THE COMPARATIVE ECOLOGY OF THE TWO BRITISH SPECIES OF THE GENUS APODEMUS (RODENTIA, MURIDAE)

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SUMMARY

Apodemus sylvaticus and *A.flavicollis* are distinct but sympatric species in Britain and parts of north-western Europe.

Much data exists on the ecology of *A.sylvaticus* in areas where *A.flavicollis* is absent. This has been summarised and compared with a new study of a mixed *A.sylvaticus* / *A.flavicollis* population in central Essex. In the presence of *A.flavicollis* the winter average population densities of *A.sylvaticus* were significantly lower than in single species populations. In other respects investigated (survival, breeding season, movements, habitat selection within woods, annual population cycle) *A.sylvaticus* ecology did not appear to be affected by the presence of *A.flavicollis*.

A.flavicollis ecology differed from that of *A.sylvaticus* in the following respects:-

a. It was rarer - representing about ¼ to 1/5 of the *Apodemus* population.

b. *A.flavicollis* was less selective of habitat *within* woods but less likely to be resident outside woodland habitats.

c. Individuals were more mobile.

d. The breeding season may be shorter.

In Essex both species of *Apodemus* are widespread but *A.flavicollis* does not spread so far into urban areas as does *A.sylvaticus* nor is it equally common in all woodland areas. There is some evidence that the most favourable woods are those in close proximity to arable land.

On a national basis the restricted range of A.flavicollis is difficult to explain but the species seems to show some tendency to favour lowland areas with a mixture of woodland and arable land. If this relationship is genuine then large edge effects must occur.

It is suggested that A.flavicollis can avoid competitive exclusion by A.sylvaticus when habitat conditions allow a partial separation of breeding habitat by the two species, and that the two species were brought into competition by man's fragmentation and intermixing of woodland and more open habitats.

PREFACE

This study was carried out between October 1966 and July 1973. During the first year of the study I was a full-time student of Royal Holloway College and wish to express my thanks to that College for a grant to cover registration fees. The remainder of the study was carried out on a part-time basis and I wish to thank my employers (North East London Polytechnic) for allowing me the time and facilities to pursue this research. The field work equipment was loaned to me by Royal Holloway College, North East London Polytechnic and the Essex Field Club.

The field work for the intensive survey study was carried out on the Coptfold Estate, Essex. The owners of the estate (Col. and Mrs P.V.Upton) have been exceptionally helpful, allowing all my requests to work on their land and providing me with accommodation while I was engaged in the field work. Many other Essex land-owners have permitted me to enter private land for the purpose of mouse trapping and I wish to express my thanks to them also.

Most of the field work I performed myself, but many friends and naturalist colleagues have assisted on occasions. In particular I wish to thank Messrs R.A.D.Cowlin, S.Harris, T.Lording, M.Nockles and R. Nockles. I also wish to thank the members of the Mammal Society, the Essex Field Club and other naturalists who assisted by taking part in the surveys of distribution.

My thanks are due to the staff of the computing section of North East London Polytechnic who tolerated and encouraged my early attempts to learn the art of computer programming, and especial thanks to my colleague Mr J.Rostron for advice on statistical matters.

Most of all my thanks are due to Dr G.I.Twigg who acted as my supervisor throughout this study and provided me with much useful advice, encouragement and constructive criticism.

I declare that, apart from the assistance acknowledged above, this thesis and the study described therein is my own unaided work. The main part of the thesis reports a new study which has not previously been published. I append copies of four papers which I have written on topics related to the subject of this thesis. One of these papers was published jointly with two other authors. These papers are offered in support of the thesis and not as an integral part of it.

In my opinion this thesis contributes to the knowledge of small mammal ecology in two main ways. It provides a critical summary of much of the British work on the ecology of A.sylvaticus, including the development of a new technique which makes easier the comparison of the population dynamics from a variety of published sources. The study of Apodemus in Essex is one of the few investigations of A.flavicollis ecology in Britain and is probably the most detailed investigation of the population dynamics of this species yet completed in Britain. I believe that the combination of extensive and intensive live-trapping surveys is a novel approach to the study of small mammal distribution and that it may be possible for other workers to use this technique to combine the results of amateur and professional studies, thus obtaining more information than can be obtained from either type of survey alone.

INTRODUCTION

Competition in co-genereric British mammals

'As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between species of distinct genera.'

(Darwin, 1859)

Since Darwin wrote the above words the idea of competition, and its possible role in ecology as well as evolution, has been much discussed. Volterra (1926), Lotka (1932) and Gause (1935) provided the mathematical proof of what has become known as 'the competitive exclusion principle'. Briefly this principle can be stated as follows:- Two similar species exploiting the same ecological resources will be in competition with each other. One or a few factors will regulate the <u>combined</u> population of the two species. One of the species is certain to be more effective (however slightly) than the other in exploiting the resources. In this case, although the total population remains constant, the more successful species will increase its proportion of the population. Eventually the more successful species will completely replace the other. If two similar, sympatric species survive indefinitely this must indicate that they are not competing for exactly the same ecological resources (i.e. the two species have somewhat different ecological niches).

The competitive exclusion principle is obviously true in the clearly defined hypothetical condition when the two species have identical ecological niches. The difficulty is that two species (if they are different enough to be recognised as specifically distinct) are extremely unlikely to share precisely the same ecological requirements. The practical question remains to be answered: How ecologically similar can two species be before competitive exclusion will occur?

As Darwin suggested, studies on pairs or groups of sympatric species from the same genus are of great importance when trying to answer this question. The genus is a subjectively defined taxon but within a well known larger taxonomic grouping it is usually safe to assume that cogeners are more similar than any pairs of species from different genera. Considering the British terrestrial mammals there are seven genera with two or more British species (Corbet, 1964). The bats and whales are not considered here as their distribution and ecology is poorly known; also consideration of competition within the limited, continental island fauna is more relevant to the subject of this thesis. For a whale or a bat Britain is little different from the rest of western Europe. Table 1 lists the British species of the seven genera and gives some information on their status.

The Sorex species have not been well studied in Britain and it is not known if they differ in food requirements. However, detailed studies in the Netherlands (Michielsen, 1966) have shown that during the winter, when food is likely to be limiting, the two species differ in their main vertical zone of activity. Sorex araneus spends four-fifths of its time below ground, whereas S.minutus spends more than half its time above ground. This partial vertical zonation indicates a difference in the ecological niches of these species. The fact that this separation of niche is associated with competitive interaction is indicated by the situation in Ireland where only S.minutus occurs. In the absence of S.araneus, S.minutus appears to be more common than in Britain. (Corke, Cowlin and Page, 1969. A copy of this paper is included as appendix 4 to this thesis.)

One of the four Mustela species (M.vison) is a very recent introduction to Britain. It is still spreading and becoming established, but its interaction with the native Mustela species remains to be studied. Of the native species M.nivalis and M.erminea, although showing an overlap of prey species, concentrate on different size categories of prey (Day, 1968). M.putorius like M.erminea, takes rabbits (Oryctolagus cuniculus (Linn.)) as one of the most important items of its diet, or at least this was so before myxomatosis reduced the rabbit population, (Southern, 1964). Thus these two species are potential competitors but M.putorius is a more aquatic species than M.erminea. The present restricted distribution of M.putorius is due to human persecution and not competition with M.erminea.

The two species of Lepus show clear separation of habitats in Britain and this is reflected in their geographical distribution (Corbet, 1971). L.timidus is a species of high, mainly northern, moorlands, while L.capensis is a lowland species. L.timidus is the only native Lepus species in Ireland (introduced L.capensis have not become widely established) and it there occupies a much wider range of habitats than in Britain. This indicates that in Britain, L.timidus has been competitively excluded from lowland habitats.

Only one species of Sciurus is indigenous to Britain, S.carolinensis being a recent introduction. The replacement of S.vulgaris by S.carolinensis over much of Britain has been well documented (Shorten, 1954 ; Lloyd, 1962). Clearly this is an example of competitive exclusion although the precise nature of the competition is in doubt. Actual combat, competition for food or variation in disease resistance are all possibilities.

Cervus nippon is a recently introduced deer while its congener C.elaphus is a native. The distribution and abundance of deer have been greatly modified by man and competition may be eliminated if man selectively culls the more abundant species. As yet the ecology of the two species in forests, where they occur together, has not been compared.

Both species of Rattus are introductions, R.rattus having arrived first, become common and then been replaced almost completely by the later introduction, R. norvegicus (Southern, 1964).

The situation in *Apodemus* is intriguing and not well understood. Despite the apparent ecological similarity between the two species, *A.flavicollis* seems to exist in competition with *A.sylvaticus* in parts of Britain. The situation has often been quoted as a contradiction of the competitive exclusion principle. For example:-

> 'There is no clear reason why the widely adapted wood mouse (*Apodemus sylvaticus*) has not entirely replaced its cogener, the yellow-necked mouse (*Apodemus flavicollis*) in Britain,..... *A.sylvaticus* would appear to be able to inhabit every woodland habitat in Great Britain, and there is no evidence to show that *A.flavicollis* is a more productive species.'
>
> (Miller, 1967)

It is this situation that I have set out to investigate. As befits the most abundant and ubiquitous of British mammals, a great deal of ecological research has been carried out on *A.sylvaticus*. However, most of this research was carried out in habitats from which *A.flavicollis* was absent. What I have attempted in this work is to summarise the known facts about the ecology of *A.sylvaticus* in habitats where *A.flavicollis* is absent, and to compare this with the ecology of the two species living in the same area. The aim has been to answer the following questions:-

1. When the two *Apodemus* species occur together are their niches sufficiently distinct to permit their indefinite sympatric existence?
2. Does the presence of *A.flavicollis* change the ecology of *A.sylvaticus*?

3 Why has A.flavicollis not extended its range further into Britain, or alternatively, been excluded completely by A.sylvaticus?

Section 1

THE TAXONOMIC RELATIONSHIP OF APODEMUS SYLVATICUS AND A.FLAVICOLLIS

It is not my intention to attempt a revision of the genus Apodemus. My main aim in this section is to consider to what extent A.sylvaticus and A.flavicollis can be regarded as separate species. Although my own investigations have been into the ecology of Apodemus in Britain, work from elsewhere is clearly relevant to the discussion - provided one bears in mind that the taxonomic (and presumably ecological) relationships between the two forms may not be the same throughout their range.

The genus Apodemus (Kaup 1829) contains fairly primitive murids with non-prehensile tails, the skin of which strips off easily if the tail is gripped. They have complex cheek teeth and a well developed rostrum. The genus is Palaearctic in distribution, the structurally very similar mice from Africa being placed in the genus Thamnomys. Apodemus shows little major variation - especially in skeletal characteristics on which so much of taxonomy is based. However, minor local and individual variation in size, body proportions and details of colouration is common. This has led to a proliferation of names for species and sub-species many of which have later been shown to be invalid.

Ellerman and Morrison-Scott (1953) list five species; these I have included in table 2 together with A.microps which is a more recent discovery. In preparing this table I have accepted Ellerman and Morrison-Scott's views on the Asian species although, as indicated below, the taxonomy of these eastern forms is uncertain. For the European species I have followed Corbet (1966) in accepting *A.microps* but have excluded the recently described *A.krkensis* (Miric, 1968) on the grounds that it is a small island population and probably has the same relationship to *A.mystacinus* as Matthews (1952) described for the discredited *A.hebridensis* with *A.sylvaticus*.

A.speciosus is restricted to Japan (Ellerman and Morrison-Scott, 1953). *A.mystacinus* is found in the Balkans and from Asia Minor to Israel (Corbet, 1966). *A.agrarius* is much more widely spread throughout most of the broad-leaved zone of Asia and in the eastern part of Europe. The details of sub-specific variation, distribution and sub-generic relationships are not yet understood, but most workers accept these three species as Ellerman and Morrison-Scott defined them (e.g. Corbet, 1966; Zimmermann, 1962).

The taxonomy of *A.flavicollis* and *A.sylvaticus* is much less settled. The main reason for the difficulty is that no skeletal characteristics which give a good separation of species have been discovered. This difficulty led Ellerman (1941) to adopt a totally arbitrary classification by size - '*sylvaticus*' type mice with an occipito-nasal length over 27 mm being regarded as '*flavicollis*'. This meant that a large number of *Apodemus* forms from eastern Asia were included with *flavicollis* or *sylvaticus*. Zimmermann (1962) has shown that these forms differ in their dental characteristics and he regards them as a species within the separate sub-genus *Alsomys*. This revision leaves the European and west Asian *flavicollis* and *sylvaticus* together with *A.microps* in the sub-genus *Sylvaemus*. The approximate ranges of the three species are shown in figure 1.

The specific distinctness of *A.sylvaticus* and *A.flavicollis* has often been questioned. Larina (1961) reported that in Russia she was able to hybridise the two species in laboratory conditions. Felten (1952) reported that it was not always possible to separate the two species in Germany, and several studies have found intermediates which have been taken to indicate introgression between the species (Englander and Amtmann, 1963; Bothschafer, 1963; Amtmann, 1965). However, Rempe (1965) showed that Amtmann's and Bothschafer's results did not differ significantly from results which can be obtained by comparing *Mustela nivalis* and *M. erminea*. These two *Mustela* species show a similar overlap but are generally recognised as good species. Also Zimmermann (1957) failed to hybridize the two *Apodemus* species in Germany.

Witte (1964) reports introgression between the two species in Yugoslavia and parts of Italy. (*A.flavicollis* is absent from most of Italy and Witte did not find any specimens which he considered 'pure *flavicollis*'.) Dalimier (1952) considered that *A.sylvaticus* is a polymorphic species and the *flavicollis* condition is one of its morphs.

In Britain, too, doubts have been expressed about the validity of A.flavicollis. For example, Harting added an editorial comment to Winton's (1894) paper reporting the discovery of A.flavicollis in Britain, stating that specific differences resting on size and colour alone were of doubtful value.

Clearly before applying the competitive exclusion principle to discussions concerning the ecology of mixed populations of sylvaticus and flavicollis it is essential to know that the species are genetically separate in the study populations. Intra and inter-specific competition are rather different processes.

The evidence that in Britain, flavicollis and sylvaticus are good species is as follows:-

1. Intermediates for the collar of orange fur are not found. Mice either have a broad, complete collar (flavicollis) or no collar, only a pectoral spot which may be completely absent (sylvaticus). If hybridisation occurred a full range of intermediates would be expected, unless the presence of a collar is determined by a simple Mendelian gene. In the latter case it could be argued that the British Apodemus population showed a genetic polymorphism for this charateristic.

2. However, flavicollis and sylvaticus are unlikely to be morphs of a polymorphic species because, if they were, litters would sometimes occur with some 'flavicollis' and some 'sylvaticus' offspring as siblings. Many workers have reared litters of Apodemus in captivity but this has never been reported.

3. Attempts to hybridise the two species, in captivity, have failed (Jewell and Fullagar, 1965). This negative evidence is quite acceptable because the experiments were carefully designed. It was possible to breed both species in captivity, but even when large specimens of sylvaticus (from St Kilda) were kept with flavicollis of a similar size, no hybrids were born.

4. DNA from sylvaticus and flavicollis can be distinguished using the technique of reciprocal DNA/DNA annealing in agar. DNA from different races of sylvaticus could not be so identified (McLaren and Walker, 1968).

Hence it can be confidently stated that in Britain A.sylvaticus and A.flavicollis are valid, genetically isolated species.

A large number of sub-specific names have been given to various races, forms or varieties of A.sylvaticus and A.flavicollis. Many of these are island races - the larger ones of these Ellerman considered to be races of A.flavicollis, but all subsequent workers have considered these to be large races of A.sylvaticus. The breeding experiments carried out by Jewell and Fullagar (1965) have confirmed this. The only islands from which A.flavicollis is known are mainland Britain and Sjaeland (Denmark) (Ursin, 1956).

Corbet (1961) suggested, and Berry (1969) has confirmed, that the Scottish island races of A.sylvaticus arose by human introductions , the differences between island and neighbouring mainland forms depending on the area of origin of the introduced mice (not always the nearest mainland), genetic drift and adaptation to the new habitat. The sub-specific names applied to these island races are of little value. The races are genetically distinct only because of their geographical isolation. Simply describing the races by the names of their island homes and attempting to indicate their mainland origins is of much greater value.

Besides these small island 'sub-species' there are several named sub-species of A.sylvaticus and A.flavicollis. These are listed in table 3. Corbet (1966) has explained the errors which can arise from the use of sub-specific names for widespread, variable species. If names are given to samples from different parts of the species range, and then efforts made to assign later collections to one or the other of the named sub-species, the picture of distribution and variation which builds up is quite erroneus. Either geographically isolated races, or races which overlap and remain distinct in the region of overlap, are indicated. The true situation is usually a cline, with a range of individual variation in any one population about a mean which itself changes across the species range. This is the situation that seems to exist in both A.sylvaticus and A.flavicollis - see figures 2 and 3. Ursin (1956) has shown that the extreme form of A.flavicollis ('wintoni') is restricted to Britain and Scandinavia. In the rest of the species range there is a transition from the typical ('flavicollis') form in the north and west to the 'princeps' condition in the south and east.

The changes that occur in the colour of A.sylvaticus are less obvious, the named forms indicating the lighter Mediterranean races. Apart from this the *A.sylvaticus* from Europe are similar in superficial appearance. Hedges (1969) has demonstrated a cline in *A.sylvaticus* populations using comparison of skull characteristics. In the same study he confirmed that *A.sylvaticus* and *A.flavicollis* become more similar in the south-eastern parts of their ranges. It is important to note that Hedges' results indicate that the south-eastern *sylvaticus* populations are more similar to the average *flavicollis* condition than are the north-western and British *sylvaticus* populations. Similarly the south-eastern *flavicollis* are more similar to the average *sylvaticus* than are the north-western *flavicollis*. This contrasts with the conclusion which would be reached from coat colour studies, where instead of both species diverging from the mean as one moves north-westwards, *flavicollis* seems to diverge and *sylvaticus* remains fairly uniform.

It probably avoids confusion to refrain from using subspecific names. The variation in the two species, in Europe, can be summarised as follows:- both species show a clinal pattern of variation on a roughly north-west / south-east axis. In addition, *A.sylvaticus* has a lighter colour in the Mediterranean region, which is presumably an adaptation to the soil colour and the more open habitats. As well as clinal variations within the species, the two species show a cline in their similarity to each other. In the central and south-eastern parts of their range they may not be genetically isolated.

There also seems to be a cline in the ecological distinctness of the two species. In central and eastern Europe it is generally reported that A.flavicollis is found in woodland and A.sylvaticus in open country. For example, in Poland Aulak (1970) found no A.sylvaticus in ten years trapping in a variety of woodland habitats in the Bialowieza National Park. During this time he caught 319 A.flavicollis. In the Wroclaw area Haitlinger (1969) caught 301 A.sylvaticus in 'ruderal' (i.e. open) terrains during fifteen years trapping. This contrasts with the situation in Britain, where it is unknown for A.flavicollis to be found in the absence of A.sylvaticus and it is rare for A.flavicollis to be more abundant (see section 5 of this thesis).

The conclusions which are most relevant to my work on the ecology of A.flavicollis in Britain are as follows:-

1. On mainland Britain A.sylvaticus and A.flavicollis are distinct species.
2. While each species shows individual variation, there is no evidence that mainland British populations contain more than one sub-species of each species.
3. Because the taxonomic and ecological relationships of A.sylvaticus and A.flavicollis differ in different parts of their range, it would be unwise to assume that information on the details of the ecology and behaviour of these two species from Europe will apply to Britain. While it is important to compare the overall situation in, for example, Poland and Britain, gaps in the knowledge of the ecology of British Apodemus cannot be

filled in from Polish sources. Only in parts of Scandinavia is the ecological relationship between the two species likely to be similar to that in Britain.

