mutually exclusive home ranges for each member of the population. There can be no doubt, however, that for most species exclusive home ranges do occur during certain phases of the annual reproductive cycle. Brown considered the breeding ranges of female *A. sylvaticus* to be the most fiercely defended of all and Getz (1972) showed that there was antagonism between breeding females of the meadow vole, *Microtus pennsylvanicus*. Healy (1967) observed well defined home range boundaries

in *Peromyscus maniculatus austerus* during the breeding season but went further to show that intraspecific strife was almost non-existent during the winter, non-breeding period. Several authors have reported small mammals living together and sharing home ranges during the winter (Burt, 1940; Nicholson, 1941; Thomson, 1945; Howard, 1949; McCabe and Blanchard, 1950).

In *A. sylvaticus* observed differences in the extent of flea transfer between the two trial populations reflected differences in their intraspecific behavioural relation-ships during the trial periods. Exclusive and defended home ranges during the period when sexually mature animals formed part of the population would have resulted in low flea transference, except between females and their litters, because social conflict between adults restricted close association at that time. Such interactions as mating and fighting would probably be of too short a duration to allow significant flea interchange. The observed similarities between breeding male and female *A. sylvaticus* with respect to *C. nobilis* index was, therefore, not due to close social contact resulting in a common flea infestation. The low extent of flea transference suggests that other factors must have controlled the male and female levels of infest-ation independently. However, the results of the inter-actions of the various factors was superficially similar.

The high incidence of transferences within the asexual population was probably due to the lowered mutual antagon-ism between members of the non-breeding population (Brown, 1966). Morris (1968) observed three *A. sylvaticus*, in winter, sharing the abandoned nest of a hedgehog. Such behaviour

would have resulted in a common flea population shared by
the animals. The high degree of mutual tolerance exhibited
by all host categories during the non-breeding period would
result in similarities in the degree of flea infestation. -
This has been shown to be the case in the present studies,
the *C. nobilis* indices for overwintering males and females
were almost identical.

Almost no quantitative data is available concerning
the length of time that fleas stay on the host. Some fleas
are thought to spend most of their time in the nest. One
such species is *R. pentacantha* (Freeman, 1942; Evans and
Freeman, 1950). Other species have been called "fur" fleas,
these spend much of their time on the host, *Leptopsylla segnis*
and *Peromyscopsylla silvatica* fall into this category (Janion,
1960 and 1961). Of the thirty-two fleas which did not
transfer to other hosts twenty were still on the original
host when the animal re-entered the traps on the following
night. The animals with marked fleas were released at about
1400 to 1500 hours and the traps were opened four or five
hours after that. It is unlikely that all the mice entered
the traps immediately after they were opened and, hence,
the fleas were probably on some of the hosts for many hours.

The application of Lincoln Index methods to the mark
and recapture data gave an estimated seventy-four individ-
uals of *C. nobilis* in the nest or on the body of each
individual *A. sylvaticus*. Davis(1934) found as many as
seventy-four specimens of *C. nobilis* in nests of *M. agrestis*
although the average number of *C. nobilis* in thirty-eight

nests was about ten. The results of Cotton (1970) gave much lower estimates for the numbers of that flea species in short-tailed vole nests.

The Lincoln Index estimate was made in the full understanding that the suitability of the data for such treatment was in doubt. For example, the periodism of feeding in fleas meant that not all members of the population were equally trappable at any one time. The released fleas, having fed, would be less likely to be found on the host than other, hungry individuals. This may have been the cause of the apparent overestimate of the population size. Furthermore, the data for both trials was pooled, in order to make it workable in the calculations, although it had been proven that the condition of the host/parasite relationship was different during the trails. The estimate was inaccurate because of these and other problems. However, other methods used for similar estimations are equally debatable. Some use has been made of nest-boxes (Haas, 1966) although it seems likely that their provision would significantly affect the rodent's nest microclimate and so alter breeding conditions for the fleas. Methods using excavation of nests involve similar levels of inaccuracy and these have been discussed by Davis (1934). During mark and recapture studies the host and parasite populations are examined under almost natural conditions. Only the stringencies of trapping and recovery of fleas alter the behaviour of the animals concerned.

EXPERIMENTAL SECTION 2

(Chapter 4)

CHAPTER 4

THE RELATIONSHIP BETWEEN HIBERNATING HEDGEHOGS

AND ARCHAEOPSYLLA E. ERINACEI

1. Introduction

The hedgehog flea, *Archaeopsylla e. erinacei* (Bouché), is a monoxenous parasite of the European hedgehog, *Erinaceus europaeus* L. (Smit, 1957). Hedgehogs often support very large populations of this flea although specimens of other flea species are very rarely found on them (Szabo, 1969; Buckle, unpublished data). It seems that the hedgehog presents a very specialised habitat as a host species for ectoparasites and, it is probable, that aspects of both its behaviour and structure make it unsuitable as a host species for parasites not adapted to it.

Much of the detail concerning the life cycle of the hedgehog flea is uncertain. Most flea species are dependent on the host's nests as sites for breeding, especially during the summer months. British hedgehogs seem to occupy no permanent nest during this period comparable with that in which they spend the major part of the winter and often use only a temporary shelter for a short time (Morris, pers. comm.). The exact site of breeding of *A.e. erinacei* is yet to be identified although some evidence has been published recently to suggest that breeding occurs in the female hedgehog's summer breeding nest (Brink and Lofqvist, 1973).

No information has been published as to whether flea populations infesting hedgehogs in autumn retain their integrity and survive through the host's period of hibernation or whether they die leaving resistant life cycle stages to overwinter. Other pulicid fleas have been seen to survive the winter period, although their hosts were

not hibernating animals. Soldatkin, Novokreshchenova
et al. (1961) found that marked specimens of *Xenopsylla*
gerbilli caspica survived from autumn until the following
April. They reported that the fleas were of a resistant
generation which was followed by a spring emergence of
another generation which existed until September. However,
other species of the genus *Xenopsylla* have been shown to be
univoltine (Kiryakova, Koptzev and Koptzeva, 1970). In
Great Britain only Rothschild and Clay (1952) have reported
that live *A.e. erinacei* were observed on a hibernating
hedgehog.

Probably the largest single obstacle to be overcome
by successful hedgehog ectoparasites is the host's period
of winter hibernation. During that time the body temper-
ature of the host animals drop and approach the ambient
temperature. It has been suggested that, in fact, the
annual cycle of the hedgehog is composed of phases when the
animal is preparing for hibernation, is in hibernation or
is recovering from hibernation (Hock, 1960). Clearly, in
such a situation, the biology of parasites would need to
be closely geared to these changing phases. However, this
view, perhaps, places too much emphasis on the effects of
hibernation in the annual cycle but there can be little
doubt that the drop in the body temperature, restriction
of the peripheral blood supply both by vasoconstriction
and reduction of heart rate and the change in blood compos-
ition must profoundly affect the ectoparasites.

It is important to note a distinction in definition which will be used throughout this chapter. In the present study, as in the work of Kristoffersson and Soivio (1964,a.), the whole winter period will be termed the "hibernation period". It is generally accepted that hibernating animals do not spend the entire hibernation period in continuous torpor but periodic arousals occur.(Hoffman, 1964). The periods between arousals, where the body temperature of the animal (T_b) approaches ambient temperatures (T_a), will be termed "hypothermic periods".

The literature concerning the length and periodicity of the hypothermic periods is somewhat confused. Herter (1938) and Proctor (1949) have recorded hypothermic periods lasting one month while Lindemann (1952) stated that he observed a period of hypothermia lasting two months. More recent work, however, indicates that the periods of torpor are not usually as long as those reported by the above authors. Kristoffersson and Soivio (1964,a and b; 1967,a, b and c) used continuous recordings of body temperature, obtained from chronically implanted sub-cutaneous thermo-couples, to investigate the periodicity of hypothermia. They found that hypothermic periods rarely exceeded two weeks and that they usually lasted between ten and thirteen days at constant ambient temperature (+ 4.2 $\pm$ 0.5^{O}C).

During the long periods of winter hypothermia the temperature of the hibernation nest, or hibernaculum, falls close to ambient temperatures. The hedgehog's body temperature remains at a degree or so above ambient unless the ambient temperature falls to zero, or below, when the hedgehog begins to thermoregulate to maintain a T_b at one or two

degrees above zero. For successful reproduction most flea species require quite high temperatures and breeding slows or completely ceases when the temperature falls much below 10°C. (see Cotton, 1970 for *C. nobilis*; Edney, 1945 for *X. brasiliensis* and *X. cheopis*; Mellanby, 1933 for *X. cheopis*).

The low nest temperature imposed on ectoparasites by their hibernating hosts is not the only adverse condition experienced during the hypothermic periods. There is some evidence that food availability is reduced during hypothermia. Soivio (1967) has shown that the blood of hypothermic animals is concentrated in certain internal organs when compared with "normothermic" and fully aroused animals. There is considerable vasoconstriction of the peripheral body tissues (Lyman, 1965), and this may result in a shut down of blood to the skin of the animals (Johnson, 1931). Furthermore, the flow of blood through the blood vessels is reduced because of the lowered heart rate which often falls to only 2-12 beats/minute (Kristoffersson and Soivio, 1964 a and b).

The composition of the blood of overwintering animals varies considerably from that of fully active summer animals. Blood glycogen decreases in winter, although its concentration in the liver increases (Mladenovic-Gvozdenovic, 1971). The number of erythrocytes per cubic centimeter of blood decreases during the hibernation period (Halil, 1970). These changes in blood constituents probably reduce its nutritive value even when it becomes available during the arousal periods.

To date all experiments concerning the periodicity of

hibernation of hedgehogs have been carried out under controlled ambient temperatures or upon restricted animals in laboratory conditions. The behaviour of hedgehogs, with respect to hibernation under natural or semi-natural conditions has received very little attention. Due to the conflicting opinions of previous authors and the lack of continuous temperature recordings from field situations it was decided to monitor the nest temperature of the hedgehogs involved in the study to determine the exact lengths of the hypothermic periods.

It was the purpose of the study to observe the conditions imposed on the fleas by the host with regard to nest temperatures and food availability and to investigate any specialised behavioural characteristics shown by the fleas which enabled them to successfully adapt to the hibernation of their hosts.

The study of the hedgehog and its flea parasite provided a very interesting contrast to the small mammal flea populations. As long as they maintain contact with a host individual small mammal fleas are provided with very good conditions for continuous feeding and reproduction. It was the purpose of these experiments to determine if the hedgehog fleas were deprived of these conditions and, if so, to study their obvious ability to overcome this disadvantage.

2. Materials and Methods

2.1. The hedgehogs and their fleas

During the late autumn of 1971 three adult hedgehogs were captured in the countryside surrounding the Department of Zoology. These animals were taken into an animal house and fed on a diet of minced butcher's pet meat and crushed rat cake in a proportion of about one to one. The animals quickly gained weight and soon exceeded 700 grammes, considerably more than the 450 grammes necessary to successfully complete a full winter hibernation period (Morris, pers. comm.)

The natural flea populations of these animals were used in all further experiments. It was impossible to remove all the fleas from a fully active hedgehog due to the "curling reflex", the following procedure was used to disinfest the hedgehogs for flea marking.

The curled animal was loosely wrapped in absorptive paper and placed in a large polythene bag. The paper was then lightly sprinkled with ether and the open end of the bag was tightly gripped. The fleas that were in the spiny area of the pelage were quickly anaesthetised as they were more exposed to the vapour than those that were protected within the curled body of the animal. The anaesthetised fleas were freed from the host by gentle shaking and were removed from the polythene bag. After a short period (usually between three and ten minutes) the hedgehog itself became anaesthetised and could be easily uncurled. The fleas infesting the furry areas of the pelage were then

collected by a careful search under a strong light source in the same way as has been described for rodent fleas in a previous chapter. The hedgehog was then allowed to recover from the anaesthetic.

After the fleas had been removed from the hedgehog those for release on hibernating hedgehogs were marked. Batches of six fleas were anaesthetised and marked by the removal of the last tarsal sub-segment of one of the legs (Mead-Briggs, 1964). The flea infestations of the three hedgehogs that were used in the overwintering experiments were marked differently. When they had recovered the fleas were put back onto the hedgehog which was caged overnight and kept in an animal house. Next morning the cage was searched for any fleas which has not survived and those were subtracted from the total released to arrive at a final infestation total.