Section 2

A CRITICAL SUMMARY OF THE ECOLOGY OF *APODEMUS SYLVATICUS* IN BRITISH HABITATS WHERE IT OCCURS IN THE ABSENCE OF *A.FLAVICOLLIS*

2.1 Introduction

If the competitive interaction of two species is to be studied, ideally the ecology of each species in habitats where the species are allopatric should be compared with the situation where the two are sympatric. As explained in section 1, taxonomic uncertainties and habitat differences make it unsafe to assume that continental *Apodemus* populations have the same ecology as those in Britain.

In the British Isles there are no known locations where *A.flavicollis* occurs in the absence of *A.sylvaticus*. There are many areas where *A.sylvaticus* is the only *Apodemus* species present, and it is in areas of this type that most of the detailed studies of *A.sylvaticus* ecology have been made. My aim in this section is to present a critical summary of these studies, concentrating on those aspects of *A.sylvaticus* ecology which will be relevant to the later discussions, and for comparison with the results of my studies of a mixed *A.sylvaticus* / *A.flavicollis* population decribed in section 3.

It is not intended to give a full account of *A.sylvaticus* ecology and several major areas of study have been omitted completely. These are:-

1. *Predators*. The detailed studies of the prey of small mustelids and owls have used methods that could not distinguish between the two species of *Apodemus*.

2. Parasites. Excellent summaries of the fungal, spirochaete, protozoan and helminth parasites of A.sylvaticus have been published in recent years. There is no comparable information on A.flavicollis parasites and my own researches have not made good this deficiency. This important aspect has had to be left for later investigators.

3. Island populations. There have been several studies concerning the origin, evolution and ecology of small island populations of A.sylvaticus. There are no small island populations of A.flavicollis and this aspect has been omitted as not relevant to the present study.

4. Regional variation. Most of the studies of regional variation have compared mainland with island mice. What evidence there is suggests that mainland A.sylvaticus populations are very uniform (Delany and Healy, 1967), although Berry (1973) has recently detected a genetic distinction between western and eastern populations from mainland Britain.

2.2 The range of habitats

Both the specific name and one of the popular English names suggests that the wood mouse, A.sylvaticus, is a woodland animal. This is indeed true in the sense that A.sylvaticus is a characteristic part of any woodland fauna. However, the species is by no means restricted to woodlands. In Britain A.sylvaticus is found over a very wide geographical area (see figure 36) and in all the main terrestrial habitat types indicated in table 4. Corbet (1971) shows that the only small rodents as widely distributed geographically as A.sylvaticus, on mainland Britain, are the two voles Microtus agrestis

(Linn.), Clethrionomys glareolus (Schreber) and the house mouse, Mus musculus Linn. Table 4 indicates that each of these species has a much narrower range of habitats than A.sylvaticus. Microtus is mainly restricted to permanent grassland habitats. Microtus habitats do not usually support a large breeding population of A.sylvaticus, but both Brown (1954) and Ashby (1967) have shown that this can occur. It is rare for A.sylvaticus to live in inhabited buildings, although Mus and A.sylvaticus may occur together temporarily in and around farm buildings. Clethrionomys is found only in woodland with undergrowth and in scrub habitats. Thus Clethrionomys habitats are included within the range of habitats utilised by A.sylvaticus and this potentially competitive situation has been much investigated.

Table 5 indicates the main areas where the detailed studies, on which this section is based, were made. With the exception of Hacker and Pearson's study, all were carried out in deciduous or mixed woodland. No long-term studies have been made in moorland habitats for example. Most of our knowledge from such areas comes from short-term trapping aimed at studying distribution or sub-specific variation.

While it is unfortunate that studies have not been made in a full range of habitats, for the purposes of this investigation it is not a serious omission. The study areas where A.sylvaticus and A.flavicollis are sympatric are woodlands, and so the woodland ecology of A.sylvaticus is the most relevant for comparative purposes.

2.3 General habits

A.sylvaticus is a strictly nocturnal animal; it is much more nocturnal than either Clethrionomys or Microtus (Brown, 1956a). The day is spent in a burrow. Cleminson (unpublished report, 1966) has shown that A.sylvaticus does not normally share its burrow with Clethrionomys and that it has a larger and more complex burrow system than the vole. The burrows are often associated with tree roots, among which the nests are constructed from any litter in the vicinity of the burrow. Stored seeds are often found, Cleminson finding up to 50 seeds in some collections, and buried at depths of about 230 mm. The amount and nature of any daytime activity which may occur below ground has not been investigated. Most studies have indicated that a high proportion of the mice present in a study area are trapped on most trapping nights. Bright moonlight may reduce catches (Kikkawa, 1964) but this is possibly related more to avoidance of open spaces under these conditions than to non-appearance of the mice above ground. This suggests that it is unusual for an animal not to come out of its burrow every night, although experiments with captive animals have shown that total activity outside the nest is reduced when decreasing day length triggered food storing activities (Miller, 1955). Both Miller's studies with captive animals and those based on frequent trap visiting in the field (Brown, 1956; Kikkawa, 1964) indicate that peak activity occurs soon after sunset with a second peak before dawn in the long winter nights. The dusk peak is highest in summer (short night) and in the long nights there is a more even spread of activity.

All the trapping studies have been based on the assumption that most Apodemus activity occurs at ground level. That A.sylvaticus can and does climb into bushes and use old birds' nests as feeding platforms has long been known (Oldham, 1899). Pollard and Relton (1970) have shown this to be a regular part of wood mouse feeding behaviour. There is, however, no evidence that A.sylvaticus lives for long periods above ground or climbs into tall trees. It appears to remain aloft only for the duration of short feeding expeditions and so at least some activity at ground level can be expected every night.

2.4 Annual cycle

Captive wood mice often live for several years (Ashby, 1967) but all the mark and recapture studies of wild A.sylvaticus agree that basically they are 'annuals'. A typical mouse which survives to breed will have been born in the summer of one year, by late autumn it will probably not have bred and will spend the winter at about 16 g. The following spring a burst of growth brings the mouse to full adult weight as it enters breeding condition. It is unlikely to survive into the next winter.

Figure 4 summarises the breeding cycle of male and female A.sylvaticus. This is derived from Baker's (1930) work and since the mice were killed and dissected the breeding condition is known with certainty. Most other workers have deduced breeding condition from external signs. The males are considered to be in breeding condition if the testes are enlarged and descended, the females are in breeding condition if obviously pregnant or if they have perforate vaginæ . Most subsequent studies agree with that of Baker, but Smyth (1966) found that in years with a good acorn crop, woodland A.sylvaticus populations contain breeding mice during the winter months.

Figure 5 shows a selection of 'disappearance curves' for wood mice, derived from a number of studies. It should be noted that if wood mice are very mobile and likely to move permanently away from the study area, then these curves will not coincide with survivorship curves. The very high disappearance in the first month after the initial capture has been interpreted (Evans, 1942) as evidence of the existence of a transient group of mice which make up a large part of the 'once-caught' category. Watts (1970a) disputes the existence of a significant proportion of transients as he found little evidence for dispersal movements in the mouse population; he considers the so called transients represent mainly mice whose home-ranges overlap only slightly with the study area. Any transients, or mice caught once only because they live at the extreme edge of the area being sampled, will cause an overestimate of the death-rate in the first few months after capture if the disappearance curves are equated with life curves. Even making some allowance for this effect, a very high early death-rate is suggested. In this respect A.sylvaticus is the same as most small mammals - juvenile and young animals having a much shorter expectation of future life than the established adult members of the population.

Figure 5 indicates that while there is some variation in disappearance rates between cohorts of mice, there is little difference between the two sexes.

2.5 Population fluctuations

The many long term studies of A.sylvaticus that have been made in the British Isles are listed in table 5.

Many of these workers have commented upon the pattern of population fluctuations over the year. A number of factors complicate comparisons of the various published results, the more important being:-

1. Differing trapping techniques have been used. Some have used prebaiting methods and others not. Various arrangements of trap lines or trap grids are involved.
2. A variety of techniques has been employed to convert the raw data into population estimates.
3. Differing frequency of trapping sessions.

In an attempt to sort out the comparable data and present them in a reasonably standard form I have adopted the following approach:-

a. Excluded studies which did not use some form of grid spacing of traps.
b. Included only studies using the standard Longworth trap (Chitty and Kempson, 1949).
c. Included only those studies where trapping sessions were at monthly intervals or less, over a period of at least 12 months. Studies with not more than three single month gaps in the monthly records have been included and the gaps filled by interpolation of results.
d. Used the number of mice caught per trapping session as an index (each trapping session being of standard effort in terms of trap-nights within any one study).
e. Converted each monthly total into a percentage of the total captures over a twelve month period. For the studies which extended over much more than twelve months the record is dealt with in twelve-monthly units.

The results of this analysis are tabulated in table 6 and shown graphically in figure 6. Note that in this table and figure, and also in the discussion which follows, the years referred to are the years in which the twelve-monthly records were started and not the years of publication. Publication dates are given in table 5. It should be emphasised that this method of analysis enables comparisons of fluctuation patterns to be made, but that the records do not give a measure nor an index of absolute population size. Population sizes are considered in section 2.6.

The monthly percentages are from 14 annual records and have been averaged and the average record displayed (figure 7) for comparison with the individual records. Taking the average records as being typical in some ways for a woodland A.sylvaticus population, then the following are the main features:-

1. A high winter population, falling slowly between November and March.
2. A falling population from March to the June/July low population state.
3. A rapid rise in the population in August and September continuing to the November peak.

This general pattern has been recognised by most workers and all the annual records follow it to some extent. As is to be expected the fluctuations are usually greater in the individual records than in the average (see table 7) although Smyth's 1961 record, Newson's 1959 (Y) and Fairley's results indicate abnormally stable populations.

There are three main ways of accounting for the observed population fluctuations:-

a. The fluctuations may simply result from the changing balance between death-rate and recruitment of young mice to the trappable population through the year.

b. Immigration/emigration may also occur. This could work to re-inforce or to partially cancel out the fluctuations introduced by (a).

c. The response of the mice to the traps may change and so the recorded catch may not be a true index of population.

Doubtless all three factors are involved to some extent, but it is interesting and important to try and determine their relative importance. Tanton (1965), by a process of elimination, concluded that (c) was the most important. He suggested that mice in summer were less interested in traps, perhaps because food was more easily available elsewhere than in the traps. Most other workers, notably Watts (1969), dispute this suggestion. Individual records for mice suggest that trappability does not change. Also some records are available of years when the summer population remained high.

The late summer onset of a population rise is strange when one considers the early (usually March) start to the breeding season. Watts states that in his study the birth rate was not deficient in the early part of the year; but using much larger samples Baker (1930) showed that the embryos per 100 adult females reach a peak in July and August, and it should be remembered that a young mouse does not become trappable until it is about a month old. Watts considers that the survival of young mice must change greatly during the year if the fluctuation in population is to be explained satisfactorily. He suggested that survival is low in early summer but that an unexplained swing in survival, resulting from an as yet undiscovered form of social interaction, favours the juveniles in late summer.

Watts based his conclusions on work at Wytham Wood, Berkshire and excluded results from a very small wood surrounded by arable land (because of migrations between habitats). He assumed that this migration did not occur between the field and the larger blocks of woodland used for his studies. He also demonstrated (1970) that dispersal was low within the wood. His rejection of immigration as an important component in the late summer population rise rested very much on this assumption. There are two points which can be used to argue against Watts' conclusions:-

a. In some studies (Crawley, 1970; Tanton, 1965) the autumn increase exceeded that which could be achieved by the resident population breeding at maximum rate and with 100% survival.

b. It has been demonstrated that A.sylvaticus moves over wide areas (see section 2.7) and colonises arable crops in the summer (Kikkawa, 1964; Pollard and Relton, 1970). The study areas on which Watts based his paper were all within an easy 'mouse's walk' of farm fields and yet a study of dispersal movements to and from farm fields was not made.

Miller (1958), Kikkawa (1964), Brown (1969) and Crawley (1970) have all mentioned the importance of migration in from farm fields at harvest time. It seems certain that a large part of the wood mouse population breeds in the fields and hedgerows and this would provide a very satisfactory model of the observed fluctuations in woodland wood mouse populations. In summary the annual cycle would be explained as follows:-

1. A large population overwinters in the favourable, woodland habitats. Rarely, breeding occurs during the winter, but fairly high survival and a continuing low rate of immigration from secondary habitats (hedgerows etc.) keeps the winter population high.
2. Onset of the breeding season is marked by an increase in intraspecific strife leading to dispersal of a large part of the population to summer field and hedgerow habitats.
3. A small resident breeding population remains in the wood during the summer.
4. At harvest time a rapid influx of mice born during the summer outside the wood, occurs. This influx continues after harvest time and is supplemented by autumn breeding in the wood. The population stabilises and breeding usually ceases by November.

If this model is correct, a study in the middle of a very large wood, uninfluenced by mouse populations outside the wood, should reveal a rather different pattern of fluctuation.

Figure 6 shows that the pattern of fluctuation varies from year to year even in the same locality. Newson's 1959 results indicate that sometimes woodland populations remain fairly high during the summer months. The variances tabulated (table 7) give a measure of the size of fluctuations. Among the most stable populations are those studied by Smyth in 1961 and Newson in 1959, in the same areas that produced violent fluctuations in 1962 and 1958 respectively. It is worth noting that the only annual record from Ireland is for the most stable population. Fairley's study area was surrounded by meadow and not arable fields. This may explain the result, but the possiblity that the absence of competing bank voles is significant should not be discounted. The only other Irish study over a period of several months (Fairley and Comerton, 1972) was not long enough to satisfy the criteria for inclusion in table 6, but also indicated that the population was unusually stable.

2.6 Population density

In considering competition between A.flavicollis and A.sylvaticus an important question is 'Is the total Apodemus density greater where both species occur than where one species occurs alone?' Before an answer can be attempted it is necessary to have good estimates of A.sylvaticus population densities, particularly woodland populations, for a later comparison with mixed population densities. There is an abundance of data on wood mouse populations but the conversion of these to good measures of population density is very difficult. Most workers have commented on the intrinsic inaccuracies of their methods, Kikkawa (1964) and Tanton (1965) especially emphasising these. The main difficulties in converting trapping data to density estimates are as follows:-

a. Obtaining an accurate estimate of the population is not easy. When a high trap density is used and the mouse population is medium or low, then probably virtually all the mice of trappable size are caught. But if there is competition for traps or the traps are so widely spaced that some mice do not meet a trap every night, then it is necessary to convert the catch record into a population estimate. This involves making certain assumptions, there are many different methods and each involves a different set of assumptions. The method used by the majority of recent students is that of Leslie, Chitty and Chitty (1953) and this involves the following assumptions:-

i. All the mice stand an equal chance of capture.

ii. A marked mouse is present on the study area on those occasions when it is not caught, but which fall between times when it was caught.

iii. A marked mouse ceases to be present on the study area following its final capture

The fact that this method gives estimates close to the number of captures, when trapping is fairly intensive, indicates that it is fairly accurate. The other methods include those of Hayne (1949) which gives good results but can only be used with certain frequencies of trapping sessions, and Manly and Parr (1968) which appears to be totally unsuitable for estimates using fairly small samples. By a suitable choice of an estimation method a worker could arrive at almost any desired estimate, even an estimate lower than the number of mice captured (see, for example, Brown, 1954).

b. Having arrived at a suitably accurate population estimate, it is necessary to know the size of the area being sampled if the density is to be calculated. This is not simply the area included in the trapping grid because mice are fairly mobile and can still be caught even if the centre of their activities is some way outside the grid boundary. Most workers have added some boundary strip to allow for this edge effect but the size of the strip used has varied. Most have chosen either half the distance between traps, or a figure based on the average detected length of movements by mice within the trapping area. With small grids the size of boundary strip chosen can dramatically affect the population density estimate obtained. A practical difficulty with boundary strips is that in some studies the habitat area is small and does not extend far outside the area being trapped. In this case the density estimate is going to be affected by the density in the habitat outside the study area.

Because of the variation in method of population estimation and size of boundary strips used, direct comparison of published densities is meaningless. I have therefore attempted to rework the published data and present them in the form of comparable estimates of population density. The same studies were used as in section 2.5 plus a few additional studies which did not fulfil the criterion of one year's regular monthly trapping, but which are suitable for winter population estimates.

In section 2.5 I have shown that the precise pattern of population fluctuations varies both in timing and size of the fluctuations. Many workers have reported the maximum and minimum densities but these are less useful for comparative purposes than the average density over periods of relative population stability. Figure 7 indicates that the average population fluctuation pattern consisted of a high stable population during the winter (November to February inclusive) and a low summer population from June to August. I have used the data from published sources to calculate average densities during these two main stages of the annual population cycle (see table 8). If the number of animals caught is taken as the estimate of population size and the grid size as a measure of the area sampled, the resulting densities are strongly correlated with grid size (figure 8). This shows clearly that errors resulting from factors (a) and/or (b) above (pages 44 and 45) have been introduced. Watts' (1969) detailed analyses of populations at Wytham used Leslie, Chitty and Chitty (1953) estimates of population size and boundary strips whose size varied with the time of year (based on range lengths for the different seasons). I have used Watts' results and a technique very similar to his to obtain the estimates included in table 8. The points of difference between my methods and Watts' are as follows:

1. When an estimate using the Leslie, Chitty and Chitty method was not given by the author (and the published data do not permit one to be carried out) the best estimate given by the author was used.
2. When a 23 m boundary strip (the winter value given by Watts) would have extended beyond the area of the wood, the size of the wood was taken as the sample area.
3. Watts' summer boundary strips were large and varied with observed population size. With low summer populations, estimates both of size of population and range length are less accurate than the winter estimates. I have preferred a more conservative method in which a 23 m boundary strip is used throughout the year (Watts' estimates have not been adjusted accordingly in table 8). Often the number of animals caught in the summer has been so low that statistical estimations of population size cannot be used. In this case the number caught is used directly as the estimate of population size.

The average winter densities are remarkably consistent and are not correlated with grid size (figure 8) indicating that at least some of the errors have been removed by this method of analysis. The two extreme values are both from somewhat abnormal areas or studies. Kikkawa's result is very high. His study wood was small and in the middle of arable fields. The evidence suggests a very large, mobile population which had crowded into the wood. Also, his prolonged trapping period (five days) will have inflated the estimates. If mice were moving in and out of the wood the number present on any one night would have been rather less than the estimate indicates.

Crawley's grid B results are lower than most of the other estimates. Grid B was in an immature wood which may account for the difference. Discounting these extreme values, winter densities of <u>A. sylvaticus</u> in typical woodland habitats average 21 per hectare and vary only between 10 and 37 ha^{-1}

Despite the authors' statement to the contrary, the two Irish studies (Fairley, 1967; Fairley & Comerton, 1972) indicate similar densities very close to the average British value. This indicates that the absence of bank voles has not led to an increase in winter densities of woodmice in the Irish study woodlands.

The low summer densities are not so consistent. For the reasons given above Kikkawa's results are very high. To what extent the variability of the other results is due to less accurate estimation of population size is difficult to judge. Watts (1969) has shown that variation in winter survival, related to the size of acorn crops, influences the spring densities and hence the timing of the decline to the low summer densities. It is quite possible that this affects the average size of the summer populations.

2.7 Home ranges and movements

Unless an animal is completely nomadic its activities are restricted to a definable home range. For small mammals the home range will include the nest or burrow - the homesite. The homesite and range may change during the animal's life. Jewell (1966) has summarised the many definitions of home range as follows:-

Home range is "the area over which an animal normally travels in pursuit of its routine activities."

This concept of home range is accepted by most workers; the difficulties and disputes surround the techniques chosen to measure the home range. These difficulties have been explained in detail by Kikkawa (1964) and many times by Brown (1956b, 1962, 1966, 1969). Most students of Apodemus home range have used grids of live-traps to reveal the range. The studies quoted above indicate that these estimates will be inaccurate for the following reasons:-

1. The spacing of the traps affects the recorded range.
2. It is difficult to convert a record of point captures to a home range without using arbitrary boundary strips or underestimating the true range by taking the minimum area as the estimate.
3. Dispersal movements may be confused with normal movements within a home range.
4. Only mice caught many times can be considered to have revealed their true home range. These mice are probably not a fair sample of the total mouse population.

Home range size is measured in two main ways: range length, being the greatest straight-line distance moved by a mouse within its range; and range area. Each may have correcting factors applied to it; which are supposed to allow for the errors introduced by trap spacing. Table 9 illustrates the range of values obtained by various workers.

Two other types of investigation have cast grave doubts on the validity of range size estimates obtained by trapping:

Homing experiments (Hacker and Pearson, 1951) showed that A. sylvaticus released away from the trap site could home quickly,(usually within one or two days) from distances up to 1 km. All the mice released up to 350 m away returned and four out of a total of 13 released between 600 m and 1 km returned. Unless the mice were getting bearings from land marks or astronomical markers, then they had a knowledge of an area wider than their supposed home range.

Tracking experiments, in which the footprints of toe-clipped mice are recorded on prepared tracking boards, without the necessity for repeated recaptures, give higher estimates of home range than do live-trapping studies (Brown, 1969). These estimates are probably much more accurate.

While it seems that trap revealed ranges have no value as an absolute measure of range size, they do have value in comparative studies. The following generalisations are almost certainly true and fit the results from all the main studies:-

Apodemus sylvaticus range sizes are:

a. larger for males than for females

b. larger in summer than in winter

c. larger than Clethrionomys ranges

d. very variable between individuals, especially between male mice.

2.8 Habitat preferences in woodland

A point that has interested many of the students of small woodland rodents is the possibility of competition between A.sylvaticus and C.glareolus. Brown (1956) and Miller (1955) have shown a separation in the times of peak activity of these two species. This has been considered to be important in the competitive interaction of these species. This is true in the sense that the two species will be exposed to a different range of predators and will minimise the possibility of aggressive interactions between vole and mouse. However, time of activity does not affect competition for food. Watts (1968) has shown differences in the diets which he considers adequate to prevent competition for food between the two species. These differences could result from occupation of different habitats, or from differing selection of food in the same habitat, or a combination of both factors.

Many workers have investigated the woodland habitats of the two species and all have found that C.glareolus is clearly associated with ground cover. A.sylvaticus is found in open habitats much more often than C.glareolus. Most workers have emphasised this distinction and failed to look closely at the possibility that A.sylvaticus is also associated with ground cover, but to a lesser extent than C.glareolus. When Fairley and Comerton (1972) detected a preference for cover in an Irish woodland A.sylvaticus population they commented that "this has never been observed in Britain, even after extensive study...." and went on to speculate that this was correlated with the absence of C.glareolus from the Irish study area.

In fact Tanton (1969) has pointed out that his results published in 1965 show that A.sylvaticus was associated with bramble in preference to open habitats during the winter; in summer shifting its preference to the non-bramble habitats which were then covered by Mercurialis and Endymion. Evans (1942) presented evidence which suggested some association of A.sylvaticus with bracken on one of his grids. However, his other grid showed the reverse effect and on balance there is no evidence of habitat preference in his study.

Ashby (1967) in a long term study of A.sylvaticus ecology did not consider that there was a correlation of captures with cover. Damp areas were avoided but in dry areas lack of cover did not seem to reduce captures. Ashby's study used traplines instead of a grid and this technique is more likely to produce erroneous results if there is any tendency for A.sylvaticus to be less abundant but more widely ranging in the open habitats.

2.9 Food of A.sylvaticus

There have only been two systematic studies of the diet of A.sylvaticus on mainland Britain. Miller (1954) found a considerable overlap in the diets of Bank voles and Wood mice but Watts (1968) has shown that Miller's very small samples and method of analysis has probably produced erroneous results. Watts has shown that A. sylvaticus concentrates on seeds and those fruits with hard seeds; whereas C.glareolus eats softer fruits and higher proportions of green and dead plant leaves and stems. However the wood mice appeared to be opportunists and when large numbers of winter moth caterpillars were available they ate these to the virtual exclusion of other items. Miller also found evidence of a partially insectivorous diet and showed that insects are eaten throughout the year.

2.10 Social behaviour

Trapping studies are not a good way of studying the social behaviour of mice. The nocturnal habits of wood mice make direct observation difficult, although Kikkawa (1964) made some observations on the behaviour of mice feeding and exploring a baited trap. He recorded that groups of mice would feed together without fighting. Studies by Brown (1966, 1969) using tracking methods have provided very interesting results. It appears that the large male wood mice which have large home ranges are dominant animals; in some unknown way they defend a territory. The use of ultrasound has been one suggestion as to how they might do this (Brown, 1966). Within the territory the smaller home ranges of the subordinate males and the females occur. Females defend small territories while they are pregnant. To what extent the dominant males monopolise the females is not known, nor is it known whether the young mice are evicted from the territorial areas. The decline in territorial activity outside the breeding season could help to explain the build-up of dense winter populations, and the dispersal of mice at the beginning of the breeding season.

Section 3

STUDIES OF A MIXED A.SYLVATICUS/A.FLAVICOLLIS POPULATION ON THE COPTFOLD ESTATE, ESSEX.

3.1 Introduction

All the major published studies of Apodemus ecology in the British Isles (those reviewed in Section 2) were carried out in areas where A.flavicollis was absent or so rare that it was not detected in many thousand trap-nights. When my study started in 1966, no work had been published reporting detailed studies on A.flavicollis populations in Britain. Since then Yalden's (1971) paper reporting a short duration study in Gloucestershire has appeared.

The first reports of A.flavicollis on the Coptfold Estate were published by Seear (1964). A brief survey of small mammals which I carried out in 1964 (Corke, 1965) indicated that this would be an ideal area for the type of detailed comparative study that I wished to carry out.

My aims were to use standard techniques, comparable with those used in the studies discussed in Section 2, to obtain information on the population dynamics, movements, habitat preferences and behaviour of the Coptfold

Apodemus populations. In this section I explain the methods used, present the results of the study and attempt to compare the ecology of the two species on my study area. In addition my A.sylvaticus results are compared with those obtained from the single species Apodemus populations described in Section 2.

3.2 The Study Area

The Coptfold Estate consists of woodlands and farmland, mainly arable fields. It is in the parish of Margaretting in Essex and is mostly contained within the Ordnance Survey grid squares TL6602 and 6603 (see figures 9 and 10 which are a large scale map and aerial photograph of the estate).

The land is 200 - 300 feet (60 - 90m) above sea level and is higher than most of the surrounding land. There are no steep hills in the area and a few hollows flood during very wet weather.

The geological survey map (Ordnance Survey, 1868) shows that Boulder Clay and London Clay are the main surface deposits on the Estate, with Bagshot Beds and Pebble Beds on the highest ground. King Wood, in which most of my work was concentrated, is at the junction of the Boulder Clay and Bagshot Beds. More recent information (Mr. R. Allen Soils Survey of England and Wales, personal communication) suggests that the Bagshot Beds are not as deep as the map indicates and are separated from the London Clay by Claygate Beds. The pebble Beds may be the upper layers of Bagshot Beds or may be the remains of preglacial pebble beds now mostly eroded away.

The woodlands are fairly typical Essex woodlands, managed for game preservation purposes. However, the area is also treated as a bird reserve and many nest boxes have been erected. The game keeping activities include releasing a few hundred pheasants each year and the control of mammalian, but not avian, (except corvid) predators. Rabbits and grey squirrels are also controlled but badgers are theoretically protected although a few were snared in fox snares.

The woodlands are mixed, with large standard deciduous trees, mainly oaks and sweet chestnuts, and occasional blocks of conifers. The scrub layer consists of coppice, rhododendron, bramble or bracken. A twenty to twenty-five year coppicing cycle had been practised but little coppicing was carried out during the period of the study.

The woodland area selected for the most detailed trapping study was the south-west quarter of King Wood. Table 10 sets forth the plant associations within the area of my woodland study grid. In range of species this area is quite typical of the Coptfold Woods although there is considerable variation in the proportions of the species present. Table 10 includes the scientific names of the plant species and these are not repeated in the text of this section. Figure 12 is a map of this study area showing the main habitats and the trapping grid described in 3.4. Figures 13 - 20 are photographs of the study area habitats. The rest of King Wood is similar to the study area except that the north-west quarter has a higher proportion of conifers and part of the south-east quarter was coppiced in 1966-67. In 1968 a small area of my study grid (part of grid square A8) was coppiced by mistake, but apart from this the distribution of vegetation types changed little during the course of my study. Annual variations in the extent of ground cover occurred especially in the more open areas and a tree fell down at D7 in 1969, causing a local increase in bramble.

The hedgerows were mechanically trimmed hawthorn hedges. Apart from those bordering roads and trackways, large standard trees were absent (see figure 10).

Most of the fields were ploughed each year and used for arable crops; usually cereal crops were grown but also leguminous and cruciferous crops on occasion. In all years except 1969 some cereal crops were grown adjacent to the woodland study grid. The crop sequence in the fields adjacent to the study area is given in Table 11.

3.3 Exploratory trappings - methods

From October 1966 a number of exploratory trapping sessions were carried out. Initially the purpose of these was to select a suitable site for the main study, but even after the main study grid was established trapping continued elsewhere to check on the range of Apodemus, and in the hope of detecting any movements to or from the grid area. The exploratory trappings used short lines, groups or small grids of Longworth traps set overnight without prebaiting. Usually the captured animals were treated in the same way as those on the study grid (see 3.5), but some in areas distant from King Wood were removed and killed. It was hoped to carry out systematic studies on gut contents and parasites but it proved impossible in the time available to do this and this line of enquiry was abandoned. Table 12 summarises the results of these exploratory trappings and Figure 11 shows the location of the trapping sites.

3.4 The Grid Studies - methods

3.4.1. Size and position of grid

The area in King Wood for the main study grid was chosen because:

a) The exploratory trappings had revealed the presence of a suitable mixed Apodemus population

b) Access was relatively easy and did not necessitate disturbance of important game areas.

c) The area was not due to be coppiced until the study was complete.

d) The area included a range of woodland undergrowth types.

e) The size of the block of woodland was slightly larger than the desired grid size.

The size of grid chosen was, of necessity, a compromise. The traps should not be spaced so widely that individual mice within the grid may not have a trap within their home range. The number of traps that can be dealt with by a lone worker is limited and if the traps are very closely spaced the grid covers a very small area and hence samples only a small population. The chosen spacing was 15m with a 10 x 10 square grid of trap points. This was similar to some of the studies listed in Table 5. Published range lengths for A.sylvaticus suggested that 15m was not too wide a spacing and it seemed a reasonable *a priori* assumption that the larger A.flavicollis would be at least as mobile.

3.4.2. The Grid Lay-out

The grid was marked out using lengths of string and small bamboo poles to mark the 100 intersections. The marker poles were only temporary markers and the grid was permanently marked by painting the grid positions on the tree, bush or fallen tree nearest to the markers. This meant that the trap points were not all exactly at 15m intervals but the errors were not great. Trees were chosen as trap-point markers because:

a) the owners of the wood did not want unsightly marker posts in the wood.

b) some trap-points, if precisely spaced, would have fallen in unsuitable location such as the bottom of the ditch.

When the second grid was established, in field C, no markers could be set up in the middle of a growing crop. The end of each row was marked and the trap-points found by pacing along the rows, taking a line of sight on markers in the far hedge. Again this technique meant that the grid was not perfectly shaped, but the errors were small and have been ignored.

3.4.3 The traps

Standard Longworth traps were used throughout the study. These traps have adjustable treadle tensions and vary in their efficiency depending on the fineness of adjustment, and probably also depending on the smell of the trap and the brightness of its metal. The treadles were adjusted every few months to a fairly fine tension (to the point where a ½d coin (5.5g) would just depress the treadle). The traps used at the beginning of the study were not new and so were not unduly shiny. When new traps were added to those already in use they were brought into use a few at a time so that there would be no sudden change to bright, new and perhaps less efficient traps. Setting the same trap always at a particular trap-point would have biased the results because of varying trap efficiency. To avoid this the grids were set and the traps collected in a different sequence at each trapping and no consistent pattern of stacking the traps in their boxes was used. This should have ensured that particular traps were not always associated with particular trap-points.

3.4.4 The number of traps per point

Whenever small mammals are abundant serious competition for traps will occur if only one trap is set at each point. If three or more traps had been used at each point the total number of traps would have been too great to deal with and so the number chosen was two per point.

That this was adequate is indicated from the usually small number of points at which both traps made a capture (table 13), but the bias caused by high trap occupancy in favoured habitats is discussed in Section 3.10.

For most of the study only 100 traps were available (plus a few spares to replace any traps in need of adjustment). This meant that each grid had to be trapped in two halves, five rows of ten points each being set each night. On a very few occasions, when field populations were very low, only one trap per point was set on the field C grid. These occasions are indicated in Table 13.

3.4.5 Absence of pre-baiting

Most live-trapping studies have used pre-baiting as recommended by Chitty and Kempson (1949) and/or trapping sessions of three or more consecutive nights. This appears to be necessary where voles are the subject of study as there is evidence (for Microtus) that a part of the population is trap shy and avoids the traps at first (Shillito, 1961). This does not seem to apply to Apodemus. Fairley (1967) demonstrated that prebaiting was unnecessary and that the first night catch was as high as later catches. All my main trapping sessions have been one night stands, the traps being set before dusk and collected during the morning of the following day. Early experience, during the exploratory trappings, indicated that if the traps were left down between trappings the bedding became damp and the trap-deaths were high (Corke, 1967). The one-night stand technique greatly reduced trap-deaths.

Also, as shown in a later section (3.6), the evidence suggests that most of the Apodemus of trappable size were caught every trapping night. I consider that my technique has provided adequate samples of the two Apodemus species but the Clethrionomys results should be viewed with greater caution. Bank Voles are partially diurnal and may be trap-shy, so the trapping will not give a fair sample of this species. Fortunately this study is not greatly concerned with Clethrionomys and the results for this species are not discussed as fully as are the Apodemus figures.

3.4.6. Effect of trapping on the population

In an ecological study it is important that the study technique does not significantly alter the ecology of the species being studied.

Watts (1970b) has shown that the provision of supplementary grain can alter the breeding seasons of Apodemus sylvaticus and Clethrionomys. While the traps in my study were well supplied with grain for the captured animal only 10 - 15 grains were placed outside the trap as bait. This, combined with the relative infrequency of the trapping sessions, should have reduced to a minimum the food supplementation effects.

If trapping sessions of several consecutive nights are used, individual mice in the population will spend long periods 'out of circulation'. This is likely to apply especially to the dominant males described by Brown (1966, 1969) which, being more mobile, are more prone to capture and whose absence from the population may alter their social status. Since any trap site was trapped at most two nights per month this effect will also be reduced.

- Shrews suffer a high mortality in traps set over-night. It seems certain that my studies exterminated the resident shrew population in King Wood, and that subsequent immigrants also died in traps. The extent or nature of any ecological interactions between shrews and Apodemus is not known, and the elimination of the shrews may have affected the mice. The only consolation is that my study is a comparative one and the workers whose studies I wish to compare with mine also killed their shrews.

3.5 Information recorded

The weather conditions on the trapping nights were recorded together with the following details of each animal captured and the grid position at which the capture was made. After examination all captured animals except those which died in traps were released at the point of capture.

3.5.1 The species

The three species most commonly caught were two Apodemus species and Clethrionomys glareolus. It is only with these three species that this study is concerned. Occasional captures of Sorex araneus, S.minutus, Neomys fodiens, Microtus agrestis, Mus musculus and Mustela nivalis occurred, these captures were noted and the animal released without further examination.

The only circumstance in which wrong specific identification is at all likely is when young Apodemus, still in their grey juvenile pelage, are captured (Southern, 1964). In fact the collar marking of A.flavicollis is visible even in juvenile animals. A code mark given to an Apodemus of one species and sex was not used again for a mouse of another species or sex, hence any misidentification of juvenile mice would become apparent if the mouse was recaught as an adult. In fact subsequent captures always confirmed the original identification (and because of the system of record keeping the original identification was not checked before the subsequent identification was recorded). However, a few cases of juveniles in which the sex had been incorrectly recorded at first capture were detected.

3.5.2 Sex and breeding condition

Except in the case of extreme juveniles mentioned above, the sex of Apodemus, even in the non-breeding season, is easily determined by examination of the external genitalia. When not in breeding condition the sexes of Clethrionomys were more difficult to distinguish. Even when I was uncertain, the animal was assigned to one sex or the other and this tentative identification was, if necessary, corrected at subsequent recaptures. The possibility that voles caught only once or twice in non-breeding condition were wrongly recorded should be borne in mind when examining the data presented later. This is why much of the data for voles is not separated by sex in the tables.

Mice were classed as juveniles if the fur was the typical grey colour (this is easily seen on the fur of the underside, which is white in adult mice). Juvenile voles are not so distinct but size and overall dull colour are normally sufficient to identify them.

Non-juvenile males are classed as being in breeding condition if the testes are enlarged and scrotal; and out of breeding condition if the testes are small and retracted within the abdomen.

Non-juvenile females were classified as follows: obviously pregnant or with a perforate vagina as being in breeding condition, not obviously pregnant and vagina closed as being out of breeding condition.

3.5.3 Marking

A combination of toe-clipping (removing the terminal phalanx of a digit) and ear-notching was used, as recommended in Southern (1964). To avoid too great a reduction in scratching ability (Smyth, 1965) a maximum of only one toe from the fore feet and one from the hind feet were clipped on any one mouse. Toe clipping was done with a pair of sharp scissors and ear-notching with a punch designed as a chicken toe punch. The way in which the marks are coded is shown in Figure 21.

The method worked well in general; it did not seem to inconvenience the animal and is simple to perform. It is the method used in most recent studies but many of the studies listed in Table 5 which date prior to 1966 used metal leg rings. This method has been discredited as causing a high incidence of death or damage to the marked animals (Fullagar and Jewell, 1965). Using the combination of toe-clipping and ear-notching it would be possible to mark 890 mice and 494 voles. Towards the end of the study I exceeded this number of mice and used two ear-notches to provide a further 98 codes.

The only difficulty using this marking technique is with voles. Sometimes the notch in the ear of a bank vole healed over and became difficult to distinguish. Also voles, when scratching to get out of a trap, sometimes damage their toes in such a way that confusion can occur between damaged and clipped toes. Fortunately there was a sufficiently large redundancy in the marking codes for, in most cases, such errors to be detected.

3.5.4. Weighing

The weight of the marked animal was recorded by placing it in a small bag of known weight on a spring balance. The balance was checked for accuracy every few months and remained accurate for the duration of the study. The weight was recorded to the nearest gram. Other possible indices of size were not used because of the difficulty and large errors involved in their measurement. (Jewell and Fullagar, 1966).