2.2. The Pens and Hibernacula

Specially constructed hedgehog pens were available at the Department of Zoology which had been used for a previous study (Morris, 1967). The pens were about ten meters square and were situated beneath a canopy of pine (*Pinus sylvestris*) and chestnut (*Aesculus hippocastanum*). The pen that was used in these experiments could be divided into four individual compartments each about five meters square. The ground layer inside the pens was grass with leaf litter. Morris (1973) has described types of nest site chosen by hedgehogs when building hibernacula. His observations showed that nests were usually composed of dry, dead leaves and were constructed beneath brambles or brushwood. In the present study each compartment of the pen was provided with a small patch of planted bramble as well as a small pile of brushwood. The dead leaves that were present in the pen were unsuitable for the building of hibernacula and a large pile of assorted dry, dead leaves were imported from other areas and placed in each compartment.

The hedgehogs, carrying their marked flea infestations, were released on 15th December 1971. They were each placed in separate compartments of the pen. All the hedgehogs constructed nests during the night of the 15/16th, two used the wood piles and one the brambles to give the essential support for the structure of the hibernaculum (Morris, 1973). The nests that were built were, in every way, similar to those described by Morris and can be stated to be the natural winter hibernacula of the species.

At intervals, throughout the winter, small amounts of

food were placed in the pen for consumption by the animals during their periods of arousal from hypothermia.

2.3. Continuous Temperature Recording

Various methods have been used for recording the periodicity of hypothermia in hedgehogs. The widely differing methods may have been, in part, responsible for the discrepancies in the results between authors. Johnson (1931) used piles of sawdust, placed outside the entrance to the hibernaculum, to detect the end of hypothermia. He assumed that hedgehogs always leave the hibernaculum during the short arousal periods. Herter (1938), Proctor (1949) and Lindemann (1952) recorded the nest temperature of animals by single, daily probings with a mercury thermometer. However, Kristoffersson and Soivio (1964a) have pointed out that 15% of all awakenings in their studies were of less than twenty four hours duration and the use of daily recordings would not detect these arousals. Furthermore, the disturbance necessary to make the recordings could stimulate the very sensitive animals into spontaneous arousal. All methods not utilising continuous temperature recorders have serious disadvantages when measuring hypothermia in hedgehogs.

Kristoffersson and Soivio (1964 a,b; 1967 a, b) used chronically implanted sub-epidermal copper-constantan thermocouples connected to a Honeywell electronic multi-pointer recorder in order to continuously monitor the body temperature of hibernating hedgehogs. However, implanted electrodes seriously restrict the movement of active hedgehogs,. In the present study it was decided to secure electrodes into the lining of the nest rather than implant them in the animal to ensure that the animals had maximum

freedom of movement.

Two separate thermistors were placed in the hibernac-
ulum and connected to an eight point Grant Recorder by
means of long insulated wires. Two other thermistors
recorded the ambient air temperature at about one half
meter above ground level within the pen. The recorder
measured and marked the temperatures of each thermistor
on a moving paper tape about once every fifteen to twenty
minutes. The nests were checked daily to ensure that the
hedgehog had not moved its nest site. When this movement
occurred the thermistors were installed in the new nest as
soon as possible.

The Grant Recorder developed faults at two separate
points during the experiment. At those times the nest
temperatures were recorded morning and evening and Herter's
"saw dust technique" (Herter, 1938) was also applied.

2.4. Reading and interpretation of the tapes

Kristoffersson and Soivio (1964a) defined the period of hypothermia as the time "from the moment the temperature (measured from the hind part of the animal by chronically implanted thermocouple) has fallen to $+6^{\circ}C$ until the slightest rise in temperature indicating arousal can be observed". This is, no doubt, a workable definition under conditions of controlled temperature. However, during the present study many instances were observed where the nest temperature (T_n), which is often a good indicator of T_b, rose to considerably more than $+6^{\circ}C$ and the animal showed no sign of arousal from hypothermia. In such cases it cannot be said that the hypothermic period had terminated. Instead a new threshold had to be defined at which point arousal or re-entry into hypothermia always occurred. In no case, when the T_n rose to exceed T_a by more than $5^{\circ}C$, was arousal not subsequently observed, and in the present experiments that point was taken to denote the end of hypothermia and the beginning of arousal. When the difference between T_a and T_n returned to $5^{\circ}C$, or less, the arousal period was said to have ended; hypothermia always ensued. All measurements concerning the length of hypothermic and arousal periods were made using the T_a to T_n difference at $5^{\circ}C$ as the point of transition from one state to the other.

It is essential to note that the thermistors in this work did not measure T_b, this fact introduced a slight possibility of error. The decline in T_n which was observed when the animals became hypothermic could have been mistaken for the decline in T_n when the animal actually left the nest.

However, usually entry into hypothermia was a very slow process taking many hours, whereas the cooling of the nest due to the aroused animal leaving the nest was comparatively swift. Similarly, the "warming-up" process was very slow compared with the sudden rise in T_n when the animal returned to its nest after a period of activity.

The Grant recorder was powered by "NiFe" cells and this introduced another area of inaccuracy. As the cells ran down the recorder tended to run more slowly, thus it was not possible to determine the exact time of day from the paper traces. All times given are approximate, being plus or minus about two hours.

2.5. Further experiments

(i) Survival of Fleas

Animals HO1 and HO2 were allowed to hibernate naturally in the pen until early spring. During March and April all the animals were removed from the enclosures and defleaed. The numbers of fleas on each hedgehog and the presence or absence of marks was carefully noted.

(ii) Position of Fleas during host hypothermia

Animal HO3 was removed from the pen on three separate dates during the hibernation periods for experiments to determine the location of flea populations during the hosts hypothermic period.

The continuous temperature recorder was inspected regularly and when the animal had been in deep hypothermia for four days it was removed from the pen. Four days was taken to represent the approximate mid-point of a hypothermic period. The hibernating animal was placed in one polythene bag and the entire nest and some of the leaf litter from below the nest were placed in another. The nest and leaf litter were placed in a Tullgren funnel for extraction of invertebrates.

On the first two occasions the animal was allowed to warm up to room temperature, which stimulated arousal, and then defleaed in the usual way. On the third occasion the animal was allowed to partially warm to about 10°C and then carefully uncurled and searched for fleas, without the use of ether. The positions and the numbers of fleas were noted.

After the experiments the animal was fed and returned to the pen having been reunited with its marked flea population. The animal usually made a nest during the following night and quickly returned to its normal hypothermic rhythm.

(iii) Feeding of fleas during hosts arousal

On March 13th 1972 animal HO1 was removed from the pens while still in deep hypothermia. The animal was taken into the laboratory and searched for fleas. Ether was not used for defleaing because on a previous occasion, a hedgehog had died during an arousal experiment and the use of ether may have been instrumental.

The fleas were anaesthetised with ether on removal from the host. Using a microscope with a camera lucida attachment and strong lighting from below the outline of the flea and its gut bolus were drawn. The fleas were then put back onto the arousing host animal.

After one hour the fleas were removed from the hedgehog and were drawn once more. This procedure was repeated after eighteen hours when the fleas were drawn for a third time. The experiment took place at external ambient temperature.

The flea infestation of a hedgehog which had been in normothermia, in an animal house, for about three weeks were drawn as controls for the above experiment.

Using dividers and allowing for the magnification of the microscope the absolute size of the fleas and their gut boli were estimated. Fig. 4.1. shows the measurements that were made on each gut blood bolus.

Fig.4.1.The details of the measurements taken from

each gut blood bolus.

width of the
descending limb

length of the
descending limb

width at the
transition

length of the
horizontal limb

width of the
horizontal limb
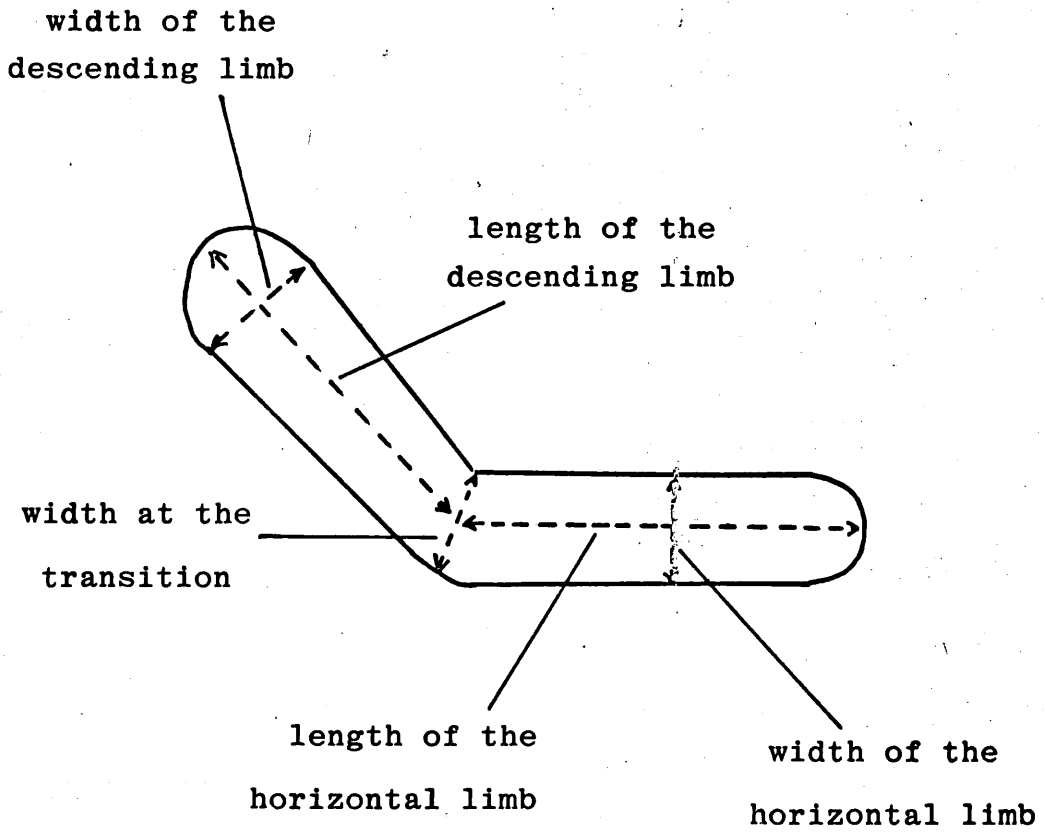
3. Results

3.1. The Weights of the Hedgehogs

The weight increases of the caged hedgehogs prior to release in the pens is shown in Fig. 4.2. All the animals were substantially heavier than the 450 gms which has been suggested as the minimum pre-hibernation weight for successful completion of the hibernation period.

Food was available to the hibernating animals at certain times during the winter. It was difficult to determine the exact amounts eaten as the food was available to other, wild small mammals living near the pens. However, large takes of food often corresponded to periods of spontaneous arousal.

Nevertheless, during hibernation the animals underwent considerable weight losses. Although animal HO3 was stimulated to arouse on three occasions for experimental purposes, these three enforced awakenings did not seem to deplete its food stores when compared with the animals undergoing natural hibernation periods. The weight fluctuations of the animals during the experiment are summarised in Table 4.1.