3.5.5. Escapes.

Sometimes an animal escaped before being individually identified. In these cases the capture was recorded but could not be included in the file of records for an individual animal. Sometimes it was possible to identify a fleeing mouse only as '*Apodemus*' without specifically identifying it.

3.5.6. Record storing and sorting

The field notes from each trapping session were numerically coded and stored on two disk files on an IBM 1300 computer. One file consisted of records classified under the individual animal's code number. This file was brought up to date by the inclusion of the new records after each trapping. The other file consisted of all the records grouped by trapping session. This file included all the information in the first file plus the records of escapes and species other than *Apodemus* and *Clethrionomys*. It is these data files which were used to prepare the tables and analyses discussed in this section.

3.6 Population Estimates and Densities in the Woodland Study Area

Many of the published methods for population estimation by mark and recapture techniques are intended for studies where a numerically large, but proportionately small, sample of a very large population is captured. For studies of small mammals, where a high proportion of the population is captured at each session, these methods are neither applicable nor necessary.

I have analysed the trapping data from the King Wood study grid to provide the following types of estimate for each session of two trap-nights (i.e. one trap-night on each half of the grid):-

a. A count (C_t) of the individual animals captured during the session. This is the minimum population in the area being sampled.

b. The number of individuals known to be alive during the trapping session (K_t). This is C_t plus those individuals not caught but known to be alive from preceeding and succeeding captures. This method of population estimation is usually called the calendar of captures method (Petrusewicz and Andrejewski, 1962).

c. The estimated population (N_t) using the method of Leslie, Chitty and Chitty (1953). This is based on the assumption that the ratio of mice marked and known to be alive at the start of the session (F_t) to the total population (N_t) is the same as the ratio of marked mice captured during the session t (S_t) to the total catch (C_t). The formula on which the program written to compute N_t was based is:-

$$N_t = \frac{F_t\ (C_t + 1)}{(S_t + 1)}$$

Table 14 lists these estimates for each trapping session and the estimates are displayed graphically in figure 22.

In making these estimates it is necessary to assume that a significant proportion of the mice and voles, on the area sampled by the grid, do not remain untrappable for their entire lives. All the estimates refer to animals which have reached a trappable size of 8 - 10 grams and not to the total population. Too great a distance between traps or trap shyness among some members of the population could invalidate this assumption. I have explained in sections 3.4.1 and 3.4.5 why I consider that these points do not invalidate the assumption.

One can obtain a measure of the efficiency of the trapping by comparing the number of animals actually caught (including escapes not individually identified) with the maximum (N_t) number estimated to be present. The overall figures for all the trapping sessions for Apodemus are: captures 1220, sum of estimates 1471.9. This means that if the values of N_t are reasonably accurate an Apodemus has only a 17% chance of avoiding capture during a trapping session.

There are important theoretical differences between the minimum estimate (C_t) and the K_t and N_t estimates. C_t is usually an underestimate of the true population as there are two groups of mice which are not included in it. These are:

a. those which were captured but escaped before being individually identified.

b. those which were present in the area sampled by the grid but which avoided capture during session t. The methods of calculating K_t and N_t will compensate for these two sources of underestimation, but they will also include animals which were alive at time t but which were at that time resident in an area outside that sampled by the grid. If mice or voles migrate off the grid area for a time, and then return, the K_t and N_t estimates will be overestimates of the resident population.

In practice the values of K_t and C_t are usually fairly close. The K_t and N_t estimates are usually close also, except when the population increases rapidly (as happens normally in the autumn with *Apodemus*) when the values of N_t may be much higher than K_t. This probably results in part from the inherent inaccuracies of Leslie and Chitty's method when used with a rapidly changing population. Also N_t may have been underestimated because of competition for traps when the big influx of mice first arrives in the wood. In the discussion which follows, comparisons are confined to those periods in the winter and summer when the N_t and K_t values are in reasonable agreement.

The difficulties of converting population estimates into meaningful density estimates have been discussed in section 2.6. As explained there, the extremes of density estimates are of less use than the average values over the winter (November/February) and summer (June/August) periods. Table 15 present the *Apodemus* and *Clethrionomys* density estimates calculated in the same way as those from published sources included in Table 8. A 23m boundary strip was chosen to make both sets of estimates comparable; the true value of the boundary strip for my study grid and the various species is discussed in section 3.9.

The most interesting question to ask concerning these density estimates is: "Does the presence of an A.flavicollis population reduce the density of the A.sylvaticus population?". The summer densities are low and are based on small samples; hence they are subject to variation on this account alone. Also the published A.sylvaticus summer densities are very variable. Whether one takes my A.sylvaticus densities or the combined densities for both Apodemus species they are well within the recorded range of variation for single species Apodemus populations. This situation contrasts markedly with Yalden's (1971) results where his A.sylvaticus densities were high and the A.flavicollis densities double those of A.sylvaticus. This occurred in the summer of three consecutive years and unless the edge effects resulting from Yalden's very small grid sizes (1.03 - 1.37 ha including a 23m boundary strip) has produced erroneous figures, then clearly our two study populations behave quite differently. This question will doubtless be resolved when Mr. C. Robert's study of Yalden's area is completed.

The winter population estimates are intrinsically more accurate as they are based on much larger samples. They are also more consistent from year to year. My A.sylvaticus densities are all within the range of the table 8 values but are noticeably below the average of the table 8 values (20.2 per hectare excluding Kikkawa's aberrant result). The significance of this observation can be tested statistically as follows: Null hypothesis: the observed winter densities of A.sylvaticus in King Wood are within the same distribution of densities found in other woodland areas. To make the test more rigorous the very high density recorded by Kikkawa has been excluded from the calculation.

An F test established that the variances of the table 8 and table 15 winter densities did not differ significantly. Hence a Student's t-test for comparing two small samples (Bailey, 1959) could be performed. Since the test is to establish whether my (table 15) values are the same as or lower than the published range of values, a one-tailed test is appropriate.

The t value calculated was 2.0399 and with 19 degrees of freedom and probability associated with this value is between 2.5 and 3.0%. It therefore appears that the Null hypothesis is invalid and that the density of the King Wood A.sylvaticus population in winter is lower than in woods where A.flavicollis is absent.

As the King Wood habitat seems similar to the woodland habitats in which the table 8 studies were made it seems reasonable to suggest that this difference in densities results from *A.flavicollis* occupying part of the niche which would normally be fully exploited by *A.sylvaticus*. Ideally this should be tested by artificially eliminating *A.flavicollis* from large, enclosed plots in King Wood and comparing the *A.sylvaticus* population in these plots with the population in similar plots in which the species are allowed to co-exist. This procedure was quite impracticable and so a less direct method of detecting competition must be used. If, in King Wood, the two *Apodemus* species have split the normal *A.sylvaticus* niche between them then the biomass of the King Wood *Apodemus* population should be similar to the *A.sylvaticus* biomass where this species occurs alone. On average an *A.flavicollis* is 1.46 times greater in weight than an *A.sylvaticus* (see 3.8). The *A.flavicollis* winter densities were multiplied by 1.46 and the combined *Apodemus* density expressed in '*A.sylvaticus* equivalents' calculated (see table 15). These density estimates were compared with the table 8 *A.sylvaticus* values using the same method as before but using a two-tailed test as there is no *a priori* reason to expect a deviation only in one direction. The calculated t value is 0.978 (again with 19 d.o.f.) and an associated probability of over 25%. Hence there is good agreement, in terms of 'sylvaticus equivalents' between the density of Apodemus in one-and two-species populations in winter.

3.7. Disappearance Rates of Mice from the Woodland Study Area

Figure 23 indicates in percentage the known survival of the species and sex groups of mice and voles in the woodland study area. As indicated in 2.4 such disappearance curves should not be regarded as true survival curves because the study area is small in relation to the probable life-time range of a small rodent (see 3.9 and 3.11). The curves simply measure the rate of disappearance (by death or emigration) of mice caught on the grid area. The data on which figure 23 is based are presented in table 16.

The disappearance curves for Clethrionomys and A.sylvaticus are quite similar. The two sexes of A.sylvaticus are also similar, with a slight tendency for females to 'survive' longer. My A.sylvaticus figures are in close agreement with those of Evans's (figure 5 section 2.4). The A.flavicollis curves indicate a much higher disappearance rate than A.sylvaticus, but this is entirely due to the very high proportion of once-caught mice. If the data are replotted (figure 24) to compare mice caught over a minimum period of two months, then the two species are seen to be quite similar. If anything, 'survival' of A.flavicollis is better up to month 4 and beyond this the numbers of A.flavicollis involved are so low that the percentage survival rates are meaningless.

The status of 'once caught' mice has been discussed in section 2.4. Whether it is Evans' (1942) explanation that a high proportion are true transients, or Watts' (1970a) suggestion that they represent mice living at the boundary of the area being sampled, that is correct is not known. But either explanation involves mobile mice: either transients or wide-ranging 'edge-livers'. So the higher proportion of once-caught <u>A.flavicollis</u> suggests that this species is more mobile than <u>A.sylvaticus</u>. More evidence to support this conclusion is presented in section 3.9.

Figure 25 indicates the survival of monthly cohorts of mice. It is difficult to compare these survival rates since such a very large proportion of both species is first caught in the autumn months (September - December). The 'survival' of these cohorts is similar to the overall disappearance curves, but this is simply because they constitute almost all the data on which the overall values are based. The size of the other cohorts is so small that detailed comparisons cannot be made. It is worth noting that no mouse of either species which was first caught before the start of the autumn influx is known to have remained on the study area until the following January.

In all three winters the disappearance rates for <u>A.sylvaticus</u> are very similar but this is not so for <u>A.flavicollis</u>. In 1968/9 (the year with the highest winter <u>A.flavicollis</u> population) 'survival' was good, better than the A.sylvaticus until the disappearance of all the overwintered mice in March/April. The January 1967 cohort of A.flavicollis (i.e. those present at the start of the study) survived well until May. In the other two winters (1967/68 and 1969/70) the A.flavicollis population consisted almost entirely of 'transient' once-caught mice. In the two years for which records are available (1968 and 1969) proportionately quite large numbers of new A.flavicollis were caught in January. This did not happen with A.sylvaticus. There is no evidence that these new arrivals were young, winter-bred mice (see 3.8) and so either these results indicate that A.flavicollis is nomadic in winter or that its home-range is very large.

3.8. Variations in body weights and breeding condition

3.8.1. Introduction

Tables 17 and 18 summarise the weight and breeding condition of Apodemus captured on either of the study grids. In this section I wish to examine the data for differences between the growth and breeding cycles of the two Apodemus species. There were very low breeding populations on the woodland grid and this is why the results from both grids are considered together. Even so, the sample size in some of the summer months is too low for the calculated average weights and the percentage of mice in breeding condition to be accurate. Besides low catches, another reason for small samples of weighed mice is that weighing can only be carried out accurately in good weather, high winds and heavy rain made it necessary to abandon weighing on some days.

3.8.2 Weights

Figure 26 shows the fluctuation in average weights and the monthly range of recorded weights. The results for A.sylvaticus are very similar to those from other studies (see for example figure 4). The mice overwinter between 16g. and 20g. and show an increase in weight during the spring. The autumn decrease in average weight is due to an influx of young mice into the population and not to individual loss of weight.

The results for A.flavicollis follow a broadly similar pattern of fluctuation but with a higher average weight, an average A.flavicollis being between 1.4 and 1.5 times the weight of an A.sylvaticus of the same sex.

Table 19 shows the monthly ratios of Apodemus weights. I examined these for signs of a changing ratio at certain times of the year. If the two species are competing seriously for food at some seasons then the more successful species might increase or maintain its average weight while the other did not. In fact there are insufficient results to detect such an effect or to be sure that it does not occur. The only consistent trend is the increase in the flavicollis/sylvaticus weight ratio from August to October. This is a result of the different proportions of young mice in the catch. Most of the results come from the King Wood study area and here the sharp increase in the late summer population occurs slightly earlier in A.flavicollis than in A.sylvaticus. In August the ratio is approximately unity but it increases as the average weight of A.sylvaticus is depressed by the later arrivals of young, slim mice. The summer ratios fluctuate widely as a result of the very small sample sizes.

3.8.3. Breeding

There must always be some element of doubt about the validity of breeding cycles deduced from the examination of external genitalia. It is very easy to decide whether a male has large scrotal or small abdominal testes but testis size and position is not perfectly correlated with fertility. The females were classified as perforate/pregnant or non-perforate; this means that early pregnancies might have been counted as mice out of breeding condition and old, parous females might occasionally have been incorrectly recorded as in breeding condition. Despite the inherent inaccuracy of this method of identifying reproductive condition useful comparisons can still be made.

Figures 27 and 28 show, respectively, the percentage of males and females recorded as being in breeding condition each month. For each species/sex group the results follow a fairly similar pattern each year (considering the small sample sizes sometimes involved). The A.sylvaticus results are similar to those from other studies (see figure 4). The presence of a few adults in breeding condition during the winter and the occasional capture of winter juveniles indicates that this species may breed during the winter, although I did not record such a high level of winter breeding as that noted in some years by Smyth (1966).

The breeding cycle in A.flavicollis was similar in broad outline to that of A.sylvaticus but the duration of the breeding season is probably shorter in the former species. The female A.flavicollis reach a high percentage in breeding condition later than A.sylvaticus and the decline in the proportion of reproductive males begins about one month earlier in A.flavicollis. A.flavicollis does not seem to breed in winter, there were no captures of juveniles and an extremely low incidence of adults was recorded as being in breeding condition.

3.8.4 Breeding in King Wood

The evidence discussed later (3.11 and 3.12) indicates that part of the overwintered populations of both Apodemus species breed outside the King Wood Study area. In both species there is a sharp autumn increase in the numbers of young, but post-juvenile , mice in the study area. This is difficult to explain in terms of late breeding within King Wood. However, some mice of both species do breed in the study area, and despite a few captures of adult and juvenile A.flavicollis in the field grid area the evidence (3.11) indicates that these are not part of a resident field population.

Table 20 summarises the captures of juvenile mice during the study. In the woodland area the proportion of A.flavicollis among the juveniles is higher than the overall A.flavicollis/Apodemus ratio. There is also slight evidence of earlier breeding in the wood, by A.flavicollis, juveniles being caught from May - October instead of June to November in the case of A.sylvaticus. It could be argued that the higher weight of A.flavicollis would mean that young would become trappable before A.sylvaticus of the same age. While this is true it is only likely to cause an error of a few days since mice grow quickly. Also, juvenile A.sylvaticus were caught during May in the field. The evidence is limited but it does seem that A.flavicollis breeds more successfully in the woodland habitat while a high proportion of the A.sylvaticus breeds in non-woodland habitats.

3.9 Movements and range size in the woodland study area

3.9.1. Introduction

I have discussed in section 2.7 the difficulties of using any live-trapping methods to reveal a mouse's home range. My data are even more than usually unsuitable for estimating home range in the conventional ways. Because I did not wish to upset the normal behaviour of the mice by prolonged trapping, a trap point was only trapped one night in 14 and later in the study only once a month. A mouse would need to be exceptionally long-lived to reveal its home range by recaptures and would have had five or more months in which to change home-site.

Therefore, I have not attempted to estimate home range areas but have simply used various indices of range length for comparative purposes.

3.9.2. Average distance moved.

The average distance moved between captures is an often used index of range size. To reduce the time between captures to a minimum, and hence the chance of a change of homesite, I included only pairs of captures from consecutive trapping nights (this does not necessarily mean consecutive calendar nights). Because the grid was trapped in two halves the only movements included will be from one half of the grid to the other. Thus the minimum detectable movement is 15m and the maximum is 190.9m with only 40 different detectable movement lengths. The great majority of recordable movements are between 30m and 50m. The calculated average distances moved are listed in table 21. It will be noted that they show a remarkable similarity - a striking example of the fact that this method of estimating range lengths is really a rather laborious way of obtaining an index of the distance between the traps! Despite this, the method is still frequently used for calculating range lengths and boundary strips. My results are an example of the errors that result from range length calculations based on regular grids of traps, made worse by the omission of zero movements.

3.9.3. Direct calculation of boundary strip size.

Fortunately, the system of trapping the grid in two halves permits a direct calculation of the boundary strip size. Because the method does not depend on the recording of actual distances moved, and because information is included about animals which have not shown a recorded movement, this method is likely to provide much better comparative indices of range length. So far as I know the method of calculation is new and so my results are not comparable with those from other studies.

During the explanation of the method of calculation reference should be made to figure 29 which shows diagrammatically the areas and distances involved in the calculation.

If each trap-point is considered to be at the centre of a 15m square then the size of each grid half (5 x 10 trap-points) is 150 x $75m^2$ ($1800m^2$). The area sampled by the traps in this half of the grid will be this area plus that included in a boundary strip of width B metres. Hence there will be an overlap in the areas sampled by the two grid halves, the size of the overlap depending on the value of B and the value of B being determined by the average range size of the rodent species in question.

The analysis includes data from mice caught at least twice as the one-catch category will have included 'transients' which were not available to be caught on both halves of the grid. For each pair of consecutive trappings the animals of each species/sex group were classified as:

i) Those caught only on rows A - E (value A_t)
ii) Those caught only on rows F - J (value F_t)
iii) Those caught on both halves of the grid (value Z_t)

All the values of A_t were added together to give an overall value 'A'. Similarly $\Sigma(F_t) = F$ and $\Sigma(Z_t) = Z$

Assuming that the number of mice caught is proportional to the area sampled the value of B can be calculated:-

The area of overlap in sample areas will be

$$(2B \times 150) + \pi B^2 = Y \text{ metres}^2$$

The area of non-overlap sampled by each grid half will be:

$$(150 + 2B)75 = X \text{ metres}^2$$

Since Z is proportional to Y (assumed)

and $A \simeq F \propto X$ (also assumed)

Then

$$\frac{Z}{A + F} = \frac{Y}{2X} = \frac{(2B \times 150) + \pi B^2}{150(150 + 2B)}$$

Let $\frac{Z}{A + F} = R$. R is a value that can be calculated from the data - see table 21.

Then $150^2 (R) + 300B(R) = 300B + \pi B^2$

Therefore $\pi B^2 + (300 - 300R)B - 150^2 R = 0$

This quadratic equation can then be solved in the normal way to provide the (positive) value of B. In table 21 7.5m has been added to each of the calculated 'B' values to provide the true boundary strip value (this is because the original assumption of 15m square with a trap-point at the centre of each adds a 7.5m strip to the area actually enclosed by the grid).

The values of the boundary strip estimates are higher than those arrived at by many other workers using different methods. My values are probably overestimates because the calculation assumes a uniform habitat and spread of animals across the whole sample area. It so happens that the dividing line of the two grid halves falls across a particularly favoured habitat (see 3.10) and so the Z values are probably too high. This will apply especially to A.sylvaticus and Clethrionomys as these species are habitat selective (3.10). Despite this the values of B are highest for the male A.flavicollis. It seems fair to conclude that male A.flavicollis are more mobile (i.e. have larger range areas) than A.sylvaticus of the same sex and that males of both species are more mobile than the females.

3.9.4. Boundary strips as an index of life-range

A calculation similar to that described above (3.9.3.) was carried out in which the values of A', F' and Z' were derived from the life-time records of the mice; e.g. a mouse included in category A' was never caught in rows F - J but was caught at least twice in the woodland study area. Because the Z' category will include mice living in the area of overlap plus those which change home-site from one half of the study area to the other, this method of boundary strip estimation will be an index of life-time range whereas the estimate in 3.9.3 was an index of home-range. Both these values are included in table 20. The results follow the same pattern as those discussed above in that A.flavicollis is shown to be more mobile than A.sylvaticus and the males more mobile than the females.

However, the proportional difference between the results for the two Apodemus species is much greater. This suggests that not only is A.flavicollis a more mobile species in terms of home-range size but it is also more likely to shift its home-range thereby giving a very large life-time range. These conclusions help to explain the differences in disappearance curves for the two species, discussed in section 3.7.

3.10 Habitat selection by rodents in the King Wood study area

All studies have shown that C.glareolus has a marked preference for habitats with ground cover but results differ concerning A.sylvaticus (see section 2.8). In this section my aim is to examine my trapping data from King Wood to detect any evidence of habitat preferences. The main categories of ground cover (open coppice, bramble and bracken) are detailed in table 10 (see 3.2) and it is these three categories which are used here. Each grid square was assigned to one of the categories; if the ground cover changed within the square the type nearest the central trapping point was used to classify the square.

There are several ways in which the proportion of mice in each habitat can be estimated. For example:

a) Total captures in each habitat type

b) Total numbers of individuals caught in each habitat

c) Total numbers of resident individuals (ignoring once caught 'transient' mice).

Trial analyses showed that each method of scoring gave similar proportions of mice in each habitat. Consequently method 'a' (total captures) has been used for the detailed analysis (table 22) because this is the method using the most bits of information and is likely to suffer from smaller proportional random errors. In table 22 the actual distribution of captures is compared with the expected distribution if the mice showed no habitat selection. The significance of the deviation of the actual from the expected results has been judged using a chi-squared test. As well as the overall captures for each species/sex group the results are further split into seasonal April/October and November/March blocks (i.e. approximately the breeding and non-breeding seasons).

Examination of the overall results shows that C.glareolus exhibits strong selection for areas of cover and against the open coppice. A.flavicollis shows no selection with respect to ground cover and the results do not differ significantly from the expected 'random' distribution. A.sylvaticus does show selection in favour of ground cover but this selection is much stronger in the males than the females.

The results for the eight periods into which the results were grouped confirm the Clethrionomys and A.flavicollis overall figures. In all the periods except when catches were so low that a significant deviation was not detected, C.glareolus showed strong selection in favour of ground cover. All except one of the 16 groups of A.flavicollis results indicated no selection. The exception was when a low catch of females showed a barely significant deviation. It should be noted that with a 5% significance level, one result in twenty will show a spurious 'significant deviation' so it seems reasonable to conclude that neither sex of this species shows habitat selection.

The situation in A.sylvaticus is much more complex and deserves closer examination. Considering the results for both sexes combined, there were two periods (both winter periods) when despite large samples there was no evidence of habitat selection. During the other six periods there was evidence of significant selection. The males showed selection in favour of cover - especially of the bramble habitats. Mostly the females did not provide evidence of habitat selection but on those occasions when the results did exhibit a low level of significance this did not arise because of selection in favour of the bramble habitat. The results are intriguing - do they represent genuine differences in habitat selection by the two sexes or is the distinction the result of differences in reaction to the traps? There is some evidence in support of the latter suggestion. Table 24 shows the number of captures in each square of the grid, the upper decile of squares being indicated for each species and sex group. The Clethrionomys and A.flavicollis figures illustrate clearly the previous conclusions about habitat selection in these species. The highest catches of female A.sylvaticus tend to be in squares adjacent to the high male capture squares. This perhaps indicates that there is competition for traps in the favoured habitats and the females are consequently caught further from home. Table 23 shows the sex ratios in the three habitat types; the great preponderance of males in the bramble habitat is noticeable, although there is also an overall preponderence of males, - a phenomenon that has been noted by most authors and is probably due to the larger boundary strip for this sex. The A.flavicollis results also show a markedly different sex ratio in the bramble habitats compared with the other two habitat types, this being further evidence of trap competition biasing the results. In figure 30 I have plotted the number (per 200 trap-nights) of males against the number of females caught in each of the habitat types for each of the six monthly periods of the study. The purpose of constructing this figure was to try to decide whether the deviations from the overall sex-ratio occurred (a) in relation to the habitat type or (b) in relation to the number of males caught (and hence presumably as a result of trap competition). The answer appears to be that both factors are responsible for the deviations. All the results from the open coppice area are below the average ratio, indicating that (a) is true; but all results where the catch of males exceeds 21 are above the average ratio and all those results where the male catch is below 9 are at or below the average ratio, indicating that (b) is true, if one assumes that the more dominant behaviour of the male and their greater exploratory drives gives them the first choice of traps.

It is unfortunate that habitat selection by A.sylvaticus has not been more closely studied in areas where A.flavicollis is absent (see section 2.8). Although selection for cover definitely occurs in Ireland in areas where C.glareolus is absent, in England most studies have not detected strong habitat preferences. Table 25 shows an analysis in which I have attempted to identify some of the factors related to the degree of habitat selection shown by A.sylvaticus in King Wood. An index of selection against the open habitats is compared with the population densities of the three rodent species. The following three empirically derived rules would predict accurately all eight values of habitat selection:

1. Low A.sylvaticus populations always show habitat selection and, other conditions being equal, show stronger habitat selection than high populations.
2. Habitat selection is never strong when a high C.glareolus population is present.
3. The A.flavicollis population is irrelevant except when the A.sylvaticus population is high and the C.glareolus population is low; then, a high A.flavicollis population increases habitat selection

by A.sylvaticus.

The multiple regression analysis in table 25 also indicates that the Apodemus and C.glareolus populations influence the degree of habitat selection by the A.sylvaticus but that the Apodemus populations are of less importance. The season of the year did not appear to affect habitat selection.

It is tempting to conclude from this that:

a) C.glareolus is a habitat-specific species whose numbers can only build up when it is competing successfully with A.sylvaticus in the ground cover habitats.

b) A.flavicollis is a mobile, habitat tolerant species which exploits a wide variety of niches and competes with both A.sylvaticus and C.glareolus.

c) A.sylvaticus is a mainly cover-dwelling species but is involved in strong competition with C.glareolus in this habitat. In the more open areas competition with A.flavicollis becomes more important.

These conclusions are very tentative and I have made no attempt to identify the 'dominant' species. There is no evidence, for example, as to whether a chance decline in the C.glareolus population allows A.sylvaticus to exploit the bramble habitat or whether it is a high utilisation of the bramble and bracken areas by A.sylvaticus which causes the C.glareolus population to decline. Also the presence of a high C.glareolus population could influence the results simply by trap-competition in the way described above for the two sexes of A.sylvaticus.

3.11 Utilisation of habitats other than the King Wood Study area

3.11.1 The above ground habitat

In 1963 Borowski reported the capture of A.flavicollis high in tall trees in Poland. Also in Poland, Olszewski (1968) showed that fallen trees were important as runways for A.flavicollis. Some of the exploratory trappings at Coptfold (table 12) were designed to check on the possibility that one or both species of Apodemus lived above ground in King Wood. The traps were set between 1 and 10m above ground on horizontal trunks or branches. The traps were held in place by elastic straps and baited in the normal way. In 79 trap-nights there were no captures of Apodemus and only one Clethrionomys (1 m high, on a tree stump) although five Blue Tits (Parus caerulens) were caught at the start of the nesting season. Most of these tree trappings were in periods of low summer Apodemus populations and so the absence of Apodemus from arboreal habitats is not proven. Indeed, Apodemus captured at ground level would occasionally climb a few metres on release; one A.flavicollis which climbed to the top of a 15m Larch tree was never trapped again.

3.11.2 Range of habitats occupied by Apodemus

The results of the exploratory trappings of a wide variety of habitats on the Coptfold Estate (table 12; figure 11) indicate that both species of Apodemus are widespread and utilise to some extent all of the habitats studied. The few areas in which A.flavicollis are not trapped are not of a particular habitat type and almost certainly the failure to detect A.flavicollis in these areas was simply a result of the small number of trap-nights used in each area. Overall, from the exploratory trappings, about 1/5 of the Apodemus were A.flavicollis compared with ¼ overall from the King Wood study grid. The difference probably results from the smaller proportion of A.flavicollis in the crop fields, a phenomenon discussed below.

3.11.3 Use of crop field by Apodemus

The exploratory trappings indicated that A.sylvaticus in particular utilised the crop field habitat. To investigate the field populations in more detail a trapping grid similar to that used in King Wood was set up in Field C and trapped for two years. The results are given in table 13. During 1969 the crop was beans and in 1970 wheat, but the trapping results were fairly similar for both years.

Although there were a few captures during the winter months the field populations (table 14) reached a peak in the summer - a reversal of the situation in the wood. Catches of Clethrionomys were very low and the proportion of A.flavicollis in the field Apodemus catch was only ⅛ (cf. 3.11.2).

The arable field habitat does not show any major difference in habitat between one grid square and the next (although the habitat shows a great seasonal change). One would not therefore expect the captures to provide evidence of habitat selection on the basis of the habitat within the grid square. But if the mice were visiting the field from a woodland home-site the proximity of the woodland may be important. The same type of test for habitat selection used in section 3.10 was applied to the field grid results, the 'habitats' being row 1 nearest the wood, row 2 which was 15m further into the field and rows 3 - 10 in the body of the field. The details of this analysis are given in table 26. These results show clearly that A.flavicollis was associated with the edge of the field and was presumably not resident in the field. While the A.sylvaticus showed a small but significant edge component, the results indicated that many mice lived deep in the field. Table 27 gives the disappearance rates for the field caught Apodemus. All the A.flavicollis were one-catch 'transients', further evidence that they were feeding but not living in the field. The A.sylvaticus results show clearly that a resident population of this species builds up in the field during the summer months. The captures of resident A.sylvaticus and juveniles in the fields showed that this is an important breeding habitat. Since the A.sylvaticus population is higher in the field than in the same area of woodland during the summer and since the area of arable land to which

King Wood is the nearest woodland is larger than the wood itself, it is certain that the arable fields are the main breeding habitat for A.sylvaticus at Coptfold.

The same does not apply to A.flavicollis where the proportion of juveniles caught in the wood is higher. The breeding population certainly exploits the field edges but does not become resident in the fields.

3.11.4 Movements between habitats

Table 28 details the recorded movements between the King Wood grid and the field grid. One of the records (mouse 723) is clearly a case where the home range incorporated both wood and field habitats with a pattern of captures alternating between the two.

Some appear to be definite migrations from one habitat to the other, but the many where there was just one capture before and after the recorded movement are not classifiable. This discussion refers only to A.sylvaticus because the recorded movements of the other species are too few to be meaningful. It is worth noting that in movements between wood and field there is a longer time lag between a wood capture and a subsequent field capture than between two captures involving a move in the other direction. This possibly indicates that the spring migration to the fields is a slow process (perhaps via temporary residence in the hedgerows) whereas the migration to the wood when the crop is harvested is more direct and sudden.

3.12 Fluctuations in the woodland Apodemus population

In section 2.5 a method of expressing the monthly catches in terms of percentage of the annual catch was used to facilitate study of annual fluctuations in the results from published studies of A.sylvaticus populations. The same method was applied to my Apodemus results from King Wood and the details are included in table 29 and figure 31. The fluctuation in the A.sylvaticus population was very similar to the published studies. In all three years the variances were well within the range given in section 2.5.

The A.flavicollis results show higher variances indicating larger fluctuations in the monthly catches. This, however, is probably a result of the smaller samples suffering from proportionately larger random errors. If the figures for the three years are combined then A.flavicollis shows a smaller variance than A.sylvaticus. This is what one would expect if a larger part of the A.flavicollis population remains in the wood to breed during the summer, as the results in section 3.11 indicate.

The pattern of fluctuation is fairly similar in the two species and is absolutely consistent in the low point during July in all years. In A.sylvaticus the July low is the only trough in the graph except for an insignificant dip in November 1968. The A.flavicollis results pick up slightly after an early spring trough, perhaps indicating a recruitment of new mice by breeding. Clearly, in July, the availability of food in the adjacent fields is so high that both species are very poorly represented in the woodland area.

Each year there was a third trough in the late autumn (October - December) in the A.flavicollis catch. Each year this is in the same month as the lowest A.sylvaticus catch during these three months and is probably a result of poor trapping weather biasing the catch.

It is noticeable that the only year in which A.flavicollis failed to show the normal autumn peak in numbers was 1969 when no cereal crops were grown adjacent to King Wood. Although this species does not become a field resident perhaps the opportunity to feed at the edge of grain crops leads to more successful breeding.

Section 4

STUDIES ON THE DISTRIBUTION AND ABUNDANCE OF THE TWO APODEMUS SPECIES IN ESSEX.

4.1 Introduction

My aim in this section is to consider the distribution and relative abundance of the two Apodemus species over a wider geographical area than that covered by the intensive study at Coptfold described in the previous section. Although the Coptfold area is a fairly typical Essex agricultural habitat it does not include all the Essex habitat types. In selecting the trapping sites for this more extensive survey an effort was made to include a wider range of habitats.

Linn (in Southern, 1964) has stated that A.flavicollis tends 'to occur in small patches among general Wood Mouse populations', although this statement appears to be based on the work of Thurlow (1958, not 1938 as stated by Linn) which involved the capture of only eight A.flavicollis and eleven A.sylvaticus. My work at Coptfold has shown that the only patchiness involved in the A.flavicollis distribution is that this species tends to avoid fields; in woodland it was less patchy than A.sylvaticus. The wider survey reported in this section will include discussion of patchiness of A.flavicollis distribution over wider areas.

Yalden (1971) detected a correlation between the proportion of *Apodemus* in the catch of rodents and the proportion of *Apodemus* which were *A.flavicollis*. I have included data on the other small (less than 50g) mammals caught during this survey, to enable such comparisons to be made. A more detailed discussion concerning these other species is included in a paper which has been accepted for publication (Corke & Harris in press).

4.2 Historical Background

The first reasonably full account of small mammals in Essex was published in 1898 (Laver). The widespread occurrence of *A.sylvaticus* was reported by Laver and although older firm records are few it seems reasonable to suppose that *A.sylvaticus* has been resident in Essex throughout historical times (see section 5 for discussion of fossil records). The same probably applied to *A.flavicollis* although this species had not been recognised in Essex in 1898. Laver discovered the species in Essex early this century (his discovery being reported by Cole, 1905). Laver (1915) hinted that the species was expanding: 'This is in a very different condition (to the practically extinct Essex polecat population) and instead of approaching extermination is more frequent apparently. It is only during the last few years that it has been so generally recognised. It is found in most parts of Essex.' Probably the increasing apparent frequency was due, in part at least to the recent discovery of the species.

4.3 Methods

For the preparation of the distribution maps (figures 32, 33 and 34) the method was simply the accumulation of all recent (post-1959) records which were reliable and locatable to a 1 kilometre grid square. Like Laver (see above) I relied to some extent on casual recording of specimens found dead, caught by cats or household mouse-traps, seen alive in the wild or reported by countrymen and naturalists. But, unlike Laver, three more recent methods supplied the vast bulk of the records:

4.3.1. Live-trapping. Standard Longworth traps set in small groups overnight with no period of pre-baiting were used to collect samples of small mammals from a very wide variety of Essex habitats. The number of traps used and the time of trapping varied and this should be borne in mind when studying the results given in table 35. For comparison the results of the Coptfold study and another fairly intensive trapping survey are summarised in table 30. These live-trapping records are by far the most important source of Apodemus records because it was only by handling the actual animal that the species could be ascertained. The following two methods provided many records of other species but Apodemus specimens could often only be identified to genus.

4.3.2 Bottle-hunting. Morris and Harper (1965) showed that it was a common occurrence for small mammals to enter discarded bottles, become trapped and die. Systematic searches by groups of naturalists and students led by myself have provided large collections of small mammal remains. Most of the bottles were collected from roadside hedges and ditches. The skulls and mandibles were easily identified using the published keys (Corbet, 1964; Southern, 1964; Morris, 1970) except in the case of the two Apodemus species. Using Fielding's (1966) method it was possible to identify specifically 44 of the 46 Apodemus skulls from the 1968 collection. All the other records remain grouped as Apodemus spp in table 31 and were not included in the maps except for a few instances where a freshly 'bottled' mouse was still identifiable from its pelage.

4.3.3 Owl Pellets. Birds of prey regurgitate the indigestible remains of their prey and the mammal remains can be identified using the same techniques as for bottle-hunting. The review by Glue (1970) shows how useful this technique can be to mammalogists but the difficulties in identification of Apodemus species have reduced the value of this method for my purposes. A set of results of owl pellet analyses from Essex localities is summarised in table 32. In no cases was any attempt made to identify the Apodemus remains specifically.

4.4. Discussion of methods

Table 33 compares the results of the four main survey methods (intensive trapping, extensive trapping, bottle-hunting and owl pellet analysis) in terms of the relative frequencies of the species recorded. The fact that each main sampling method (traps, bottles and owls) reveals a different 'most common' species indicates that care is needed in the interpretation of the results. Basically the results could differ because:

a) The sampling techniques have different biases.

b) The survey methods have been used to sample different habitat types.

c) The samples were collected at different times of the year.

Probably a combination of all three factors is involved. Differences resulting from (b) and (c) are real differences in relative abundance which I do not wish to ignore. Factor (a) however, generates spurious differences which I wish to minimise, therefore a discussion of the likely biases of traps, bottles and owls as small mammal samplers is necessary.

Live-trapping. Overnight trapping is likely to increase the proportion of nocturnal species caught. This means that live-trapping will indicate too high a proportion of Apodemus, an effect that is likely to be reinforced by any trap-shyness shown by voles (see 3.4.5). A.priori I would expect live-trapping to underestimate the abundance of the above ground living Micromys minutus but in fact a higher proportion of the catch consisted of this species than was the case with the other sampling methods. Very light animals are likely to be underestimated as they have a much greater chance of leaving the trap without firing it. This is likely to cause an underestimate of the shrews, and this will be made worse if the bait used (whole oats) attracts rodents more than shrews. A marked difference will be noted in the proportion of shrews in the intensive and extensive trapping surveys. This results from the high death-rate of shrews in the traps. In a series of trappings in the same area recaptures of rodents will increase the catch rate for that species but shrews, which normally die at the first capture, are only counted once. The extensive survey results are therefore more likely to give a more realistic indication of the relative abundance of shrews.

Bottle-hunting. Since bottles are effective as traps over a long period they may overestimate species (such as *Neomys fodiens*) which migrate through the habitat being sampled but which have a low or non-existent resident population. Unlike live-traps, the bottles are not likely to be biased against small species; the reverse will be the case with narrow-necked bottles. There is likely to be variation among the various small mammal species in the propensity to enter and ability to escape from bottles. Live-traps are not baited with shrew food but bottles soon attract an insect fauna (especially once an animal has died in the bottle) and this may be a further attraction to shrews.

Owl Pellets. The proportion of each species in owl pellets is likely to reflect the relative abundance of the species in habitats hunted by owls (the habitat not being known with certainty, but since owls are territorial it is likely to be the habitat near where the pellets were found) and the feeding preferences of the particular individuals and species of owls. Many of the pellets were collected on an island (Foulness) where C.glareolus may be absent (Corke and Harris in press).

It appears that the methods differ greatly in their ability to catch shrews and, there is probably much less difference in bias between different species of rodents. In table 36 the results are reworked to compare the proportions of rodents caught (omitting island owl pellets). Differences are still present but for the most part these can be accounted for in terms of habitats sampled. The owls (barn and short-eared) which provided most of the pellets, hunt over open grassland, a habitat favouring M.agrestis.