Fig.4.2 The weights of the hedgehogs prior to release in the pens.
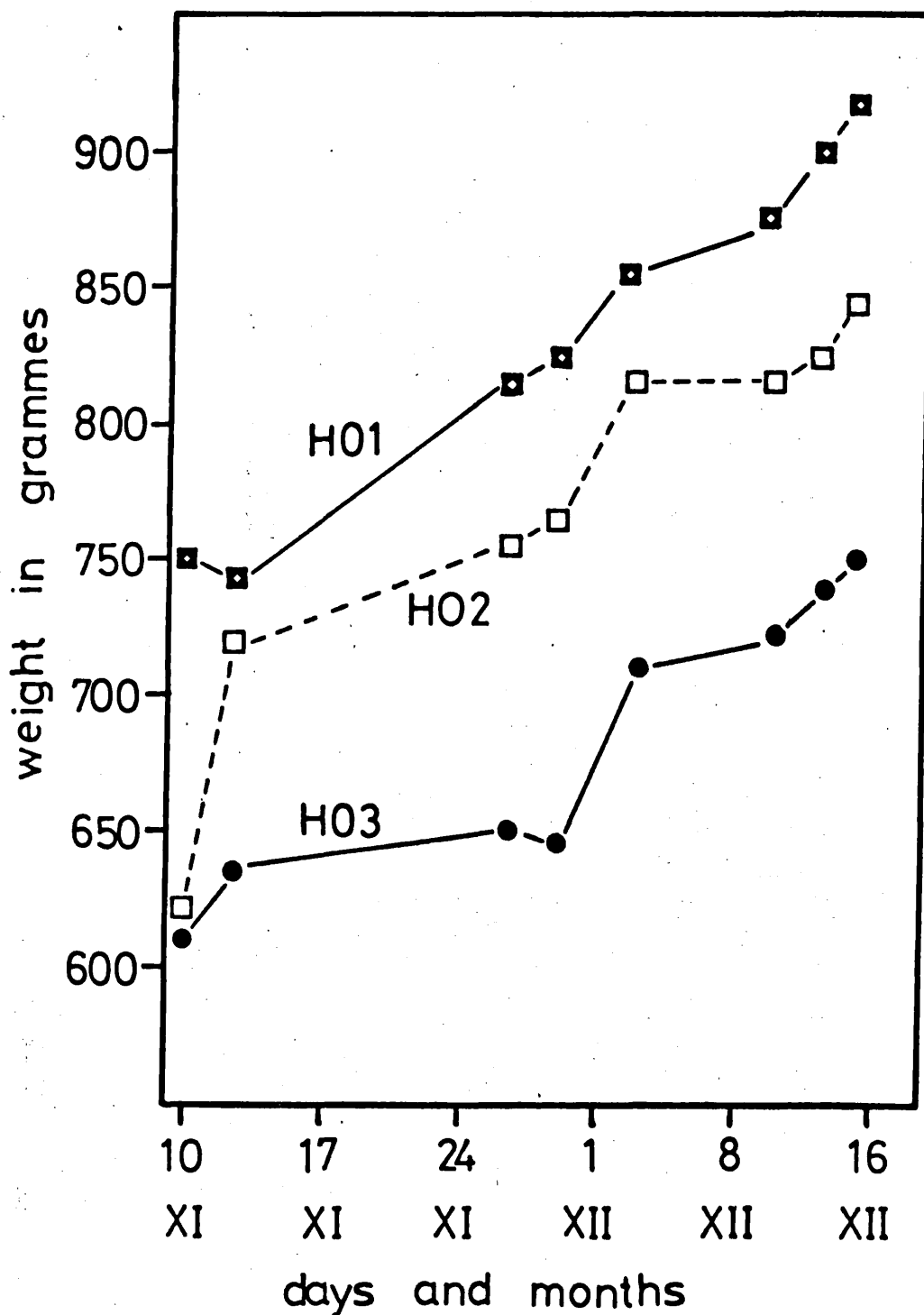
. Table 4.1.

Weight changes of the hedgehogs during the experimental

period

	HO1	HO2	HO3
Initial weight 10.11.71	750gms.	622gms.	610gms.
Weight on release 15.12.71	920gms.	845gms.	749gms.
% of original weight gained	22.7	35.9	22.8
weight after hibernation	530gms.	509gms.	455gms.
% of pre-hibernation weight lost	41.3	39.8	39.7

3.2. The Hibernation Periods

Only animals HO1 and HO2 were suitable for determination of the frequency of hypothermia during hibernation as HO3 was artificially stimulated to arouse on three occasions. Each animal underwent ten hypothermic periods and ten arousals. When the lengths of the hypothermic periods and the arousal periods of the two animals were compared no significant differences were detected (Mann-Whitney "U" Test, p > 0.05, in both cases). The mean length of the periods of hypothermia in hours was 195.6 ± 45.9 for animal HO1 and 189.6 ± 108.5 for animal HO2. The periods of arousal were, as would be expected, much shorter being 21.90 ± 9.5 for HO1 and 22.4 ± 9.5 for HO2. The lengths of the hypothermic periods tended to be quite variable and, consequently the mean values are not very meaningful. The range of readings is probably more significant. For animal HO1 128 hours (about five days) was the shortest hypothermic period while the longest was about twice that length (236 hours or ten days). Animal HO2 tended to be more variable. The first period of hypothermia of HO2 lasted only about two days (forty-two hours) and the one that followed was the longest period recorded (360 hours or fifteen days).

The length of the periods of arousal were also very varied. For HO1 eight hours was the shortest and twenty seven hours the longest arousal period, while HO2 gave twelve hours for its shortest and fo rty-one hours for its longest time awake. The distribution of arousal and hypothermia during the hibernation period of the two animals is shown in Fig.4.3.

Fig.4.3 The periodicity of hypothermia during the hibernation period of two of the experimental animals,(breaks indicate arousal).
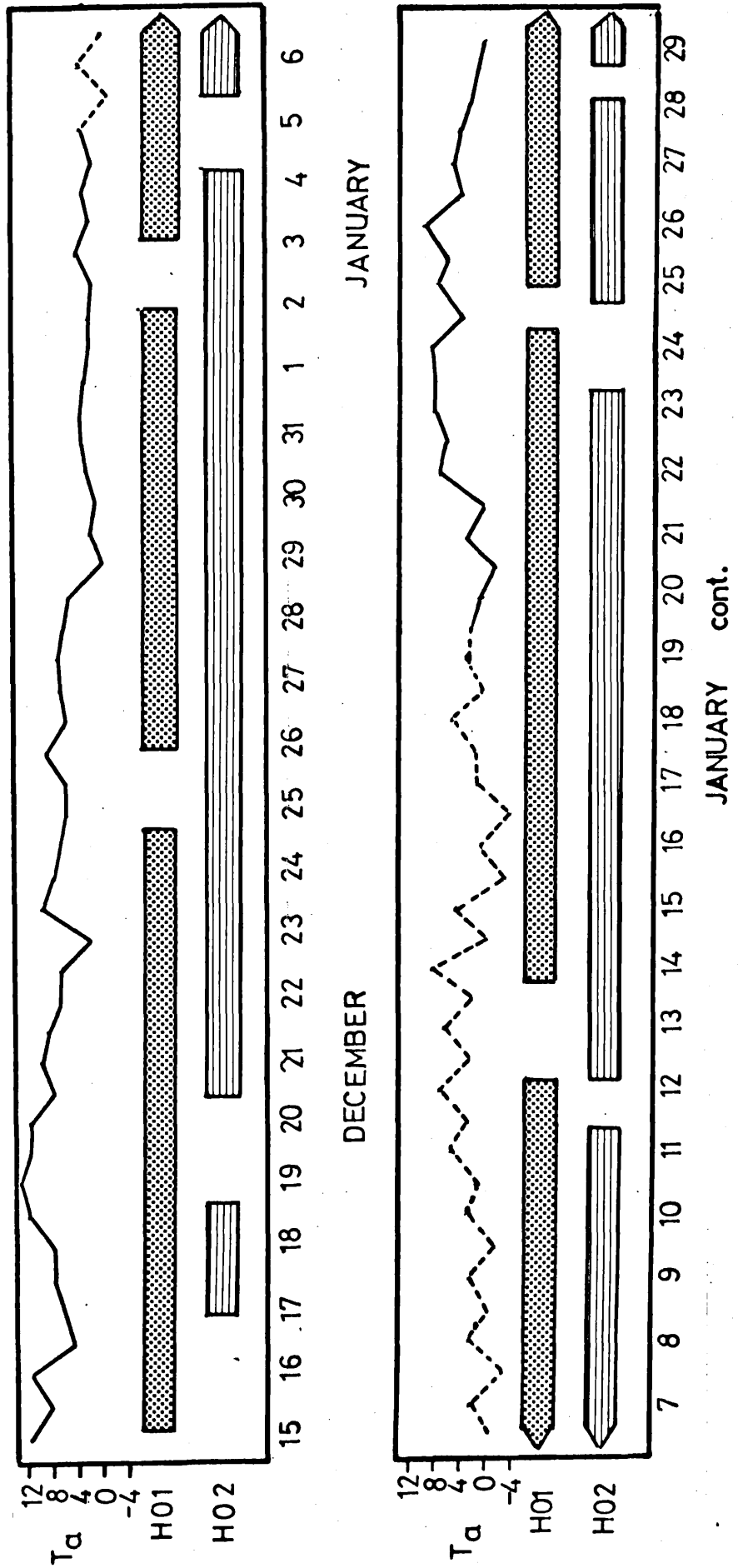
Fig. 4.3 cont.
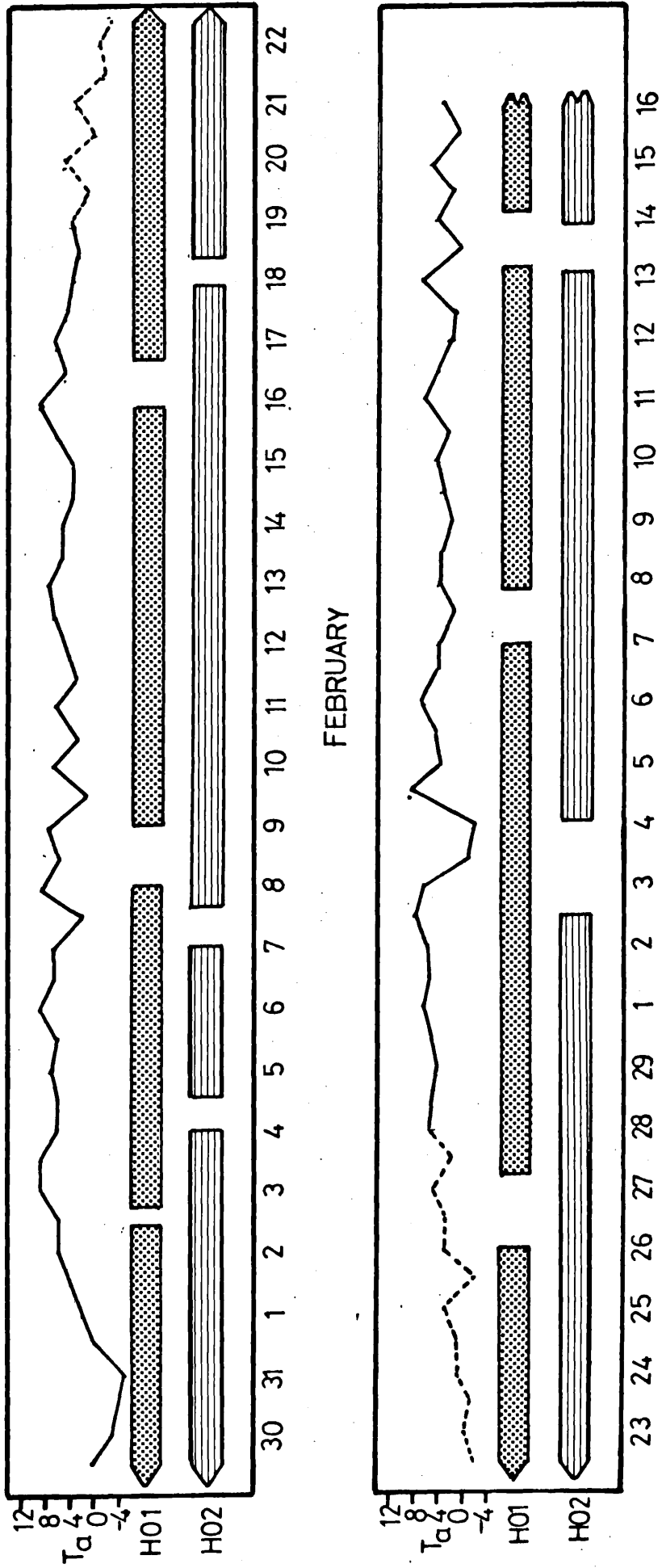
--- T$_a$ recorded by max/min thermometer,
— T$_a$ recorded by continuous temperature measurement

The experiment ran for ninety-two days and both
animals spent a little over nine days awake (HO1 - 9.13
days and HO2 - 9.33 days awake). Thus the animals were
hypothermic for about 90% of the duration of the experiment.
Fig.4.4. shows a typical arousal from hypothermia.