The bottles were almost all collected from roadside hedges and ditches with a very few from mature woodland. The hedgerow habitat is favoured by C.glareolus. The live-traps were set in as wide a variety of habitats as possible, but rather more in woodland than is 'fair' in terms of the proportion of Essex covered by woods.

4.5 The Proportions of Rodents Caught

Figure 35 shows the relationship between the proportion of rodents which were Apodemus and the proportion of the Apodemus catch which was A.flavicollis for the main Coptfold habitats and the extensive Essex trapping survey. The results from King Wood tend to confirm Yalden's (1971) report that there is a positive relationship between these two ratios. This effect is simply a result of investigating habitats in which there are only three rodent species. The C.glareolus are restricted to scrub and woodland with ground cover while the A.flavicollis are more evenly dispersed in the woodland. This difference will automatically generate the effect shown by Yalden and the failure of C.glareolus to colonise the arable fields explains why the field results do not fit the pattern.

The sample sizes from the extensive survey localities are small and so the proportions vary as a result of random errors to a greater extent than the Coptfold results. Even making some allowance for this there seems to be little evidence for the Yalden relationship applying to these results. All that can be said is that A.flavicollis occurs in woods where Apodemus constitutes a fairly high proportion of the rodents. In other habitats the proportion of Apodemus (sylvaticus) varies widely.

4.6 Geographical Distribution of Apodemus in Essex

The maps (figures 32, 33 and 34) show the distribution of the two Apodemus species in Essex together with C.glareolus for comparison. Before examining the maps for evidence of restricted distributions it is important to realise that the survey is not complete. For example C.glareolus appears at first glance to be more widespread than A.sylvaticus but this is simply the result of the availability of a large number of C.glareolus records from the bottle-hunts, most of the Apodemus remains from this source not being specifically identified. However, looking at the distribution of live-trapping captures the two species seem equally widespread except that C.glareolus does not extend so far into urban London as does A.sylvaticus. Comparing the distribution of the two Apodemus species there is no real evidence of the absence of A.flavicollis from any large area of mainland Essex except the built-up area of London.

At first sight this absence of A.flavicollis from built-up areas seems strange in view of this species known propensity to enter human habitations. Laver (1915) states 'If a long tailed Field Mouse (i.e. Apodemus spp) is caught in a storeroom in a house in this county (Essex) it is generally of this species. It cannot be said that the ordinary sylvaticus never enters houses, for it does so at times, but much more rarely than the Yellow-necked variety or species.' Recent reports confirm Laver's impression that A.flavicollis is prone to enter country houses; there are records of this happening at Little Leighs, Coptfold Hall, Norsey Wood, Alresford, Colchester Museum and the Flatford Mill area. At Little Leighs, where records were kept, the mice invaded the loft in the autumn soon after harvest-time. When they were removed new arrivals did not appear until the following autumn. It appears that household populations of A.flavicollis only occur where the house is adjacent to a free-living population, and that invasion takes place at the same time of year when there is a rapid change in habitats and a build-up in the woodland Apodemus populations. Possibly the greater success shown by A.flavicollis at colonising houses is due to a greater climbing ability than is possessed by A.sylvaticus.

4.7 Habitats Occupied by A.flavicollis

The overall ratio of A.flavicollis/Apodemus is much lower from the extensive trapping than from the King Wood study area. If the results from only those habitats in which

A.flavicollis was caught are considered then the ratios are more similar, 1/5 from the extensive trapping and 1/4 in King Wood. This would appear to indicate that A.flavicollis has a restricted range of habitats in which it is fairly common, but is absent from other habitats. The question which I wish to try to answer in this section is 'what particular features of a habitat make it suitable for A.flavicollis?'

At Coptfold it appeared that most of the A.sylvaticus bred in the crop fields leaving only small populations to compete with the A.flavicollis in the woods. Could it be that the proximity of arable crops is necessary to allow this separation of the two species during the breeding season? Table 37 shows results from the 'arable' and 'non-arable' habitats trapped in the extensive survey. These indicate that there is a highly significant degree of selection by A.flavicollis in favour of 'arable' areas. The difficulty is that the choice of 400m as the dividing line for the proximity of arable land is quite arbitrary and no Essex rural habitat is more than two or three kilometres from arable fields. It is particularly rare for fairly mature woodland to be far from arable land so there is no guarantee that the presence or absence of nearby arable land is the only difference between the 'C' and 'D' habitat categories.

It is often stated that A.flavicollis occurs in more mature woodlands (e.g. Southern, 1964; Corbet, 1966) and this would agree with the Coptfold results in so far as A.flavicollis showed no selection against the more open ('mature') parts of the study wood. Table 38 includes all those results from habitats in or at the edge of woodlands for which full details of date, trap-nights and catch of Apodemus are available. This list includes all the table 35 areas where A.flavicollis was caught except for three localities where the necessary details are incomplete. With such small samples in most of the areas, it is difficult to be certain whether failure to detect A.flavicollis results from its genuine absence from the area or simply chance failure to catch any. The analysis in table 38 attempts to compensate for these small samples. Taking as a Null Hypothesis the suggestion that all Essex Woodland habitats have both species of Apodemus present at the same level of abundance as in King Wood at the same time of year, and that the catch per unit trapping effort is a valid index of abundance, it is possible to predict the numbers of the two species that one would expect to catch for a given trapping effort in a particular month. For each trapping the actual numbers caught are given together with:

a) The probability of not catching any A.flavicollis based on the probability of catching an A.flavicollis in one trap-night in King Wood.

b) The probability of not catching any A.flavicollis based on the probability of catching an A.flavicollis for each Apodemus capture in King Wood.

c) The expected number of A.sylvaticus caught if the Null hypothesis is true.

d) The expected number of A.flavicollis caught if the Null hypothesis is true.

e) The expected number of _A.flavicollis_ caught if the species has the same abundance relative to _A.sylvaticus_ as in King Wood.

Each of these estimates can then be summed and the expected number of habitats in which _A.flavicollis_ should have been caught can be compared with the number in which the species was detected. Both methods (a) and (b) suggest that _A.flavicollis_ should have been detected in more than 20 habitats instead of the actual figure of 13. Also an actual total capture of 22 _A.flavicollis_ compares with an expected catch of over 56 by both methods (d) and (e). The actual number of _A.sylvaticus_ slightly exceeded the expected number from estimate (c).

It seems, then, that the Null hypothesis is not true. The second part of the Null hypothesis 'that the catch per unit effort is a valid index of abundance' does not need to be true for estimates (b) and (e) which depend on relative measures only, and yet these estimates agree fairly well with (a) and (d) respectively. It is, therefore, reasonable to conclude that _A.flavicollis_ is _not_ as abundant or widespread in Essex woodlands generally as it is in King Wood.

It appears that in Essex _A.flavicollis_ is most likely to be found in woodland habitats with adjacent arable fields. There may well be other factors involved in limiting the distribution and abundance of the species but my study has not been detailed enough to detect them.

Section 5

STUDIES ON FACTORS RELATED TO THE DISTRIBUTION OF A.FLAVICOLLIS IN BRITAIN

5.1 Introduction

A study of the distribution pattern of the two British species of Apodemus should throw some light on the nature of the ecological differences between the two species. If similarities between the distribution pattern of A.flavicollis and any other physical or biological factors can be found, these may help explain the restricted distribution of this species.

Before attempting a discussion of the possible reasons for the restricted distribution of A.flavicollis it is necessary:

a. to establish a reasonably accurate picture of the species true range.

b. to consider whether the range is changing.

For these reasons this section begins with a review of the history of Apodemus in Britain and a discussion of the likely errors involved in the distribution survey.

5.2 The History of Apodemus in Britain

It is generally accepted that A. sylvaticus has been present in the British Isles continuously since the late Pleistocene (Barrett-Hamilton and Hinton, 1910-1921). Descriptions of mice which probably refer to this species occur in early European literature (e.g. Gesner, 1551). There appears to be considerable doubt about the date and method by which A.flavicollis arrived in Britain. Corbet (1964) listed the species in a checklist as '? introduced' but gave no evidence. Lawrence and Brown (1973) list the species as 'introduced in 1894' a statement which is quite untrue as 1894 was the date of the discovery of the species in Britain (de Winton) at which time it was widespread.

Whereas A.sylvaticus was recognised by Linnaeus (as Mus sylvaticus, 1758) it was not until 1834 that Melchior described his Mus flavicollis from Denmark. This description was ignored for many years and so it is not really surprising that the first definite records of A.flavicollis in Britain do not date before 1894. However, early descriptions of mice (e.g. Pennant 1793) "..... Field Rat.....breast of ochre colour; belly white; length from tip of nose to tail 4½ inches; tail 4 inches.." is more likely to refer to A.flavicollis than any other species.

The fossil history of Apodemus in Britain is peculiar. Fragmentary remains of late Pliocene and early Pleistocene Apodemus have been referred to A.whitei which closely resembles the living A.sylvaticus (Barrett-Hamilton and Hinton loc. cit). Apodemus was, apparently, absent during the middle Pleistocene but in the late Pleistocene two forms were present. In addition to the small A.sylvaticus-like fossils, larger skulls and jaws referred to A.lewisi were found at Ightham, Torquay and the Forest of Dean. A.lewisi closely resembles A.flavicollis but no more closely than do the skulls of the large extant island races of A.sylvaticus. However, there is now good evidence (Berry, 1969) that the island races of A.sylvaticus are recently evolved and since A.lewisi existed contemporaneously with a smaller Apodemus species it seems reasonable to regard it as the ancestral stock of A.flavicollis. If this is so it is interesting that A.lewisi occurred in Devon - an area from which A.flavicollis appears to be absent today (see 5.3).

It thus seems reasonable to regard A.flavicollis as a native species. If it was introduced then this must have happened so long ago that A.flavicollis has had a long time in which to colonise potentially suitable habitats.

There is no evidence for a changing range between the early records of de Winton's time and today. A.flavicollis can be found in all the old localities (except Northumberland, but see 5.3) and the new records are from previously unexplored areas rather than newly invaded regions.

5.3 Accuracy of present distribution maps

Figures 36 and 37 show the distribution of A.sylvaticus and A.flavicollis respectively, as recorded in the Mammal Society survey (Corbet, 1971) with a few minor corrections to incorporate recent records. Before using such maps as the basis for any discussion it is important to establish to what extent the recorded distribution pattern is an artefact resulting from uneven distribution of recorders. All the available evidence indicates that *A.sylvaticus* is to be found in any rural area and most urban habitats. Certainly a full survey would detect *A.sylvaticus* in virtually all mainland 10 km national grid squares and on many of the small islands. Hence the *A.sylvaticus* map (fig. 36) may be taken as a reasonable map of mouse recorder distribution. The large gaps in Norfolk, Lincolnshire, South Wales and parts of Scotland and the Borders indicate absence of recorders in these areas. Thus when examining the *A.flavicollis* map (fig. 37) a gap in the apparent distribution of *A.flavicollis* which coincides with a gap in the *A.sylvaticus* map simply means that no search was made in that area. It is not even safe to conclude that *A.flavicollis* is genuinely absent from areas where *A.sylvaticus* is present but *A.flavicollis* has not been recorded. This could simply result from the fact that *A.sylvaticus*, being more common, will be detected by casual recorders who may miss *A.flavicollis* However, large gaps in the *A.flavicollis* map, which correspond with fairly well recorded *A.sylvaticus* areas, may reasonably be assumed to be areas from which *A.flavicollis* is absent. On this basis *A.flavicollis* is absent from all small islands so far examined, from Ireland, Scotland, the north-west of England, the Midland area around Oxford and the South-west peninsula.

The apparent recent distribution of *A.flavicollis* falls into two main blocks:- (1) south-east of a line from Portland Bill to Norwich and (2) the Welsh Marches. The south-east of England contains a high proportion of the Mammal Society members and a block of records in that region is a common feature of the distribution maps for most widely distributed mammals. Many of the records from Wales and its borders result from a survey by Matheson (1964) and it will be noted that *A.flavicollis* was recorded from several squares from which no-one has bothered to record *A.sylvaticus*. Because of the absence of recently active recorders it is not safe to assume that the old records from Cheshire, Derbyshire, Lincolnshire and Leicestershire represent mistaken identification or extinct populations. The Northumberland record is old but the specimen still exists and is considered to be a genuine record (Corbet, 1971). I carried out a short trapping survey at the same site in April 1969 and did not find any *A.flavicollis*. Only a few *A.sylvaticus* were caught and the trapping was not intensive enough to provide any real evidence of the absence of *A.flavicollis*.

Figure 38 shows a probable distribution map for *A.flavicollis* in which I have made some effort to eliminate the effects of uneven recording. The true range may be more restricted than is shown in this map but it is unlikely to be less restricted.

5.4 The distribution of *A.flavicollis* in Britain

Despite the inadequacies of existing distribution maps it seems certain from the above discussion that *A.flavicollis* has a restricted distribution and there must be some reason for this. A priori any of the following factors could account for a restricted distribution:-

(a) The present distribution is a transitory stage in the expansion of A.flavicollis from its centre(s) of introduction into Britain.

(b) A.flavicollis may not be able to colonise some potentially suitable British habitats due to the fragmentation of habitats by man.

(c) Climatic, geological or biological features (which are likely to be related) restrict the habitats which are naturally suitable for A.flavicollis.

(d) Man has affected the ecology of certain habitats in such a way as to affect their potential suitability for A.flavicollis.

The above four factors cover all the possibilities. Either A.flavicollis is expanding (a) or has a relatively stable distribution pattern explicable by some combination of factors b, c and d. It could be argued that the range is decreasing as a result of competition or changing habitats but if this is so then the fact that the species has disappeared from some areas and, as yet, remains in others is to be explained in terms of b c or d.

I consider (a) to be unlikely. As explained in section 5.2 A.flavicollis is either a native or an introduction of long standing. It would be difficult to explain the very slow rate of spread which must be occurring if (a) is true.

Possibilities b, c and d are rather more likely. It is difficult to test possibility (b) except by experimentally introducing A.flavicollis into apparently suitable habitats from which it is known to be absent. This has yet to be done. The most plausible argument for this possibility would be as follows:

A.flavicollis would have been restricted to the south of England after the last Ice Age, living in the large forests which developed as the Ice Age ended. Mature forests are the typical habitats of this species in central Europe (see section 1). The destruction of woodlands by man began very early in the history of man in Britain and few areas have been afforested continuously since the forests first appeared after the ice age. A.flavicollis was able to persist in areas where forests remained or where forests regenerated near enough to reservoir habitats of the mice. But natural or artificial reafforested areas remote from A.flavicollis colonies would not be recolonised.

The main arguments against this view are that A.flavicollis, while being basically a woodland animal, does move along hedgerows and often invades houses. It seems to be no less mobile than most other small mammals and no other species have ranges restricted by habitat fragmentation.

The only other mainland British small mammals with restricted ranges are the dormouse (Muscardinus avellanarius) and the harvest mouse (Micromys minutus). The dormouse is mainly a southern species and this could be explained purely in terms of climate (perhaps a requirement for a warm winter or a reasonably long summer feeding season) although the hazel coppice woodlands which are the main habitat of the dormouse are mainly southern in distribution. The harvest mouse has a mainly southerly and easterly distribution and this probably results from its requirement for a dry climate for successful breeding; wet weather can destroy the breeding nests and young (Adams, 1913 and Harris personal communication).

To see if similar explanations could apply to A.flavicollis I compared the distribution map with all available climatic, geological, sociological, land-use, botanical and zoological distribution maps. (The main sources being the Oxford Atlas of Britain (Bickmore & Shaw, 1963), Perring and Walters, Atlas of the British Flora, 1962 and the interim distribution maps from the Biological Records Centre).

None of the recorded distributions of wild species (plant or animal) shows much similarity with that of A.flavicollis. This is so even when records from the mainland of Britain alone are considered (to allow for the differential ability of various species to colonise islands). The most closely similar plant distribution is that recorded for Campanula trachelium (figure 39). This is a woodland plant associated mainly with lowland woods on fairly heavy soil (Clapham, Tutin and Warburg, 1962).

It is also noticeable that among the geological, soil and altitude maps only the map of lowland areas (fig. 40) in Britain shows much similarity with the A.flavicollis map.

No single meteorological map corresponds well with the A.flavicollis map. It is, however, possible to combine temperature and rainfall information to generate a map which shows some similarity with A.flavicollis distribution (see figure 41 which indicates those areas with a February mean daily minimum above 34.5° F and an average annual rainfall below 40 inches).

It seems unlikely that small differences of temperature and rainfall would have a direct effect on A.flavicollis and so if the relationship between climate and A.flavicollis distribution is cause and effect it is likely to be an indirect relationship working via the distribution of some other habitat factor.

In section 4.7 I discussed evidence from Essex which indicated a possible relationship between land use and the presence of A.flavicollis. Examination of the national pattern of agriculture seems to support this suggestion. There appears to be a positive correlation (figures 42, 43, 45) between the presence of A.flavicollis and:

(a) the amount of land devoted to cereal growing
(b) the density of farm labour
(c) density of gamekeepers

and a negative correlation with the amount of land used as permanent pasture and rough grazing (fig. 44). Thus it would seem that A.flavicollis favours areas of intensive arable farming where woodlands exist as game preserves. Since this type of agriculture occurs in lowland areas with the appropriate climate this also explains the relationship between A.flavicollis and these other factors. Presumably the explanation for this restriction of A.flavicollis would be that it can only co-exist with A.sylvaticus where the opportunity for breeding season habitat separation occurs, as happened in the Coptfold study area (see 3.11.3)

5.5 A survey of A.flavicollis distribution and abundance in Britain

The national mammal distribution survey (Corbet, 1971) was a simple presence or absence survey with no attempt being made to consider the relative abundance of the different species in various habitats. In an attempt to gather more detailed records of Apodemus distribution I carried out a survey among Mammal Society members and other interested naturalists.

The survey form and accompanying letter (figure 46) was carefully designed to persuade participants to include any possibly relevant information and to avoid 'leading' the naturalists into only sending records which supported my hypothesis of an association between arable land and A.flavicollis.

No effort was made to check the identification of the specimens recorded, but most Mammal Society members are knowledgeable field naturalists who could be expected to identify the two Apodemus species correctly. This applied with added force to those who take the trouble to use small mammal traps.

When a few forms which had been wrongly or incompletely filled in had been eliminated there were 98 completed record sheets remaining. These form the basis of the summary and analysis in table 39.

This table shows clearly that A.flavicollis has a more restricted range of habitats than does A.sylvaticus. In particular A.flavicollis avoids non-woodland, non-garden habitats. In and around houses A.flavicollis is about as common relative to A.sylvaticus as it is in woodland, but almost all reports of Apodemus in occupied houses (mostly casual reports not included in the survey) are of A.flavicollis.

When considering all the records there is no evidence that A.flavicollis is more frequent in woodland near arable land than in other woodlands. In fact there is a slight indication that the reverse is true.

Considering records only from areas where A.flavicollis was known to be present there is still no indication that A.flavicollis represents a higher proportion of the Apodemus population in 'arable' rather than 'non-arable' woods. It is unfortunate that many of the results for 'non-arable' woods came from one general area (New Forest) and at one time of the year (May/June). The Essex results (table 38) indicate a great difference in the sylvaticus/ flavicollis ratio at different times of the year. For this reason the survey results were reworked to eliminate those records obtained only in May/June. This final analysis does give a higher proportion of A.flavicollis in arable woods than in non-arable woods where both Apodemus species occur but the difference is not significant at the 5% level.

Thus this survey does not support my original hypothesis and suggests that differences in the proportion of A.flavicollis in the C and D habitat categories in Essex may have resulted from some factor other than the proximity of arable land.