Fig.4.4 Ambient and nest temperatures during a typical arousal from hypothermia. Animal HO2, 28–30·1·72.

3.3. Nest Temperatures

The recorder thermistors were placed in the nest as close to the animal as possible. Hibernating animals are quite sensitive and easily aroused from hypothermia by disturbance during certain periods of a hypothermic cycle and it was possible to check the position of the thermocouples only during periods of arousal. The temperatures recorded represent the temperature of the nest (T_n), as close to the animal as possible, they were not direct records of the animal's body temperature (T_b).

It was rather difficult to decide the exact effect of the ambient temperature (T_a) on the T_n because of the large numbers of variables involved. The proximity of the animal to the thermocouple and the state of the animal, that is whether it was entering, leaving or in deep hypothermia are important in this respect. However, some generalisations can be made.

Fig. 4.5 presents the results of the study of the two animals throughout their hibernation period. Only the T_n and T_a at about mid-day and mid-night are included for sake of clarity.

The highest T_n that was reached during arousal varied from 14°C to 27°C (mean 18.59 ± 4.0°C, for twenty arousals). Kristoffersson and Soivio (1964a) show the highest T_b, taken at the posterior part of the animal, to be about 27.5°C. The 27°C recorded in the present experiments meant that, in that case, the thermistor was extremely close to the animal.

Fig.4.5 The relationship of ambient with nest temperatures (only midday and midnight records given).
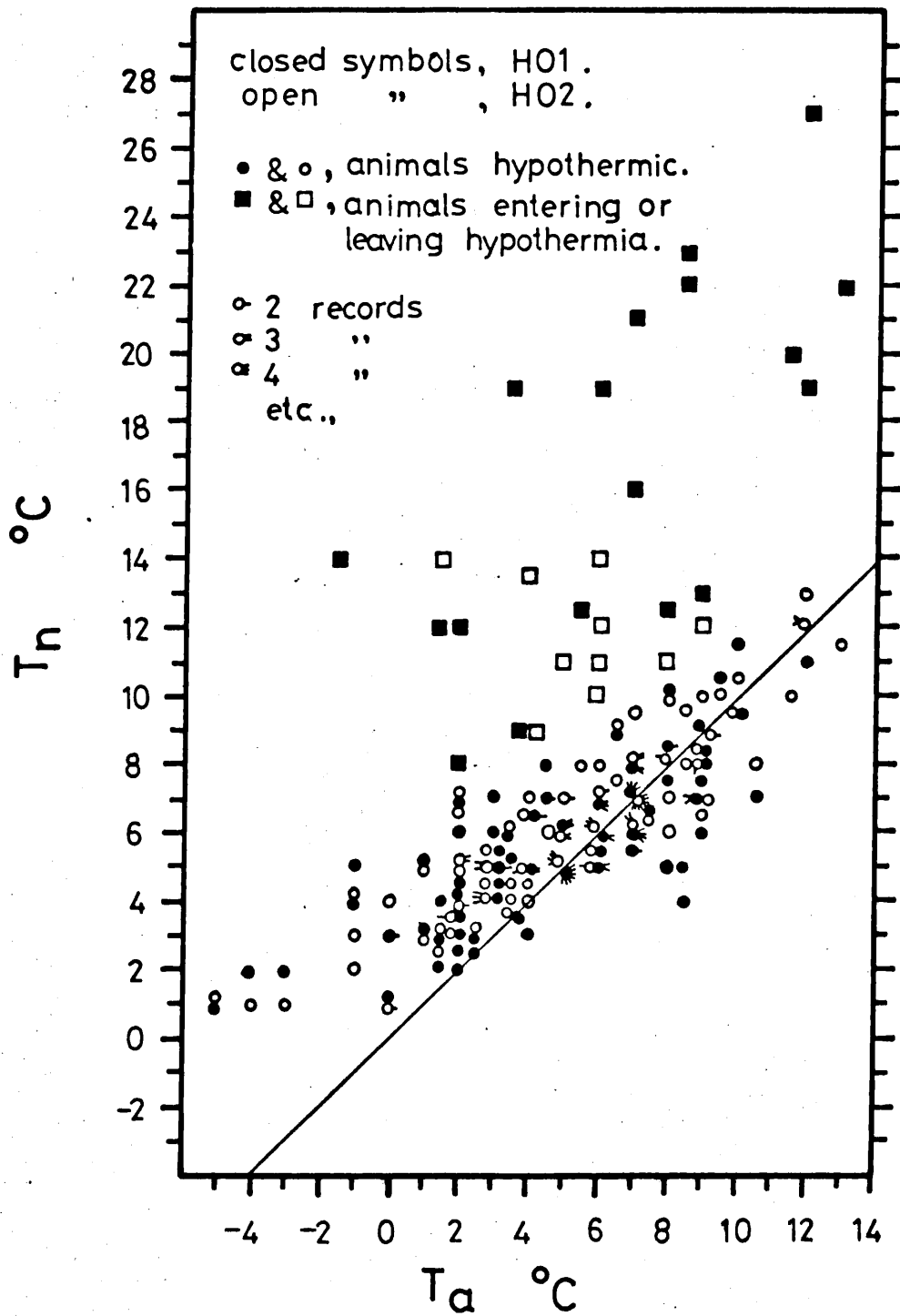
During hypothermia the temperature of hedgehogs approached T_a. A clear relationship of T_n with T_a was visible, taking into account the fact that the animals begin to thermoregulate when the T_a nears freezing.

When T_a was above about 7.0^oC T_n tended to be below the T_a recorded simultaneously. As T_n approached 7.0^oC, T_n became closer to T_a and usually, with T_a at below 5.0^oC, T_n was almost always higher than T_a. The difference between T_a and T_n increased as T_n grew less until at about -4.0^oC the difference was as much as five degrees (see Fig. 4.5.).

Usually ground temperature is a little higher than air temperature (T_a in the experiments). Also, at constant temperatures of 4.0^oC, the T_b of experimental animals is always about $0.2 - 0.8^oC$ above ambient (Kristoffersson and Soivio, 1964a). These two factors should have ensured that T_n never fell below T_a, but this was not found to be the case. However, of the occasions where T_a exceeded T_n significantly more records were observed at midday than at midnight ($\chi^2 = 8.70$, $p < 0.01$). Fig.4.6 shows a typical day/night cycle where, at times, T_a exceeded T_n.

Fig.4.6 Example temperature recordings to show the protection given by the hibernaculum against sudden changes in ambient temprature.

3.4. The Survival of the Flea Populations

A total of 136 *A.e. erinacei* were released on the three experimental animals. The fleas infesting the animals HO1 and HO2 were left completely undisturbed throughout the period of the study. Animal HO3 was removed from the pen and underwent enforced arousal on three occasions during its hibernation period.

A total of eighty-eight fleas survived the hibernation period of their hosts. This figure represents 64.7% of the number initially released. Survival varied on the three host animals. The proportion of survivors was similar on HO1 and HO3 ($X^2 = 0.99$, $0.20 > p > 0.50$). However, more fleas survived on HO2 than on the other two animals ($X^2 = 4.68$, $p < 0.05$).

There was no observed difference of survival of male and female fleas during the experiments. Fifty-three male fleas were released of which thirty-two survived (61.5%) and eighty-three females were released of which fifty-six lived through to the following spring (67.5%). When compared by means of Chi-square analysis the observed greater survival of females was not significant ($X^2 = 0.71$, $0.20 > p > 0.50$). Table 4.2 summarises the results of these experiments.

Four unmarked fleas were recaptured. These were probably individuals that had been overlooked during de-fleaing in the autumn, although they may have been transferred from other hedgehogs approaching the outside of the pen or may have been the results of successful winter or early spring breeding attempts by the flea populations

already infesting the animals. Nevertheless, from the point of view of this study recruitment into the flea populations was almost negligible during the hibernation periods of the animals.

Table 4.2.

The results from the mark and recapture experiments on *A.e. erinacei* infesting penned *E. europaeus* during the winter of 1971/2.

Serial No. of animal	Date of release into pen	No. of fleas		Total released	Date of defleaing	Marked fleas recaptured		Unmarked fleas recaptured		Total recaptured
		♀	♂			♀	♂	♀	♂	
HO1	15.12.71	49	19	68	13.3.72	30	8	2	-	40
HO2	15.12.71	22	16	38	24.4.72	19	11	-	-	30
HO3	15.12.71	12	18	30	13.3.72	7	13	1	1	22
TOTALS		83	53	136		56	32	3	1	92

3.5. Position of Fleas during Hibernation

At the beginning of the experiments thirty fleas were released on HO3. On three occasions the animal was removed from its hibernaculum while in deep hypothermia. Both the animal and its nest were searched for fleas. Table 4.3. shows the distribution of fleas between the animal and the nest on these occasions.

In every case almost all of the fleas were found on the body of the hedgehog.

In the final experiment the animal was defleaed before it had returned to normothermia. All of the twenty fleas infesting the animal were clustered into a single, well defined area of the pelage. The animal had hibernated, curled up on its left side, and all the fleas were found in the small furry area, between the spines and the almost bare belly, on the left side of the animal.

TABLE 4.3.

Date	fleas on animal		fleas in nest		Total
	♀	♂	♀	♂	
19.1.72	9	16	2	0	27
8.2.72	9	14	0	0	23
13.3.72	7	12	0	1	20
TOTAL	25	42	2	1	

3.6. <u>Feeding Experiments</u>

The gut of fleas is typical of many insects being divided into five major regions. A long narrow oesophagus terminates at a bulbous proventriculus which is, in fleas, specially adapted as a valve to prevent blood from leaving the next region, the very large, distensible mid-gut. The mid-gut, in turn leads to a narrow hind-gut which finally opens into the rectum with six rectal papillae.

In fleas the wall of the mid-gut is quite thin and the blood bolus, if present, is easily seen through them. The mid-gut is an approximately "L" shaped tube with a descending and a horizontal limb which join at an angle of about 135° in most cases. This organ can be viewed through the integument, with the aid of strong lighting from below and drawn by means of a camera lucida. The size of the mid-gut is a good indicator of the amount of blood which has been taken in due to the very small bore of all the preceeding organs (Ioff, 1949).

In the present study populations of fleas were collected and the measurements of absolute body size and the dimensions of the gut bolus were taken. The measurements were averaged for the population under investigation and resulted in an average size for the fleas and a "gut diagram" (see Fig.4.1.). The dimensions of female fleas were larger than those of male fleas, this resulted in bigger differences between the populations under comparison. Male fleas generally mirrored the results from female fleas but differences between populations were less well defined. Hence, only females were used to study the alimentary relat-

ionships of the fleas with their hosts.

Fig. 4.7 shows the gut diagrams for the control flea populations from non-hibernating hosts (a) and the diagrams derived from the three different sampling stages of the experimental insects (b, c and d).

The control fleas showed a distinctive gut diagram. The diameter of the whole mid-gut was about the same and the horizontal limb was larger than the descending limb. The gut took the shape of a parallel sided tube. It must be remembered that few of the animals in the sample had gut shapes of this form, but the fact that individuals were in all stages of intake and digestion of a blood meal meant that this "average" shape resulted. The gut diagram took the appearance of the mid-gut half-way between completed digestion, as seen in hungry fleas, and total distension, as seen in recently gorged fleas. Repetitions of these measurements gave similar results.

The gut diagram of the flea sample taken from a hibernating hedgehog showed some interesting variations from the gut diagram of the control insects. Overall, the bolus was quite small and the width of the gut at the transition from the descending to the horizontal limb was significantly less than in the controls. Similarly, the horizontal limb was narrower and shorter.

After the host had been arousing for an hour the fleas were once more removed, drawn and a gut diagram produced. The blood bolus was larger, in several dimensions, than the bolus of fleas from the hibernating host. The descending limb had not significantly increased in size but the width of the bolus at the transition between descending and

horizontal limbs had increased as had both the width and
the length of the horizontal limb. The descending limb was
both longer and wider than in control insects.

The population was studied finally after eighteen
hours on the aroused host. Only the length of the horizon-
tal limb of the bolus had changed; this had increased.
The gut diagram was very similar to the control diagram
except that the descending limb was still wider and the
horizontal limb not as long.

Table 4.4. summarises the changes in size, between the
different populations, of the gut bolus as shown by the
gut diagrams; it gives results of statistical comparisons
of the dimensions by "t" test.

The changes in the dimensions of the gut bolus contain-
ed within the mid-gut affected the overall size of the
abdomen of the fleas. The inter-segmental membranes allowed
the segments to "telescope", increasing the depth and length
of the body. In general, increase in the length of the
horizontal limb of the mid-gut resulted in an overall
increase in the length of the insect's body and increase in
size of the descending limb resulted in an increase in
depth of the abdomen.

Fig. 4.7 Diagrammatic representation of the measurements of the gut boli of fleas during the arousal experiments.
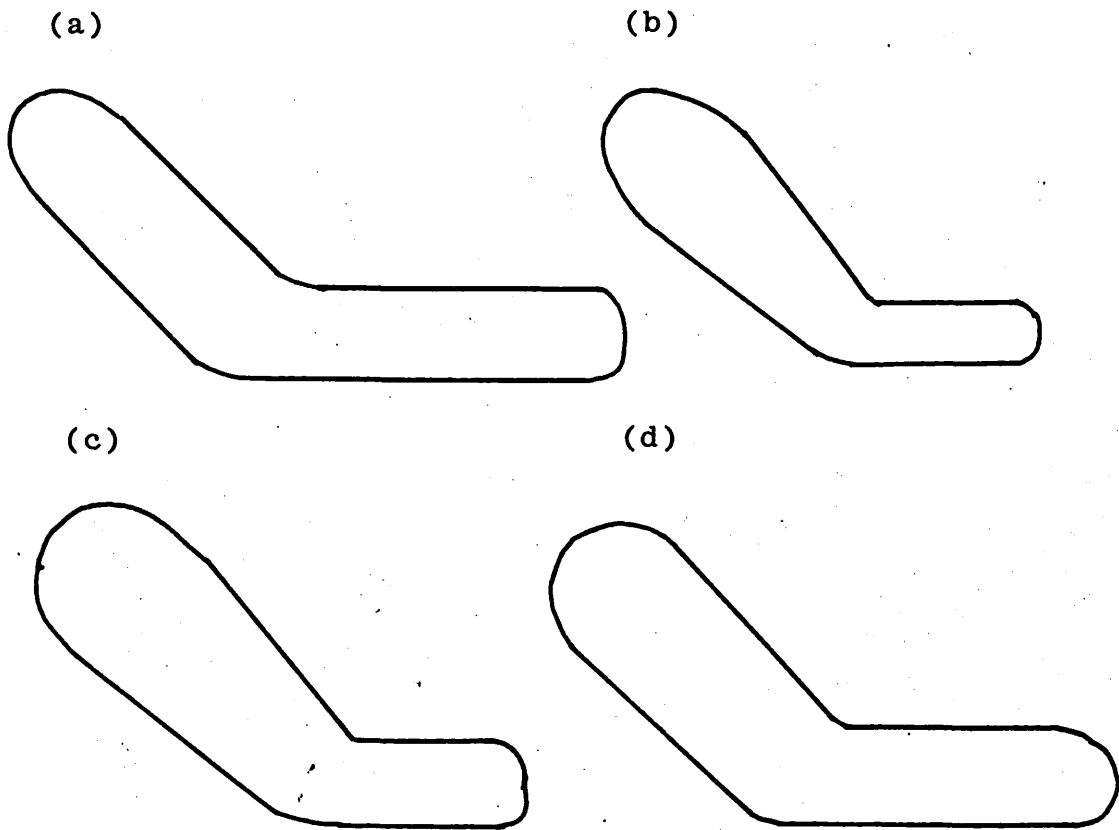
(a) Fleas infesting normothermic host.

(b) Fleas infesting hypothermic host.

(c) Fleas infesting host 1hr. after start of arousal.

(d) Fleas infesting host 18hrs. after start of arousal.

1 mm.

Table 4.4.

The dimensions (in mm.) of the different areas of the
gut blood bolus of *A.e. erinacei*.
   (n = number of insects in sample)

Also significant:- 1_a x 1_c : t = 2.37, p < 0.05

                      2_a x 2_c : t = 2.97, p < 0.01

                      3_a x 3_c : t = 2.50, p < 0.05

                      4_a x 4_c : t = 6.06, p < 0.001

                      4_b x 4_d : t = 4.64, p < 0.001

                      5_b x 5_d : t = 4.35, p < 0.01

Table 4.4.

The dimensions (in mm.) of the different areas of the gut blood bolus of *A.e. erinacei*
(n = number of insects in sample)

	a control n = 14		b hibernating host n = 19		c 1hr. after start of arousal n = 17		d 18hrs. after start of arousal n = 17		a control n = 14
1 Length of descending limb	0.771 +0.184	N.S.	0.823 +0.167	N.S.	0.930 +0.203	N.S.	0.870 +0.221	N.S.	0.771 +0.184
2 Width of descending limb	0.296 +0.084	N.S.	0.352 +0.105	N.S.	0.388 +0.095	N.S.	0.378 +0.095	t = 2.56 p < 0.05	0.296 +0.084
3 Width at transition	0.313 +0.063	t = 5.36 p < 0.001	0.174 +0.071	t = 3.16 p < 0.01	0.258 +0.071	N.S.	0.276 +0.084	N.S.	0.313 +0.063
4 Length of horizontal limb	1.045 +0.253	t = 6.27 p < 0.001	0.524 +0.203	t = 2.87 p < 0.01	0.560 +0.208	t = 4.07 p < 0.001	0.841 +0.200	t = 2.43 p < 0.05	1.045 +0.253
5 Width of horizontal limb	0.252 +0.032	t = 5.53 p < 0.001	0.158 +0.063	t = 2.62 p < 0.05	0.221 +0.071	N.S.	0.265 +0.071	N.S.	0.252 +0.032

Discussion

During the weeks immediately preceeding entry into
hibernation hedgehogs accumulate large quantities of food
reserves which are stored in the form of fat (Herter, 1933;
Kristoffersson and Suomalainen, 1964; Kristoffersson, Soivio
and Suomalainen, 1965). This occurrence accounts for the
rapid weight gains observed in the animals in this study.
The amount of weight gained by the animals in the present
experiments closely compared with the weight gained by
hedgehogs in similar experiments in Finland (Kristoffersson
and Soivio, 1967). Respiratory quotient analysis has
shown that the metabolism of hibernating hedgehogs is based
mainly on decomposition of fats (Suomalainen, 1962) and the
vast fat stores become diminished as hibernation continues.
The observed weight loss of about 40% in the present study
agrees with the amount of weight lost by animals in similar
experiments (Kristoffersson and Soivio, 1964 and 1967).

The Finnish authors Kristoffersson, Soivio, Suomalainen
and their associates have published a series of papers
concerned with the physiology and periodicity of hedgehog
hibernation. Their experiments were performed on laboratory
animals. The papers adequately introduce previous studies
of the subject. The results of this study on penned animals
under naturally fluctuating ambient temperature are similar
to those of the above authors on animals kept at constant
or controlled ambient temperatures. Kristoffersson and
Soivio (1964a) found the normal length of a period of hypo-
thermia to be about eight days (range two - thirteen days)

which agrees closely with results from the present study. The length of arousal periods was slightly different. Kristoffersson and Soivio reported the average length of arousal to be about two days whereas the hedgehog under fluctuating environmental temperatures were awake for an average of only twenty-one to twenty-two hours. It has been shown that long arousals cause increase in weight loss of animals over the hibernating period (Kristoffersson and Soivio, 1964c). Kristoffersson and Soivio provided neither food nor water for the hibernating animals. These were provided in the present study. It is possible that the Finnish animals searched for food and finally gave up after some time and returned to hypothermia, whereas the English animals found food on awakening and immediately returned to hypothermia. The amounts of energy expended on awakening probably need to be replaced or even extended by feeding to make that aspect of behaviour, during hibernation, valuable to survival of the animals.

The nest temperature during hibernation fluctuated depending on the ambient temperature and the physiological state of the occupant. It is widely accepted that when the environmental temperature approaches the freezing point of water the hibernating animal steps up its basal metabolic rate and always maintains its body temperature above freezing without awaking from hibernation (Lyman, 1963). Suomalainen (1954) recorded the lower limit of the body temperature of hypothermic hedgehogs, measured from the ventral body, surface, at +1°C. However, Kristoffersson and Soivio (1964b) have shown that electrodes implanted in

the interscapular region, never fall below +2.5°C, while

electrodes in the hind part of the body fell to below zero.

In the present study the nest temperature was always at

+1°C or above.

The difference between the nest and ambient temperat-

ures was greatest when the environmental temperature was

below freezing, the temperature of the nest was maintained,

at times, up to six degrees above ambient by the increased

body metabolism of the hibernating animal. When the ambient

temperature was at about +5 —+6°C the nest temperature

tended to lie close to the ambient. Above 6°C nest temper-

atures were frequently recorded at considerably less than

ambient. This is a rather surprising result when analysed

in isolation. The normal purpose of a nest is to "buffer"

the occupant against sudden drops in temperature by forming

an insulating layer between the animal and its environment.

It has been shown that during certain stages of the hedgehogs'

hypothermic periods the animals react to sudden rises in

the environmental temperature by arousal (Kristoffersson

and Soivio, 1964b). Sudden rises in the ambient temperature,

such as those that frequently occurred during daytime after

a very cold night, would have resulted in spontaneous

awakening. In these circumstances the nest acted as a

buffer to the sudden rises in ambient temperature. The nest

slowed down the warming up of the occupant and prevented

arousal. Fig. 4.6. shows a good example of the nest's

insulating properties. Morris (1967) reported similar

results and further observed that the nest protects the

animals from extremes in the environmental temperature and

from rapid thermal changes (Morris, 1973).

The preceeding paragraphs outline the conditions that are presented to hedgehog ectoparasites during the period of the host's hibernation. It is now possible to comment upon the effects of these conditions on the winter survival of the fleas.

Rothschild and Clay (1952) have noted active fleas on a hibernating hedgehog but gave no further details of the observation. The three flea populations released on the experimental animals after marking survived three months of hibernation on their hosts with about 35% mortality among the populations. There was almost no replacement of losses by individuals. It appears from this information that fleas undergo a sexually inactive winter period. Losses of 35% over a period of three months is probably quite low and it is possible that the inactivity of the host allows survival of fleas as opportunities for defleaing behaviour are much reduced.

When the hosts near the end of hibernation the fleas are ready to lay eggs. Nineteen fleas were taken in mid-March from a hibernating host to be drawn and they laid thirty-seven eggs in a little under one hour. It is not known if fleas continue to lay eggs during the winter which then remain dormant or hatch to produce another life cycle stage which undergoes dormancy. Further experiments would be necessary to elucidate this point.

During hibernation hedgehog fleas remain in direct contact with the body of the host rather than going into the nest. The population congregate on the side of the animal's body which is touching the bottom of the nest and not on the

more exposed upper side. These aspects of hedgehog flea
behaviour probably have considerable survival value.

The temperature of the host animal, more particularly
its anterior body parts, never falls below the freezing
point of water. The host's body remains four or five
degrees above ambient when the temperature is below freezing,
this fact undoubtedly increases the chances of flea survival
during the long winter periods of very cold weather.

It has been shown that hedgehogs often move their nest
site during their periodic arousals from hypothermia (Morris,
1973). The animals warm up very quickly and leave the nest,
this process may take less than one hour. If the hedgehog's
flea population inhabited the nest during hibernation it
might take them some time to detect the rise in the host's
body temperature and to recover their position on the host's
body. Many fleas would probably be left behind in the
abandoned nest, during a period of harsh environmental
conditions, if they had not maintained close contact with
the host's body.

There are many reports in the literature of fleas
leaving the bodies of dead hosts. This movement has usually
been attributed to the fleas ability to detect the decreas-
ing body temperature of the host. The hedgehog "dies" many
times during a hibernation period and yet the fleas retain
their association with the host. Thus, *A.e. erinacei* has
overcome what appears to be a basic piece of flea behaviour,
that is leaving the cooling body of a dead host, in order
to ensure that individuals are available to take advantage
of the next period of normothermia.