The conflict between the survey results and the mapping correlations (see 5.4) can only be resolved if it is suggested that the correlation between land use and A.flavicollis presence and abundance operates only on a very broad level with large edge effects. If it is the balance of woodland/arable land over a very wide area which determines whether A.flavicollis can maintain a viable population anywhere in the area, then the above survey would fail to detect this. Clearly the situation is complex and my work has not satisfactorily solved the riddle of A.flavicollis distribution.

Section 6

GENERAL DISCUSSION

6.1 Introduction

My main aim in this section is to attempt to answer, in the light of the research detailed in this thesis, the questions I posed in the introduction. In addition I wish to compare briefly what is known of the ecology of *A.flavicollis* in Britain with the situation on the continent of Europe, with a view to speculating on the origin of the differences between the ecology of *A.flavicollis* and *A.sylvaticus* in Britain.

6.2 Competitive Exclusion?

"When the two *Apodemus* species occur together are their niches sufficiently distinct to permit their indefinite sympatric existence?".

The short answer seems to be yes. The pattern of population fluctuations at Coptfold did not suggest that either species was in a period of decline and replacement by the other. Also the survey of distribution at the national level has failed to reveal any changing distribution of *A.flavicollis* since its discovery at the end of the last century. So there is no reason to suppose that the two species cannot co-exist indefinitely and thus it is axiomatic (if the Volterra - Gause principle is correct) that the two species occupy adequately distinct niches.

I have not investigated all aspects of A.flavicollis ecology, but of those which I have investigated the main points of difference from A.sylvaticus are as follows:

a) Range sizes. The Coptfold A.flavicollis individuals ranged widely, overlapping the areas occupied by the less widely ranging A.sylvaticus in the woodland habitats.

b) Breeding habitats. The results from Coptfold indicate that a high proportion of the A.sylvaticus breed in the crop fields while the majority of the A.flavicollis breed in woods or hedgerows, only making occasional forays into the fields and not becoming resident there.

c) Winter habitat preferences. In winter both species are woodland residents but whereas A.sylvaticus shows a distinct preference for areas with undergrowth cover, the A.flavicollis occupied open and undergrowth areas equally readily.

I have not investigated the food and predators of Apodemus (and there is no published information on these aspects of A.flavicollis ecology in Britain) but as a result of the observed differences in breeding areas and winter habitat preferences it seems highly probable that small differences in food and predators could be detected. But since the diet of A.sylvaticus is so varied, the species being an opportunist feeder (Watts, 1968), the differences are likely to be small.

In some respects the relationship of the two species fits the 'included-niche' model (Miller, 1967), the niche of the basically woodland A.flavicollis being included within the niche of the eurytopic A.sylvaticus. The situation is more complicated than this since, when the woodland habitat is taken alone, the A.sylvaticus niche is to some extent included within that of the more widely ranging A.flavicollis.

Despite these observed differences in the ecology of the two species it is noticeable that the niches are very similar: more similar than any other pair of British terrestrial small mammals with the possible exception of the two Sorex species. So the question must be asked: "why are the two sympatric populations not regulated by the same factor(s) - a process that would normally lead to the eventual elimination of one species?"

Probably the niches are different enough for the regulatory factors to favour one species in its niche and the other elsewhere. This is the classical Volterra - Gause type explanation of such a situation. But it is worth considering an alternative explanation of how two very similar species can persist sympatrically.

If one makes the following assumptions about two ecologically very similar (and possibly identical) species:-

a) Each is successful enough (when occurring in the absence of the other) to produce surplus offspring, the population being regulated by territorial behaviour forcing surplus young out of the main habitat.

b) The size of territory defended (by individuals or groups) is related to the food requirements.

c) Territory is defended against members of the same species only.

Then, when the two species come into competition, they will have overlapping territories. Each will be 'stealing' food from the other. In this situation each species is likely to enlarge its territory size (since selection will favour those that compensate for the food lost to the other species) and hence reduce the population density. If this happens then the two species can co-exist indefinitely irrespective of whether there is a difference in reproductive potential between the species.

It seems to me that this could explain the co-existing *Sorex* species, where the two British species are known to be strongly territorial and ecologically very similar (Michielsen, 1966); and in which interspecific territoriality does not occur because of the rapid avoidance of *S.araneus* by *S.minutus* individuals whose territories overlap (Crowcroft, 1957). In *Apodemus* little is known of the occurrence or nature of territorial behaviour, although territoriality by small groups led by a dominant male is a possibility (Brown, 1969). If such territoriality does occur it could explain the sympatric co-existence of the two *Apodemus* species, but could not explain why the two are not sympatric throughout Britain.

6.3 Effect of A.flavicollis on A.sylvaticus ecology

"Does the presence of *A.flavicollis* change the ecology of *A.sylvaticus*?"

Based on my work at Coptfold the answer appears to be 'not much'. Published results from studies of single species Apodemus populations indicate that a great deal of variation in population dynamics, range size and habitat choice is normal in A.sylvaticus. The only difference I detected between the Coptfold A.sylvaticus and those not living in association with A.flavicollis was a slightly lower average winter population density. This can be explained if it is assumed that the two Apodemus species are competing for the same food resources; either directly or via territorial behaviour as suggested above.

6.4 Range restriction in A.flavicollis

"Why has A.flavicollis not extended its range further into Britain or, alternatively, been excluded completely by A.sylvaticus?"

The fact that the restriction in range of A.flavicollis does seem to be a stable and not a transitory situation indicates that the co-existence of the two species must, to some extent, depend upon them occuping somewhat different niches. The pattern of distribution of A.flavicollis can be explained fairly satisfactorily if it is assumed that only in lowland agricultural areas with a varied mixture of woodland and agricultural land, can the two species maintain distinct niches. Based on the Coptfold study an important aspect of this niche separation could be the separation of breeding habitats, something that can only occur when arable land occurs in close proximity to woodlands.

6.5 A.flavicollis ecology in Europe

There have been few studies of mixed Apodemus populations in Europe. The two main population studies are those of Bergstedt (1965, 1966) in Sweden and of Mermod (1965) in Switzerland. In both these studies the populations behaved in a similar way to the Coptfold populations. In Bergstedt's study the relative abundance of the two species was about the same as in Essex (except in two of the six winters when the Swedish A.flavicollis captures greatly exceeded the A.sylvaticus catch). Also Bergstedt detected migration of A.sylvaticus to and from the crop fields. Mermod's study was only of twelve months duration but did indicate that the woodland A.flavicollis remained fairly high while the A.sylvaticus catch decreased during the summer months. In this respect (but not in the high relative frequency of A.flavicollis in the Swiss area) the results were similar to my Essex results.

Hoffmeyer (1973) has published the results of some interesting experiments concerning habitat selection by captive Apodemus. The choice of habitat was between open (woodland) type and 'grassland' with reasonable ground cover. A.sylvaticus preferred the ground cover while A.flavicollis was equally active in both habitats. These results agree well with my conclusions drawn from the distribution of captures of free-living Apodemus in King Wood.

Other studies of A.flavicollis ecology (as distinct from studies of distribution and taxonomy) are nearly all from areas with a single Apodemus species. Most such studies were made in Poland and other eastern European countries where it appears to be the norm for A.flavicollis to occupy mature woodland and A.sylvaticus to occupy the more open habitats. Girons (1966, 1967) has suggested that in France the two species are segregated vertically, A.flavicollis occurring mainly on higher ground than A.sylvaticus. This is the reverse of what happens in Britain, but it should be noted that A.flavicollis is comparatively a very recent discovery in France and its distribution is far from fully mapped.

It seems reasonable to suppose that the original situation was similar to that which pertains in eastern Europe today:- a separation of basically allopatric woodland and open habitat species. In the more intensively farmed parts of western Europe woodlands are small relics scattered among the open habitats. Thus what were originally allopatric species have been forced to be sympatric when the habitats became small in relation to the size of individual animals' movements. In this situation there are three possible results:-

a) Competitive exclusion of one species (which does not seem to have happened in this case).

b) Introgressive hybridization resulting in one species. (There is some evidence that this occurs in Germany and North Italy - see section 1 of this thesis.)

c) Changing ecology of one or both species resulting in a new type of competition reduction and the sympatric survival of both species as distinct entities. If this does happen (rather than introgression) then character displacement is likely to occur since selection would operate against any tendency to hybridize. It is noticeable that it is in those parts of Europe (Scandinavia and Britain) where the two species exist in the closest sympatric conditions that the morphological differences between the two species are greatest.

Table 1 Names and status of the species of dispecific and polyspecific British terrestrial mammal genera

GENUS	SPECIES	STATUS
Sorex	araneus Linn.	Native
	minutus Linn.	Native
Mustela	erminea Linn.	Native
	nivalis Linn.	Native
	putorius Linn.	Native
	vison Schreber	Feral since 1950s
Cervus	elaphus Linn.	Native
	nippon Temminck	Feral since late 19th century
Lepus	capensis Linn.	Native
	timidus Linn.	Native
Sciurus	vulgaris Linn.	Native
	carolinensis Gmelin	Feral since 1890s
Apodemus	sylvaticus (Linn.)	Native
	flavicollis (Melchior)	Unknown
Rattus	rattus (Linn.)	Feral since about 12th century
	norvegicus (Berkenhout)	Feral since about 1730

(Data from Corbet, 1964)

Table 2 The species of the genus *Apodemus*

mystacinus	Dunford and Alston 1877
speciosus	Temminck 1845
agrarius	Pallas 1771
flavicollis	Melchior 1834
sylvaticus	Linnaeus 1758
microps	Kratochvil and Rosicky 1952

Table 3 The important subspecies of *A.flavicollis* and *A.sylvaticus* from Europe and mainland Britain

(all other island forms have been excluded)

A.flavicollis	Range
flavicollis (Melchior, 1834)	Denmark and elsewhere on southern side of Baltic
wintoni (Barrett-Hamilton, 1900)	Britain and Scandinavia
princeps (Barrett-Hamilton, 1900)	South and East Europe
alpicola Heinrich, 1952	Alps
A.sylvaticus	
sylvaticus (Linnaeus, 1758)	Most of Europe including Britain
dichrurus (Rafinesque, 1814)	The Mediterranean region of Europe
callipedes (Cabrera, 1907)	The pyrenees
clanceyi Harrison, 1947	Basses-Alpes

Table 4 The main habitats of the four most widely distributed British rodents

Habitat Type	A.sylvaticus	M.musculus	C.glareolus	M.agrestis
permanent grassland	r	–	–	+
heather or ling	+	–	–	+
gorse	+	–	r	+
reedbeds	+	r	–	+
scrub or hedge	+	r	+	r
deciduous wood	+	–	+	–
mixed wood	+	–	+	–
coniferous wood	+	–	+	–
crop fields	+	r	r	r
urban gardens	+	+	r	r
uninhabited buildings	+	+	–	–
human habitations	r	+	–	–

Sources:-
1. studies listed in table 5
2. Southern, 1964
3. the Essex survey (section 4 of this thesis)
4. the complete run of 'Notes from the Mammal Society, 1956 to 1971

Key
+ normally present
r rarely present
- no more than the occasional wanderer present

Table 5 The locations and durations of the major studies of *A.sylvaticus* ecology on mainland Britain and Ireland

Study area	Student	Duration	Aspects studied	Publications
Wytham or Bagley woods Berkshire	Elton	Sep 1925/Apr 28	Parasites	et al, 1931
	Baker	Sep 1925/Apr 28	Breeding cycles	1930
	Evans	Oct 1936/Feb 39	Population ecology	1942
	Southern	1949 - 1966	Owl/prey relationship	& Lowe 1968; 1970
	Miller	Jan 1950/Mar 51	Food, activity, population	1954; 1955; 1958
	Kikkawa	Sep 1955/Feb 57	Movement, activity	1964
	Newson	Apr 1958/Oct 59	Populations	quoted in Watts 1968
	Smyth	Dec 1960/Dec 62	Populations	1966; 1968
	Watts	Nov 1963/Oct 65	Food, dispersal, populations	1968; 1969; 1970
	Flowerdew	1967 - 1970	Populations	1972
County Durham	Ashby	1954 - 1966	Populations and woodland regeneration	1967
	Crawley	Mar 1963/Jan 65	Populations	1970
	Cleminson	1964 - 1966	Populations and burrows	Thesis, private report 1966

Table 5 continued

Study area	Student	Duration	Aspects studied	Publications
Monkswood	Tanton	Apr 1962/Nov 64	Populations	1965; 1969
Huntingdon	Pollard & Relton	Dec 1967/Jan 70	Use of fields and hedges	1970
Silwood Park	Brown	Sep 1949/Sep 51	Activity, range, population	1954; 1956; 1956
Studland Dorset	Hacker & Pearson	1937 - 1939	Growth, movements, habitats	1944; 1946; 1951; 1952
Poorstock	Brown	1961 - 1966	Movements, social behaviour	1966; 1969
Co. Down	Fairley	Feb 1963/Mar 64	Populations, habitats	1967
Co. Galway	Fairley & Comerton	Oct 1970/May 71	Population, breeding	1972
Exeter	Huband	?	Use of arable fields	private report 1965

Table 6 Population fluctuations in *A.sylvaticus*

Explanation of table

Source of data: from published results of the authors listed in 'Study' column. Details of studies are listed in table 5

Criteria for selection of studies are given in section 2.5 of the text

Year column gives the year in which the twelve monthly samples began (not the year of results publication).

The upper figure in each pair is the percentage of the annual catch caught in the month in question.

The lower figure in each pair is the actual number of mice caught. Interpolated results are in parentheses.

If more than one trapping session was held in the month the two results are averaged (hence the occasional fractions of mice caught).

Table 6 continued

Study	Year	Jan	Feb	Mar	Apr	May	Jun	Jly	Aug	Sep	Oct	Nov	Dec
Crawley (A)	1963			6.5 21	2.8 9	1.6 5	0.9 3	2.8 9	2.5 8	3.2 10	8.7 28	10.9 35	16.2 52
		21.5 69	22.7 (73)										
Crawley (A)	1964		15.5 (73)	16.4 77	10.0 47	4.9 23	3.2 (15)	1.5 7	1.5 7	5.1 24	10.9 51	13.6 64	10.4 (49)
		7.2 34											
Crawley (B)	1964	12.5 (22)	10.8 19	13.1 23	11.4 (20)	9.7 17	2.8 5	3.7 (6.5)	4.6 8	5.7 10	8.5 (15)	11.4 20	5.7 10
Fairley	1963				10.1 57	8.0 45	6.5 37	3.5 20	6.0 34	8.3 47	9.7 56	12.0 68	12.2 69
		9.4 53	8.5 48	5.8 33									
Kikkawa	1956	5.0 58	3.3 (38)	1.6 18	3.0 35	2.3 (26)	1.6 18	10.1 117	5.6 65	18.4 212	17.9 207	16.4 188	14.7 170
Miller	1950	9.1 28	7.8 (24)	6.5 20	5.9 18	6.2 19	7.2 22	0.7 2	7.2 22	15.6 48	15.6 48	15.6 48	2.6 8
Newson (b)	1958				0.5 1	0.5 1	0.5 1	1.0 2	8.1 4	5.2 10	5.7 11	16.8 13	10.9 21
		17.2 33	26.0 50	23.4 45									
Newson (B)												4.3 13	7.0 21
	1959	10.9 33	16.6 50	14.9 45	13.6 41	9.3 28	4.6 14	5.3 16	3.3 10	5.6 17	4.6 14		

Table 6 continued

Study	Year	Jan	Feb	Mar	Apr	May	Jun	Jly	Aug	Sep	Oct	Nov	Dec
Newson (Y)	1958				0.5 1	0.5 1	0.5 1	1.0 2	5.1 10	7.1 14	1.5 3	11.7 23	9.1 18
		20.3 40	21.3 42	21.3 42									
Newson (Y)												5.8 23	4.5 18
	1959	10.0 40	10.6 42	10.6 42	14.1 56	10.3 41	8.5 34	7.5 (30)	6.8 27	4.0 16	7.3 29		
Smyth													10.2 39
	1961	12.3 47	10.5 40	9.9 38	9.2 35	7.3 28	4.7 18	5.5 21	2.9 11	6.8 26	9.2 35	11.5 44	
Smyth	1962	9.0 13	4.2 6	9.0 13	2.8 4	4.2 6	3.5 5	2.1 3	2.1 3	11.1 16	11.1 16	17.4 (25)	23.6 34
Tanton	1962				2.6 8	2.2 6.7	2.5 7.5	1.3 4	0.3 1	2.6 8	17.0 52	14.7 45	27.5 84
		10.3 31.5	9.8 (30)	9.2 28									
Tanton													13.8 61
	1964	10.6 47	3.8 17	4.7 (21)	5.6 25	6.8 30	4.5 (20)	2.3 10	1.6 7	13.2 58.5	15.9 (68)	17.6 78	
Average of all 14 percentages		11.8	11.8	10.9	6.6	5.3	3.7	3.5	3.7	8.0	10.2	12.1	12.0

Table 7 Size of population fluctuations in *A.sylvaticus*

The studies given in table 6 are listed in order of increasing size of fluctuations as measured by the variance and standard deviations of the 12 monthly percentages

Study	Variance	Standard deviation
Fairley	6.57	2.6
Smyth 1961	8.38	2.9
Newson (Y) 1959	8.53	2.9
AVERAGE	12.31	3.5
Crawley (B) 1964	13.55	3.7
Newson (B) 1959	21.21	4.6
Miller	24.54	5.0
Crawley (A) 1964	27.31	5.2
Tanton 1964	31.85	5.6
Smyth 1962	45.33	6.7
Kikkawa	45.58	6.8
Crawley (A) 1963	61.28	7.8
Tanton 1962	67.31	8.2
Newson (Y) 1958	71.66	8.5
Newson (B) 1958	83.72	9.2

Table 8 Population estimates and densities of *A.sylvaticus*

Notes:

Source of information: those studies listed in table 5 which satisfy criteria (see section 2.5 and 2.6)

Year: the year given is the year of the summer population estimate. The winter estimate is from the given year November to February of the following year.

Min. area is the area in hectares enclosed by the traps area + boundary is minimum area plus a 23m boundary strip or the size of the study wood if this is smaller.

Av. winter catch is average catch from November to February

Av. summer catch from June to August.

Av. summer and winter populations are authors best population estimates (method of Leslie et al. in most cases).

Densities are in mice per hectare derived from population estimate and area + boundary strip.

Final column is winter denstity estimate obtained from total catch and minimum area.

The second part of this table gives average winter and summer densities taken from the figures in Watts (1969) and converted to mice per hectare. N.B. winter estimates used a 23m boundary strip but the summer estimates used slightly larger and variable sized strips.