The "gut diagrams" represent an over-all picture of the state of feeding of the populations. When a population includes a spectrum of all the stages from engorgment to starvation the gut diagram will be similar to that for the control animals. When fleas were sampled as the host animal emerged from hibernation important changes were visible in the successive gut diagrams indicating that the fleas were feeding in a co-ordinated rather than a random manner. Feeding of the control fleas was not co-ordinated and the constant changing in the feeding state of single individuals did not affect the overall picture. The co-ordinated diagrams of fleas on the animal emerging from hypothermia was strong evidence that fleas infesting hibernating animals cannot feed. This is possibly due to a partial or complete shutdown in the epidermal blood supply of the host. The periods of hypothermia meant that fleas were starved for periods of up to fourteen days. The fleas only fed during the periods of host arousal.

The three stages in the gut diagram of the experimental animals closely approximate to the feeding sequence in an individual flea. The enlarged descending limb of the gut indicated that fleas began feeding almost as soon as arousal was initiated. The descending limb was enlarged at stage one but the horizontal limb was still very short and thin. At stage two the descending limb was even larger and the blood had passed down to begin to fill the horizontal limb. Finally in stage three the horizontal limb had continued to enlarge although it had not reached the length of the control fleas. The descending limb remained distended. This co-ordinated feeding clearly indicates that feeding is initia-

ted almost simultaneously throughout the population
possibly due to the detection by the fleas of the increase
in the host's body temperature.

The study of the survival of *A.e. erinacei* on hiber-
nating *E. europeus* has provided a very interesting comparison
with the behaviour of overwintering rodent flea species.
It has shown that the hedgehog flea has adapted its behav-
iour in several respects when compared with other flea
species in order to overcome the difficulties imposed upon
it by its host, and it may, in part, explain why attempts
to colonise the hedgehog by other fleas do not appear to be
successful.

C H A P T E R 5

GENERAL DISCUSSION

GENERAL DISCUSSION

Evans and Freeman (1950) commented upon the necessity for simultaneous study of both host and epifaunistic animals. This approach formed the basis of the work presented in this thesis concerning the ecological relationship between epifaunistic insects and their mammalian hosts. It was possible to observe changes that occurred in the behaviour and ecology of the mammal species and to identify synchronous changes that occurred within the communities of epifaunistic insects. For example, the levels of infestation of *C. nobilis* were seen to vary with time of year, host sex and age category, host species, home range size and, in some cases, settlement of hosts. These phenomena, among others, have been discussed in detail in the preceeding chapters. However, some aspects of the work deserve special comment particularly in the light of some previously published observations and suggestions for future study.

The basic technique, upon which all other analysis is founded, is the collection of insects from the bodies of the hosts. Techniques that have been used for collection of epifaunistic insects are rarely completely efficient. Ulmanen and Myllymäki (1971) have stated that it is probable that the numbers of fleas recorded on hosts are always underestimates and this may be true for other epifaunistic groups. Where collections are made for distributional, taxonomic or structural studies of insects complete accuracy is rarely required. However, during ecological studies, especially where infestation levels are low, the need for

efficiency of collection cannot be overstated. It is
accepted that techniques where hosts are captured alive,
sacrificed and searched must give the most accurate assess-
ments of infestation levels. However, it is probable that
anaesthetisation of hosts approaches the above method in
its level of accuracy.

The technique of "blowing", first described in detail
by Balthazard and Eftekhari (1957), has been frequently
used in this country in ecological studies of ectoparasites,
(see for example Evans and Freeman, 1950; Cotton, 1965 and
1970). Humphries (1967a and b) has expressed the opinion
that certain flea species, which are equipt with combs
consisting of regular rows of spines, are able to withstand,
to some degree, attempted dislodgement from the host's
pelage. In the present study it was observed that anaesth-
etised individuals of the genera *Megabothris* and *Malaraeus*,
which do not have genal combs, often fell from the host's
fur during defleaing. Whereas, individuals of the genera
Ctenophthalmus, Rhadinopsylla and, most especially, *Peromyscopsylla,*
which have genal combs, often had to be removed with the
aid of forceps. These observations seem to indicate that
"blowing" may not be equally efficient at removing all flea
species from the bodies of the hosts because of differen-
tial abilities to resist dislodgement.

No less important is the collection of those insects
which leave the host after its capture. Cowx (1967) has
shown that large numbers of fleas frequently leave the host
and enter the bedding material which is provided in traps
of the Longworth design when they are set. In the present
study it was observed that certain flea species were found

among the trap contents more frequently than others.
Adequate provision must be made in any collecting scheme
for these evasive insects. Both the ability of some fleas
to resist dislodgement and the readiness of fleas to leave
captured hosts merit further investigation.

Many authors have observed higher levels of flea
infestation during the summer months (e.g. Evans and Freeman,
1950 for infestation of *A. sylvaticus*; Cotton, 1970 and
Ulmanen and Myllymäki, 1971 for infestation of *M. agrestis*).
In the present study this general trend was also noted but
the high infestation of individuals with *C. nobilis* was
particularly pronounced during the pre-breeding season.
Miller (1958) has shown that home ranges are very large and
the high level of activity is probably linked with the fact
that females become fecund at that time, after the over-
wintering asexual phase of the annual cycle. It has been
suggested that emergence of coccooned *C. nobilis* from
abandoned nests may be the cause of sudden increases in
levels of infestation (Cotton, 1970). There can be little
doubt that during pre-breeding, when small mammal population
density is at its lowest (Southern, 1964), the numbers of
abandoned nests must be very high. Thus, it seems that these
two phenomena combine to ensure that the small mammals which
will found the new breeding populations are highly infested
with fleas. However, it is interesting to note that it is
male *A. sylvaticus* which harbour most fleas during pre-breed-
ing and this may be explained by the fact that males are
usually more active than females as determined by home range
size (Brown, 1966).

Mohr (1961) was able to demonstrate a relationship between the level of infestation of *Microtus californicus* with chiggers (Trombiculidae) and the host's home range size. During the breeding season a similar relationship was observed between individuals of *A. sylvaticus* and their flea infestations. This appears to be the first direct observation of correlation between home range and infestation levels in fleas. As has been pointed out by Mohr (1961) such relationships are unlikely to be simple and they may be linked with such factors as age, body size and maturity of the host's nest.

Smit (1957) has suggested that there are indications that *Apodemus* or its ancestors were the original principal hosts of *C. nobilis*. During the present study individuals of the species *C. glareolus* were more heavily infested with *C. nobilis* during both breeding and overwintering periods. Only among pre-breeding populations did the level of infestation of *A. sylvaticus* reach that of *C. glareolus*. This appears to suggest a possible preference of *C. nobilis* for the bank-vole. Further evidence for this theory was provided by the observation that, on *A. sylvaticus*, female *C. nobilis* outnumber males whereas, on *C. glareolus*, there were similar numbers of the two sexes. Evans and Freeman (1950) state that in some flea species females live longer than males. This is probably especially true during adverse conditions and it may be that the nests of *C. glareolus* are better suited for the survival of *C. nobilis* than are the nests of wood-mice. However, much more information is required before this view can be confirmed. Host specificity is an extremely

complicated aspect of the biology of fleas and Smit (1957)
has suggested that conditions within the host's nest
probably determine breeding success in many flea species
and, hence, fleas may be said to be nest-specific rather
than host-specific. Also, evidence involving sex ratios
must be viewed with some caution until information is
obtained concerning original sex ratios and possible sex
differences in the affinity of fleas for hosts.

Very little is known about the behaviour of small
mammals in the field. The use of mark and recapture of
fleas may provide useful information in this respect. The
results presented in Chapter 3 from the two limited trials
indicate that the technique is workable and that significant
numbers of fleas can be recaptured. Russian workers have
used recapture of marked fleas to indicate "contact" of
hosts (e.g. Sviridov, 1963). This idea is based on the
assumption that observed incidences of flea transfer are
indicative of host contact. In the light of work by
Vaughan and Mead-Briggs (1970), who showed that rabbit fleas,
S.c. cuniculi, could move only up to 9m towards urine baits
in short grass enclosures, it seems that this assumption
may be valid. Various authors have shown that fleas can
detect their hosts directly only over very small distances.
However, it should be noted that rabbit fleas are considered
to be semi-sedentary despite the fact that Mead-Briggs (1964)
has demonstrated a high degree of flea interchange between
hosts. Furthermore, Bates (1962) and Humphries(1968 and 1969)
showed that some species of bird flea are capable of quite
long movements in order to increase the chances of their

encountering a host. Thus, there may be some debate concerning the assumption that observed instances of flea transfer are indicative of contact between hosts. Nevertheless, it seems reasonable to assume that, in a majority of cases, interchange indicates close spatial or even physical contact. There is little doubt that the use of mark and recapture of fleas is a fruitful area of research worthy of further study.

Attempts to quantify numbers of fleas infesting small mammals in the nidicolous environment are rare in the literature. Only Davis (1934) and Cotton (1970) have studied this important aspect of flea ecology in this country. Difficulties in identifying host species, age or sex categories mean that a direct approach, that is searching for and studying actual nests, will have limited value. Release of marked fleas is an indirect method of investigating nest flea populations when used in conjunction with the equation of Lincoln (1930). However, application of the equation requires three assumptions: (i) that there is no population change through immigration, emigration, natality and mortality between the sampling periods (ii) all animals within the population are equally catchable and (iii) the marked animals mix freely with the rest of the population and are subsequently unaffected by the marking being neither easier nor more difficult to obtain than the marked ones. Clearly none of these assumptions can be made with certainty until more work has been carried out on the dynamics of nest flea populations.

Our ability to compare the levels of infestation of

different host categories with fleas has been restricted
because techniques are often both tedious and inaccurate.
Cole and Koepke (1947) have shown that standard statistical
methods are difficult to apply to results derived from
ectoparasite studies because of the marked skewness of
frequency distributions. Having realised this Evans and
Freeman (1950) and Ulmanen and Myllymäki (1971) used trans-
formation techniques in order to compare samples. Other
investigators have chosen to ignore the problems altogether.
The use of the Mann-Whitney "U" Test offered distinct poss-
ibilities in its application for comparison of levels of
infestation being a "distribution-free" test. However, when
applied in its standard form it was extremely unwieldy. A
tabular method was developed in the present study which
proved to be extremely quick and comparatively accurate.
Blank tables can be produced by photocopy and the relevant
values inserted. With the aid of only a small desk-top
calculator it was possible to complete statistical compari-
son of two samples in a matter of minutes.

During the non-breeding season voles of the species
M. agrestis inhabit "permanent" nests where microclimatic
conditions permit fleas to reproduce throughout the winter
(Cotton, 1970). This is almost certainly true for the other
small mammal species studied in this investigation. The
continuous winter activity of the hosts provide their epi-
fauna with a constant source of food and warmth. This is
most certainly not the case for insects infesting hibernat-
ing hedgehogs. During the present study the hedgehogs were
in hibernation, their body temperature close to ambient,

for about 90% of the winter period (mid-December to mid-March). Observations on the feeding activity of the fleas infesting the hibernating animals and normothermic control animals indicated that feeding of fleas occurred during the host's periods of arousal from hypothermia. However, many fleas were able to survive these conditions and in spring were ready to lay eggs. It is probable that this is the main overwintering method of the hedgehog fleas although other mechanisms cannot be ruled out. Humphries (1969) has shown that sand martin fleas, *Ceratophyllus styx jordani*, overwinter mainly as coccooned adults in old breeding nests and are stimulated to emerge by the exploratory habits of the sand martins newly returned from overwintering abroad. Although it seems unlikely that mammal fleas would undergo unforced separation from their hosts, emergence of imagines from abandoned nests may explain the high infestation with hedgehog fleas of some other mammal species, for example the fox, *Vulpes vulpes* L., (Buckle and Harris, unpublished data).

The work that has been described in this thesis has shown that, by close simultaneous examination of both mammal and insect communities, it is possible to increase our knowledge of the relationship between the mammal hosts and their epifauna. These findings and the techniques used to arrive at them provide a basis for the improved understanding of, and further investigations into, many aspects of this complex ecological relationship.

A P. P. E. N. D. I. C E S

I.   Some of the results of Trap Period A (1971).

II.   An example calculation using a tabulated system of
"U" analysis to compare the levels of infestation
of two small mammal samples with fleas.

III.   The numbers of captures of the three rodent species
during the twelve samplings of Trap Period B
(1972/3).

Appendix Table 1a (i)

The percentages of different flea species in monthly samples of rodents

(actual numbers in parentheses)

Flea species	MAR	APR	MAY	JUN	JUL	AUG	SEP	TOTALS
(i) A. sylvaticus								
C. nobilis	86.84 (33)	93.33 (70)	89.05 (122)	79.77 (71)	83.96 (110)	84.90 (45)	87.50 (21)	86.28 (472)
M. turbidus	-	-	8.75 (12)	17.97 (16)	12.97 (19)	9.43 (5)	12.50 (3)	9.68 (53)
R. pentacantha	13.16 (5)	5.33 (4)	2.18 (3)	-	-	-	-	2.19 (12)
M. penicilliger mustelae	-	1.33 (1)	-	-	-	-	-	0.18 (1)
R. silvatica spectabilis	-	-	-	2.24 (2)	3.05 (4)	-	-	1.09 (6)
H.t. talpae	-	-	-	-	-	5.66 (3)	-	0.54 (3)
TOTALS	38	75	137	89	131	53	24	547

Appendix Table 1a(ii)

The percentages of different flea species in monthly samples of rodents

(actual numbers in parentheses)

Flea species	MAR	APR	MAY	JUN	JUL	AUG	SEP	TOTALS
(ii) C. glareolus								
C. nobilis	55.66 (59)	80.95 (34)	73.07 (19)	65.71 (23)	83.33 (5)	66.66 (2)	33.33 (5)	63.09 (147)
M. turbidus	-	-	-	-	-	33.33 (1)	20.00 (3)	1.71 (4)
R. pentacantha	25.47 (27)	2.38 (1)	-	-	-	-	6.66 (1)	12.44 (29)
M. penicilliger mustelae	13.20 (14)	16.66 (7)	26.92 (7)	25.71 (9)	16.66 (1)	-	-	16.30 (38)
P. silvatica spectabilis	-	-	-	-	-	-	20.00 (3)	1.28 (3)
H.t. talpae	5.66 (6)	-	-	-	-	-	13.33 (2)	3.43 (8)
M. walkeri	-	-	-	8.57 (3)	-	-	6.66 (1)	1.71 (4)
TOTALS	106	42	26	35	6	3	15	233

Appendix Table 1b

The sex ratio of flea species from *A. sylvaticus* and

C. glareolus during Trap Period A (1971)

Species	No. of Fleas		Total No.of Fleas	% male	χ^2	p
	♀	♂				
(i) **A. sylvaticus**						
C. nobilis	293	179	472	37.92	27.53	<0.001
R. pentacantha	7	5	12	41.66	0.33	>0.05
M. turbidus	33	20	53	37.73	3.18	>0.05
P. silvatica spectabilis	4	2	6	33.33	-	-
M. penicilliger mustelae	1	0	1	0	-	-
H.t. talpae	3	0	3	0	-	-
(ii) **C. glareolus**						
C. nobilis	87	67	147	40.81	4.95	<0.05
R. pentacantha	14	15	29	48.27	0.01	>0.05
M. turbidus	2	2	4	50.00	-	-
P. silvatica spectabilis	1	2	3	66.66	-	-
M. penicilliger mustelae	25	13	38	34.21	3.79	>0.05
H.t. talpae	5	3	8	37.50	-	-
M. walkeri	2	2	4	50.00	-	-

Appendix Table Ic.

The numbers of host captures and the numbers of

L. testaceus taken from the Trap Period A. (1971)

HOST SPECIES	HOST SEX	HOST CAPTURES	No. OF BEETLES
Apodemus	♂	286	93
sylvaticus	♀	163	36
	BOTH	449	129
Clethrionomys	♂	63	3
glareolus	♀	27	0
	BOTH	90	3

Appendix Fig. I a. The numbers of *Apodemus sylvaticus* and *Clethrionomys glareolus* individuals captured during Trap Period A. (1971)
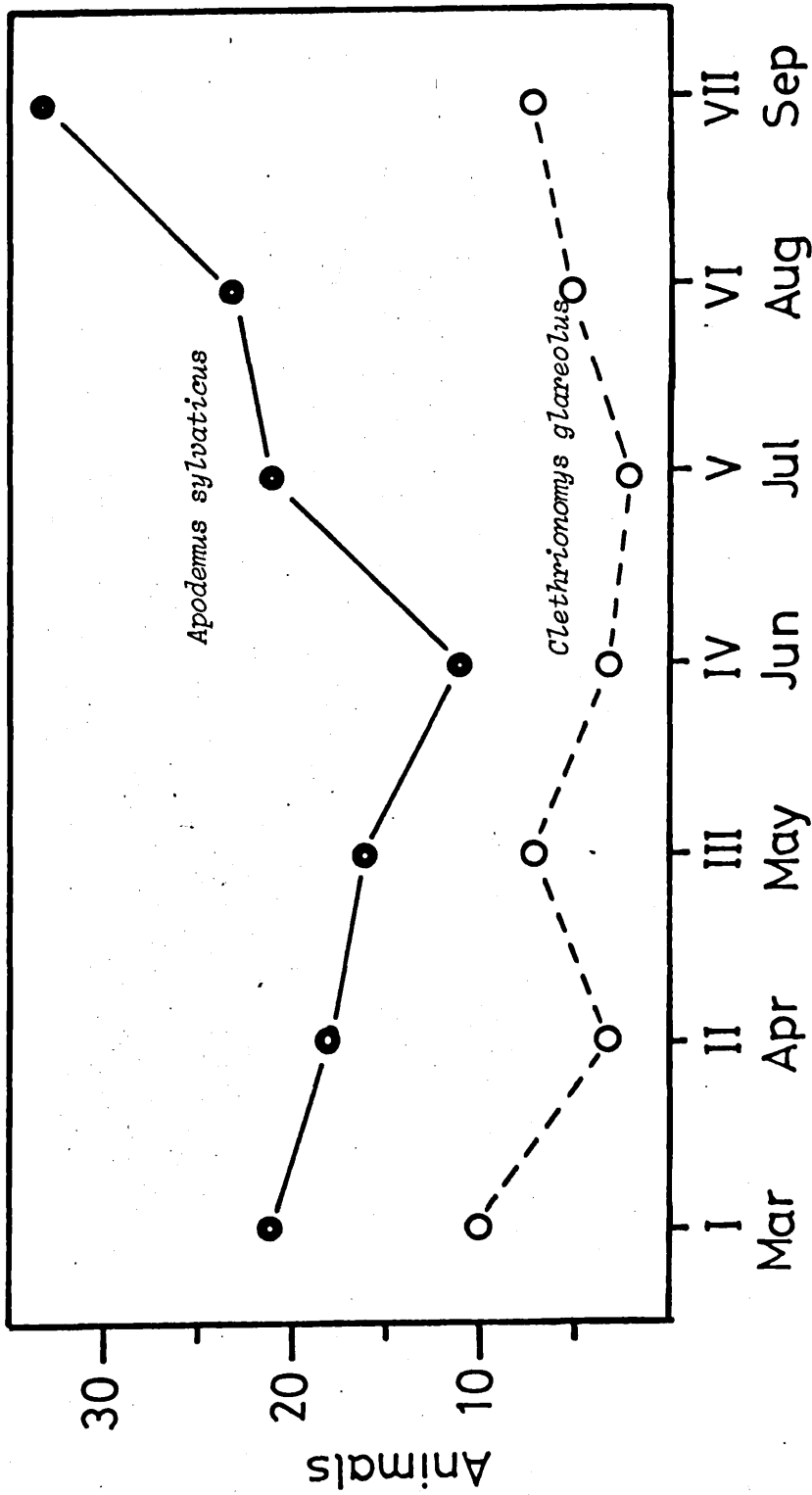
Appendix Fig. I b. The infestation index and percentage infestation of
C.nobilis on captures of *A. sylvaticus*. Trap Period A. (1971)
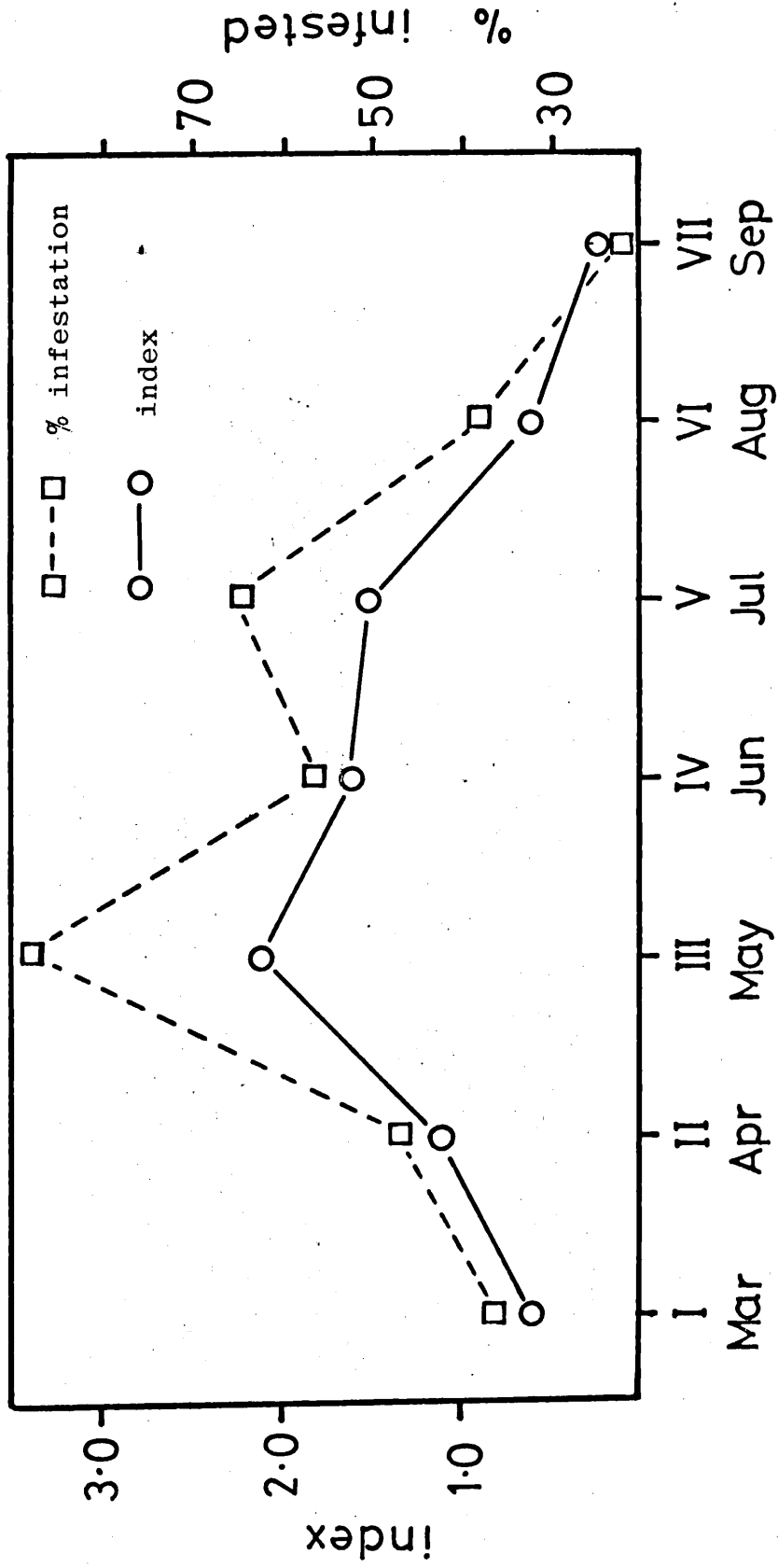
Appendix Fig I c. The *L. testaceus* index on *A. sylvaticus* for Trap Period A. (1971). Dotted lines indicate the index during Trap Period B. (1972/3).
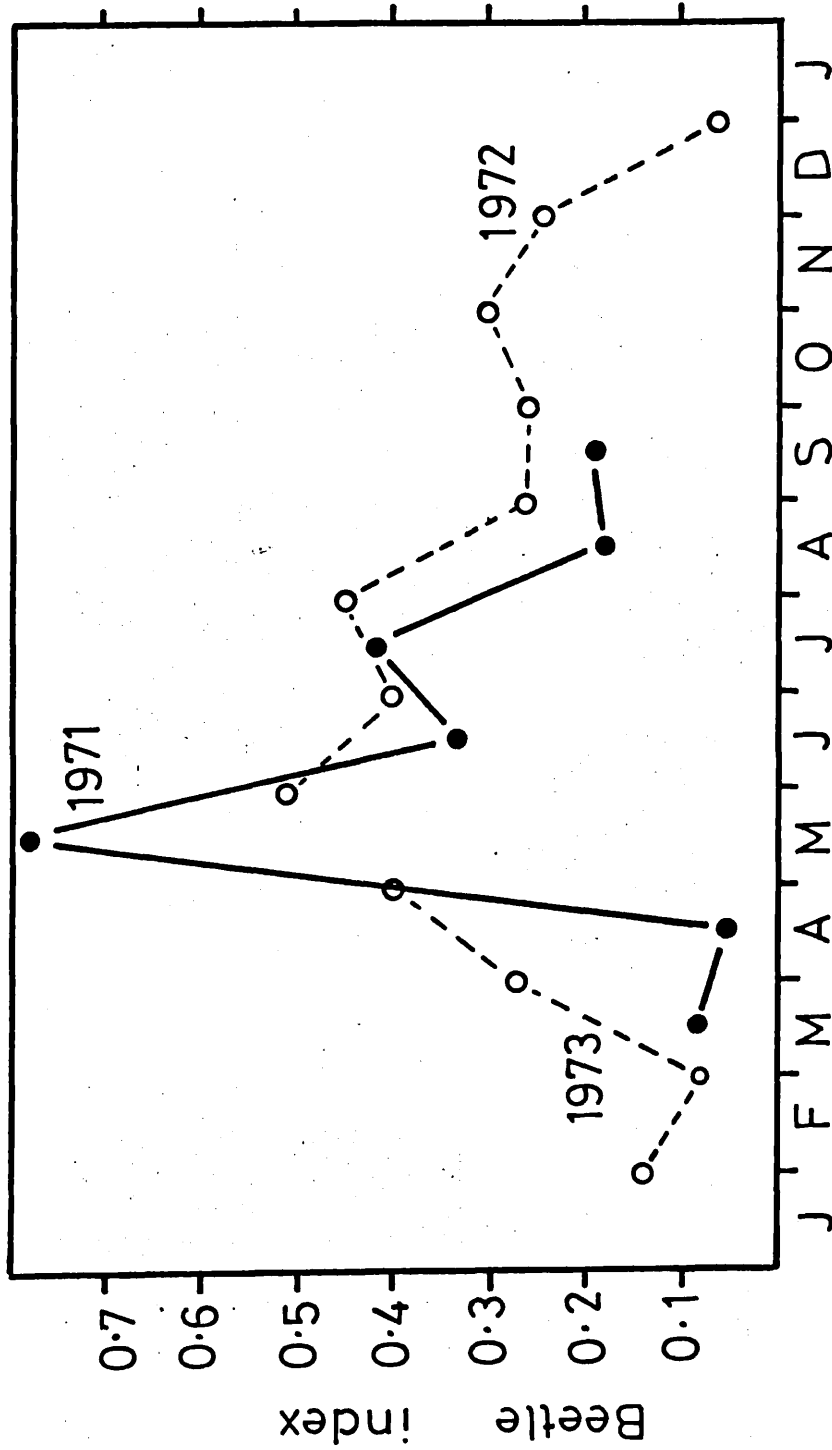
Appendix Fig. III. The numbers of captures of the three rodent species during the twelve samplings of Trap Period B (1972/3).

Appendix II

An example calculation using a tabulated system of "U"

analysis to compare the infestation of two samples with

fleas.

The two samples for comparison are set out in a table

of distribution (rows 1,2 and 3, Table II). The total

number of counts at each frequency for the populations is

added in row 4. The number of inferior ranks for each

distribution frequency can be obtained by summing all the

previous counts in row 4. Thus, the 328 zero counts have

no inferiors, But, all the zero counts are inferior to the

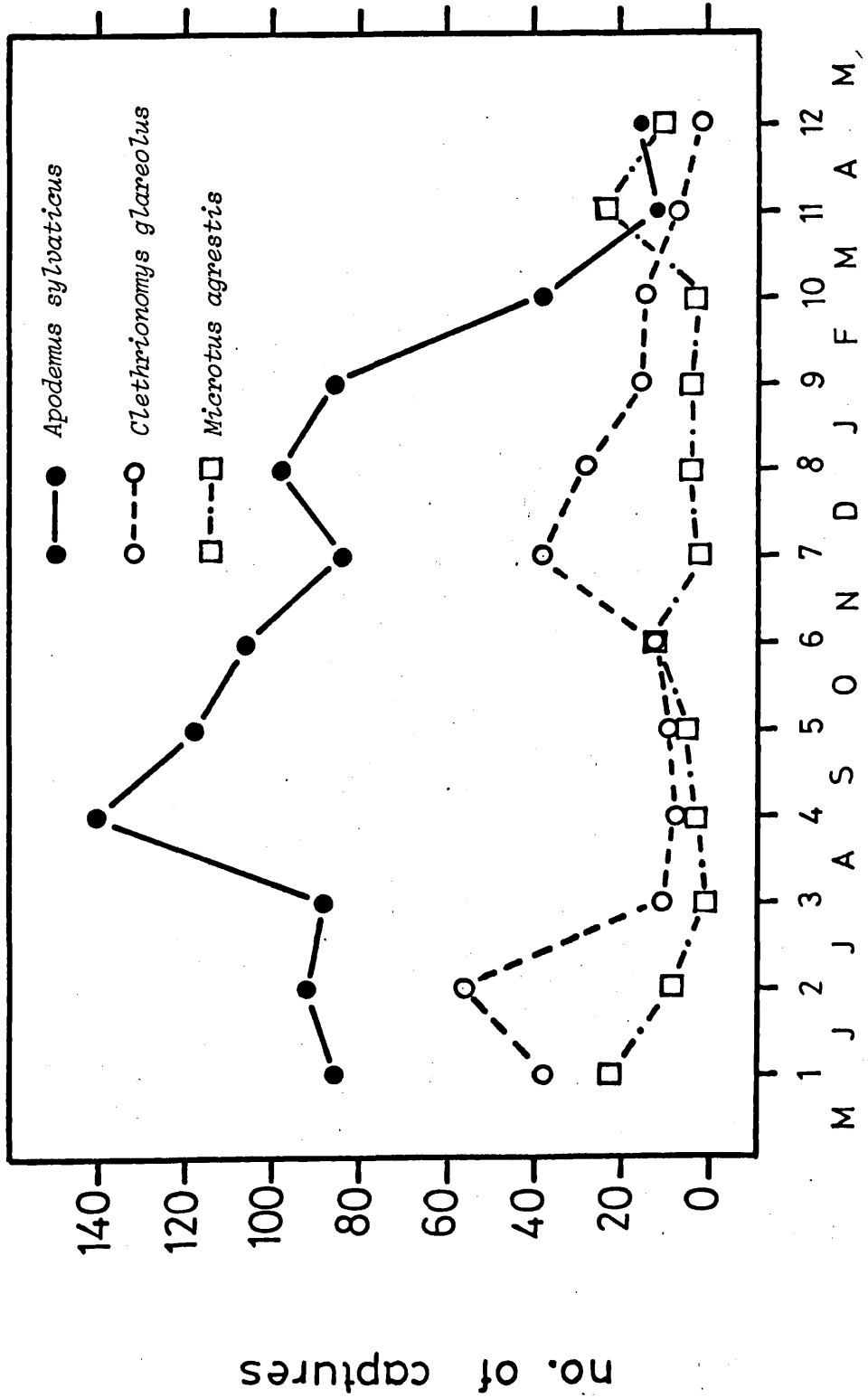counts of one and the 328 counts for zero and the 164 counts

of one are inferior to the counts of two, and so on. All

the tied counts must be given the rank of the average of

all the total ranks of the tied counts. For example, the

zeros will occupy ranks one to 328 and, therefore, the

average zero rank is 164.5. There are no inferior ranks and

the rank of each zero count is 164.5. The counts of one

will occupy ranks 329 to 492. The average of the tied

counts is 82.5 but the 328 inferior ranks give each count

of one a rank of 410.5 (328 + 82.5). The actual ranks of

each frequency of the distribution are then calculated in

that manner.

"R" is now calculated for each population. Each R is

the sum of all the ranks in the population.

"U" can be calculated in the normal way (Elliott, 1971).

$$U_1 = n_1 n_2 + \frac{n_2(n_2 + 1)}{2} - R_2$$

$$U_2 = n_1 n_2 + \frac{n_1(n_1 + 1)}{2} - R_2$$

Table of "U" cannot be used when N_1 and N_2 are very large, as in this case. The sampling frequency of "U" approaches the normal frequency distribution with mean, $\frac{n_1 n_2}{2}$. Therefore the normal deviate is calculated.

$$d = \frac{U - (n_1 n_2)/2}{\sqrt{\dfrac{n_1 n_2 (n_1 + n_2 + 1)}{12}}}$$

In the above test the null hypothesis is that the two samples are, in fact, drawn from the same parent distribution. Ho is rejected at 5% level ($p = 0.05$) when d is greater than 1.96, at the 1% level ($p = 0.01$) when $d > 2.58$ and at 0.1% level when $d > 3.29$. In the above example $d = 3.92$ and therefore Ho is rejected ($p < 0.001$).

The use of the Mann-Whitney "U" test in this case has two distinct advantages.

(i) The test makes no assumptions as to the distribution of the sample. It is a "distribution-free" test and no transformations are needed, and, hence, it is not necessary to calculate the best-fit to any parent distribution.

(ii) The test takes into account the frequency distribution of the sample. The low numbers of very high infestaations are reduced in their importance in the overall results. Thus, in the above example the counts of 23

Appendix Table II

A worked example of the Tabulated Mann Whitney "U" Test

		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	>18	>23
1	No. of Fleas	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	>18	>23
2	Frequency of sample I.	140	83	67	37	23	10	9	4	3	5	4	-	-	-	2	-	-	-	1
3	Frequency of sample II.	188	81	39	25	16	6	8	8	-	2	1	-	-	-	-	-	1	1	1
4	Added frequency distributions	328	164	106	62	39	16	17	12	3	7	5	-	-	-	2	-	2	1	1
5	inferior ranks	0	328	492	598	660	699	715	732	744	747	754	-	-	-	759	-	761	763	764
6	Average of tied ranks	164.5	82.5	58.5	31.5	20	8.5	9	6.5	2	4	3	-	-	-	1.5	-	1.5	1	1
7	rank for each count	164.5	410.5	550.5	629.5	680	707.5	724	738.5	746	751	757	-	-	-	760.5	-	762.5	764	765.0

$R_1 = 161196.5$

$R_2 = 132564.5$

$n_1 = 389$

$n_2 = 377$

$U_1 = 389 \times 377 + \dfrac{377 \times 378}{2} - 132564.5 = 85341.5$

$U_2 = 389 \times 377 + \dfrac{389 \times 390}{2} - 161196.5 = 61311.5$

taking smaller value of U, i.e. U_2

$d = \dfrac{61311.5 - 146653/2}{\sqrt{\dfrac{389 \times 377 \; (389+377+1)}{12}}} = 3.924$

$p = \; < 0.001$

Table II continued

fleas for a single animal are, comparatively, insign-

ificant when compared with the counts of one. Whereas

in Chi-square analysis the counts of 23 would carry

more than $\frac{1}{4}$ of the weight of the 83 or 91 counts for

one flea.

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those used in the World List of Scientific Periodicals.
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