Table 8 continued

Author	Study year (march/feb.)	min. area (ha)	area + boundary (ha)	av. winter catch	av. winter population	av. summer catch	av. summer population	winter density	summer density	winter catch / min. area
Crawley (A)	1963	0.9	2.05	52	75	6.7	7.0	37.3	3.3	57.8
	1964	0.9	2.05	42.5	49.5	7.0	7.0	24.6	3.5	47.2
(B)	1963	0.9	2.05	22	22	2.7	2.7	10.9	1.3	24.7
	1964	0.9	2.05	15	15	6.5	6.5	7.5	3.2	16.6
Tanton	1962	5.2	7.6	47.4	132.1	4.2	4.2	17.4	0.6	9.1
	1963	5.2	7.6	59.8	76.1	34.7	48.6	10.0	6.4	11.5
Kikkawa	1956	2.1	2.2	145.5	156.3	66.7	113.3	71.0	51.5	83.1
Miller	1950	2.1	2.2	32.0	47.0	15.3	17.7	21.4	8.0	15.0
Fairley	1963	2.6	3.9	59.5	89.3	30.3	40.7	22.9	10.4	23.2
Fairley & Comerton	1969	3.2	3.6	41.6	74.7	-	-	20.6	-	13.0
Brown	1949	2.7	3.0	36.5	38.0	-	-	12.7	-	13.5
	1950	2.7	3.0	92.0	108.5	-	-	36.0	-	34.0
	1951	2.7	3.0	32.5	50.0	-	-	16.7	-	12.0

Table 8 continued

Watts' density estimates

Year	Summer density	Winter density
1961/2	5.2	10.1
1962	0.7	-
1964/5	0.4	20.0
1965/6	9.9	24.7
1958/9 (Area B)	1.5	30.3
1958/9 (Area Y)	1.0	19.8

Table 9 Estimates of *A.sylvaticus* home ranges from published sources

Range length (metres)

Author	Males			Females		
	av.	min.	max.	av.	min.	max.
Brown (Silwood)	53	27	110	47	27	110
Miller	61	10	170	35	4.5	80

Range area (hectares)

Author	Males			Females		
	av.	min.	max.	av.	min.	max.
Brown (Silwood)	0.21	0.07	1.2	0.1	0.06	0.8
Miller	0.29	0.008	2.3	0.1	0.002	0.25
Kikkawa	0.18	0.03	0.43	0.11	0.026	0.27
Brown (Poorstock)						
Trapping		0.008	0.44			
Tracking		0.048	1.4	0.08		

Table 10 The plant associations on the King Wood study area

Notes: No attempt was made at a complete botanical survey; this table simply lists the main components of the three major habitat types. See figure 12 for the distribution of these habitat types.

Habitat Type	1. Coppice	2.Bramble	3. Bracken
Tree layer	Oak (*Quercus robur* L.)	Oak	Larch (*Larix decidua* Mill.)
	Sweet Chestnut (*Castanea sativa* Mill.)	Sweet Chestnut	Silver Fir (*Abies* sp.)
	Larch (few)		
	Silver Fir		
Shrub layer	Sweet Chestnut coppice	Bramble (*Rubus fructicosus* agg.)	*Rhododendron ponticum* L.
	Birch (*Betula pubescens* Ehrh)	Sweet Chestnut	
	Hornbeam coppice (*Carpinus betulus* L.)	Rhododendron	
	Honeysuckle (*Lonicera periclymenum* L.)		
Field layer	Bramble (scattered)	Bramble (dense)	Bracken (*Pteridium aquilinum* (L.))
		Nettle (*Urtica dioica* L.)	Bramble (little)
		Male Fern (*Dryopteris felix-mas* agg.)	

Table 11 Crop sequence in the fields adjacent to the King Wood study area

See figure 9 for the positions of the fields.

Year	1967	1968	1969	1970
Field A (east)	Sugar beet	Wheat	Sugar beet	Barley
Field B (west)	Wheat	Barley	Sugar beet	Barley
Field B	Oats	Mustard	Beans	Wheat
Field C	Wheat	Wheat	Beans	Wheat

Table 12 Results of the exploratory trapping sessions on the Coptfold Estate

Key The species are listed by the initial letter of their scientific names:

As	*A.sylvaticus*	Af	*A.flavicollis*	Cg	*C.glareolus*
Sa	*S.araneus*	Sm	*S.minutus*	Nf	*N.fodiens*
Mm	*M.musculus*	Ma	*M.agrestis*	Mn	*M.nivalis*

i) Trappings on the King Wood study area before the standard grid was established.

Date	Trap-nights	As	Af	Cg	Sa	Others
30.10.66	60	2	2	1		
3.11.66	60	5		3	6	
5.11.66	60	18	2		8	
22.11.66	75	12	2	2	1	
13.12.66	50	16	3	9	2	Mn 1
1.1.67	50	24	1	4		Sm 1
Total	405	96	12	21	17	

ii) Trappings in King Wood in which the traps were set in trees, 1 - 10m above ground.

Date	Trap-nights	As	Af	Cg	Sa	Others
10.4.67	25					
15.5.67	20			1		(1m above ground)
4.6.67	12					
15.10.67	10					
19.5.68	12					
Total	79			1		

Table 12 continued

iii) Exploratory trappings in a wide variety of habitats.

See figure 11 for map of trapping locations.

Date	Trap-nights	Loc.	Habitat	As	Af	Cg	Sa	Others
14.12.67	24	1	Field	4				
14.3.67	24	1		4				
13.7.67	10	1				1		
4.8.68	10	1						
9.8.67	10	2	Field	1				
13.7.67	10	2					1	Mm 1
16.8.67	10	2		1				
10.8.67	10	2		1				
13.7.67	20	3	Field edge		1	1		Ma 1
9.8.67	20	3				1		Ma 1
10.8.67	20	3						
16.8.67	20-	3		2		2		
9.8.67	10	4	Field edge				2	
22.6.68	10	4		1				
23.6.68	10	4						
4.8.68	10	4			1			
26.2.67	10	5	Field edge					
13.7.67	10	5			2			
10.8.67	10	5					1	
21.10.67	10	5		4			1	
4.8.68	10	5						
4.8.68	10	6	Field			1		
4.8.68	10	7	Field	1				

Table 12 continued

Date	Trap-nights	Loc.	Habitat	As	Af	Cg	Sa	Others
22.6.68	10	8	Field edge					Mm 1
23.6.68	10	8			3			Mm 2
30.6.68	10	8		1	2			
4.8.68	10	8						
18.7.67	10	9	Hedge	1		1		
10.8.67	10	9		1				
16.8.67	10	9				2	1	
9.8.67	10	9				1		
21.10.67	10	9		4				
4.5.68	20	9						
30.6.68	10	9		1				
4.8.68	10	9						
14.2.67	17	10	Wood	2				
26.2.67	10	10						
14.3.67	17	10						
19.4.67	17	10		2				
21.5.67	10	10				1		
18.7.67	10	10						
21.10.67	10	10		3				
4.5.68	10	10		2			1	
23.5.68	10	10		1				
26.8.70	40	10		3	4			
18.7.67	10	11	Field					
9.8.67	10	11		1				
10.8.67	10	11						
16.8.67	10	11						
30.6.68	20	11		1				
4.8.68	20	11		1				

Table 12 continued

Date	Trap-nights	Loc.	Habitat	As	Af	Cg	Sa	Others
3.5.67	20	12	Field	1				
18.7.67	20	12		1	2			
9.8.67	10	12						
10.8.67	10	12		3				
16.8.67	10	12		1				
21.10.67	10	12		2				
22.6.68	10	12		1				
23.6.68	10	12		1				
30.6.68	10	12				1		
4.8.68	10	12				1		
26.2.67	10	13	Hedge	1				
21.6.67	20	13		1				Ma 1
21.10.67	10	13		1				
4.5.67	10	14	Wood	1	1	1		
10.5.67	10	14		1				
23.5.67	10	14				3		
21.10.67	10	14		3	1	1		
26.2.68	10	14		4				
5.5.68	20	14		1				
4.5.67	10	15	Hedge					
23.5.67	10	15		2				
21.6.67	20	16	Hedge	1	1			
15.7.67	40	16		2				
21.10.67	10	16		2				
5.5.68	20	16		1				
4.5.67	10	17	Hedge		1			
23.5.67	10	17					1	

Table 12 continued

Date	Trap-nights	Loc.	Habitat	As	Af	Cg	Sa	Others
4.5.67	10	18	Wood	2	1			
10.5.67	10	18		2				
23.5.67	10	18		1				
15.10.67	10	18		1	1			
24.4.68	40	18		2				
19.5.68	40	18		1	2			
4.5.67	10	19	Hedge					
23.5.67	10	19						Ma 1
15.10.67	10	19		2				
4.5.67	10	20	Wood	3				
23.5.67	10	20		2				
14.2.67	16	21	Wood	1		1		
14.3.67	16	21		4		4		
19.4.67	16	21		2				
14.2.67	23	22	Wood	1				
26.2.67	10	22		3		2		
14.3.67	23	22		1				
4.5.67	10	22		3		2		
23.5.67	10	22		1		1	1	
21.6.67	10	22				2	2	
15.10.67	10	22		2		2		
21.10.67	10	22		3		2		
27.8.68	40	22		2	2			
14.2.67	17	23	Wood	3				
14.3.67	17	23		2				
Total Field				25	2	3	1	
Total Field edge/Hedge				28	11	9	6	
Total Wood				65	12	22	4	
Overall Group iii total				118	25	34	11	

Table 13 Results of the main grid trapping sessions on the Coptfold estate

Notes:

The date is the day when the traps were examined, having been set on the previous day. Each session consists of 200 trap-nights on one grid half (W-1 and W-2 being the King Wood grid and F-1 and F-2 being the field grid).

Mice classified as '*Apod*' escaped before being specifically identified.

The column headed x2 gives the number of trap-points at which both traps were occupied. An asterisk (*) indicates those sessions when only one trap per point was used.

See key to table 12 for the species codes.

Date	Grid	As	Af	Apod	Cg	Sa	Sm	Others	x2
5.1.67	W-2	19	4	1	5	2	1	Mu 1	6
6.1.67	W-1	19	4		16	2	1		11
29.1.67	W-2	15	3		13				6
1.2.67	W-1	15	2	1	15	1			8
9.2.67	W-2	12	5		9				6
12.2.67	W-1	12	4		16				8
19.2.67	W-2	14	3	1	8				4
21.2.67	W-1	16	2		14				5
5.3.67	W-2	8	1	1	4				3
7.3.67	W-1	11	1		7				3
24.3.67	W-2	8			2				1
27.3.67	W-1	11			3				1
8.4.67	W-2	10	1	1	3				
9.4.67	W-1	12	1						1

Table 13 continued

Date	Grid	As	Af	Apod	Cg	Sa	Sm	Others	x2
26.4.67	W-2	4	2		3				
30.4.67	W-1	8	1	1	2				1
7.5.67	W-2	4	2	1	2				1
11.5.67	W-1	11	1	1	7		1		3
29.5.67	W-2	9	4	1	9		1		5
1.6.67	W-1	3	2	2	17	3			3
9.6.67	W-2	4	1		7				1
13.6.67	W-1	2	1	2	19				2
29.6.67	W-2	2	1		11				2
30.6.67	W-1	5			17	2			3
27.7.67	W-2	1		1	1				
28.7.67	W-1	3			2	1			1
2.8.67	W-1	6			3	2			
3.8.67	W-2	4	1	1	13	2			4
8.10.67	W-1	30	5	5	5				9
12.10.67	W-2	31	9	6	4			Nf 1	13
5.11.67	W-2	32	8	4	14	2			15
12.11.67	W-1	19	7	6	16			Ma 1	14
26.11.67	W-2	20	4	14					7
31.11.67	W-1	30	8	8	10				15
20.12.67	W-2	11	4	3	3				3
29.12.67	W-1	20		5	14				7
21.1.68	W-2	11	3	1	8				1
22.1.68	W-1	17	8	1	14				10
4.2.68	W-2	10		1	8				1
12.2.68	W-1	7		1	14				4
3.3.68	W-2	6	1	1	3				2
7.3.68	W-1	8			6				

Table 13 continued

Date	Grid	As	Af	Apod	Cg	Sa	Sm	Others	x2
17.3.68	W-2	7	3		4				3
8.4.68	W-1	5			2				1
9.4.68	W-2	3			1			Mn 1	1
26.4.68	W-1	3	1						
4.5.68	W-2	3	2						1
5.5.68	W-1	4	1	1					1
19.5.68	W-2	1							
25.5.68	W-1	1							
9.6.68	W-2	1	2						
15.6.68	W-1		3		2				
22.6.68	W-2	2	2		3				
23.6.68	W-1		2	1	5				1
6.7.68	W-2				1				
7.7.68	W-1				4				
29.7.68	W-2	1				2			
30.7.68	W-1		2			2			
15.8.68	W-2	1	7	1	2	3			1
22.8.68	W-1	3	8	2	2	2			2
5.9.68	W-2	9	13	2	1	1			3
6.9.68	W-1	9	17	3	2	2			6
10.10.68	W-2	15	7	1	1	1			5
13.10.68	W-1	19	8	1		4		Ma 1	6
11.11.68	W-2	10	5						1
23.11.68	W-1	18	2						2
17.12.68	W-2	14	5	2	1				4
18.12.68	W-1	25	7			1		Mn 1	3
19.1.69	W-2	16	8		2				5
26.1.69	W-1	17	5		2				3

Table 13 continued

Date	Grid	As	Af	Apod	Cg	Sa	Sm	Others	x2
16.2.69	W-2	9	4		1				2
22.2.69	W-1	12	7		4				3
2.3.69	F-1	3							
9.3.69	F-2	3							
2.4.69	W-2	5			3				2
3.4.69	W-1	9			8				4
24.4.69	F-1	3							
31.4.69	F-2								
11.5.69	W-2	6	2		1				1
17.5.69	W-1	6			2	1			1
25.5.69	F-1	5	1						
28.5.69	F-2	3	1						
15.6.69	W-2	2	2	1	1				1
16.6.69	W-1	5		1	2				
17.6.69	F-1	4							
18.6.69	F-2	4	3						
16.7.69	W-2	1		1	11	2			2
17.7.69	W-1				13	2			2
17.7.69	F-1	3		1					
18.7.69	F-2	3	1						
15.8.69	F-1	9		2				Mn 1	
16.8.69	F-2	5	1			1			
17.8.69	W-1	1	1		15	3			3
18.8.69	W-2	2	1		6			Mn 1	
15.9.69	F-1	5		1		1			1
16.9.69	F-2								
16.9.69	W-2	9	3		2	2		Mn 1	1
17.9.69	W-1	2	2			6		Nf 1	1

Table 13 continued

Date	Grid	As	Af	Apod	Cg	Sa	Sm	Others	x2
15.10.69	W-2	6	1						
16.10.69	W-1	11	1		1	5			1
16.11.69	F-1								*
17.11.69	F-2								*
16.11.69	W-2	12	1			2			2
17.11.69	W-1	16	4	1	1				5
22.12.69	F-1	4							*
22.12.69	F-2	2							*
22.12.69	W-2	26	1			1			4
23.12.69	W-1	23	3		1	1			5
10.3.70	W-2	9	3		5				3
10.3.70	W-1	5	2						1
30.5.70	F-1	4	2	1					
30.5.70	F-2	7		1					
8.7.70	W-2	2	1						
8.7.70	W-1		1		5				
12.7.70	F-1	11	4	1	1				
12.7.70	F-2	7	2	1					
6.8.70	W-2	13	7	2	5	1			3
7.8.70	W-1	8	7	1	12	1			4
9.8.70	F-2	9			3	1			1
9.8.70	F-1	3							
26.8.70	W-2	13	16		6		1		7
30.8.70	W-1	15	14	5	10				11
12.10.70	F-1	5							1
12.10.70	F-2								
31.1.71	W-2	15	4		4				
31.1.71	W-1	11	3		6	1			

Table 14 Estimated populations of rodents on the two study grids

Notes:

The Catch figure is the total catch during the trapping session of 200 trap-nights. It includes recaptures of the same individual and mice which escaped before being individually identified. These two categories are excluded from the Individual figure.

See section 3.6 for the explanation of Known population and Estimated population.

Marking of *C.glareolus* began in February 1967 and continued to the end of July 1969 only.

When an estimate cannot be calculated the column is left blank. The final figures for Estimated population (Jan. 71) are inaccurate because subsequent captures are needed for an accurate estimate to be obtained. The figures for Estimated population are given to the nearest whole number.

Table 14 continued

1967 Woodland Results

Months	Janua		Febru		March		April		May		June		Jul	Aug	Oct	Novemb		Dec
Session	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
A.sylvaticus																		
Catch	39	31	24	31	20	19	23	13	17	15	8	7	5	11	74	60	62	39
Individuals	27	24	18	21	15	15	16	7	9	7	5	5	3	8	55	43	43	24
Known alive	27	28	25	26	22	19	18	10	11	9	8	11	10	11	58	54	53	35
Estimated pop.		29	25	26	22	19	18	10	11	9	8	14	28	12	93	72	57	36
A.flavicollis																		
Catch	8	6	9	5	2	0	2	3	3	6	2	1	0	1	14	15	12	1
Individuals	6	5	6	3	2	0	2	3	3	5	1	1	0	1	11	12	8	0
Known alive	6	7	10	8	7	6	7	7	6	7	2	1	0	1	11	15	8	1
Estimated pop.		8	11	9	7	6	9	7	6	8	2	1	0			39	8	1
C.glareolus																		
Catch	21	29	25	22	11	5	3	5	9	26	26	28	3	16	9	30	24	18
Individuals			13	16	10	5	2	4	6	21	17	19	3	14	6	23	18	14
Known alive			13	19	17	15	14	14	16	23	21	20	7	19	12	24	21	18
Estimated pop.				21	19	17	14	14	20	24	22	20	8	35	25	24	24	21

Table 14 continued

1968 Woodland Results

Months	Jan	Feb	Mar	M/A	Apr	May		June		July		Aug	Sep	Oct	Nov	Dec
Session	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
A.sylvaticus																
Catch	30	19	15	12	6	7	2	1	3	0	1	7	23	36	28	41
Individuals	23	13	11	9	4	4	1	1	1	0	1	4	14	29	27	35
Known alive	29	18	13	10	7	7	4	3	3	3	4	7	16	30	34	43
Estimated pop.	30	18	13	10	7	7	4	3	3	3	6	10	18	30	40	49
A.flavicollis																
Catch	11	0	1	3	1	3	0	5	4	0	2	15	30	15	7	12
Individuals	8	0	1	2	1	3	0	3	4	0	2	11	21	14	7	11
Known alive	9	1	1	2	3	5	2	4	5	3	4	14	21	21	15	17
Estimated pop.	9	1	1	2	4	6	2	4	5	3	5	24	20	45	22	20
C.glareolus																
Catch	22	22	9	6	1	1	0	2	8	5	0	4	4	1	0	1
Individuals	14	13	7	3	1	1	0	1	6	4	0	2	4	1	0	1
Known alive	19	16	10	8	5	5	5	5	8	6	3	4	5	2	1	2
Estimated pop.	27	18	11	8	5	5	5	5	9	6	3	5	5	2	1	2

Table 14 continued 1969/71 Woodland Results

Months	Jan	Feb	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mar	Jul	August		Jan
Session	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
A.sylvaticus																
Catch	33	21	14	12	9	2	3	11	17	29	50	14	2	24	33	26
Individuals	30	17	9	8	4	1	3	10	14	24	38	9	1	16	25	25
Known alive	35	21	11	8	4	2	4	11	17	29	41	10	4	19	26	25
Estimated pop.	36	21	11	8	4	2	4	11	25	34	43	10	4	26	26	(20)
A.flavicollis																
Catch	13	11	0	2	2	0	2	5	2	5	4	5	2	14	30	7
Individuals	12	10	0	2	2	0	1	5	2	5	3	5	2	12	26	7
Known alive	17	10	0	2	2	0	1	5	2	5	3	5	4	12	28	7
Estimated pop.	19	10	0					3				3	6	10	32	(4)
C.glareolus																
Catch	4	5	11	3	3	24	21	3	1	1	1	5	5	18	16	10
Individuals	3	5	7	3	3	15	15	3	1	1	1					
Known alive	5	8	9	6	7	20	18	4	2	1	1					
Estimated pop.	8	12	9	8	8	29	21	4	2	1	1	—	—			

Table 14 continued

1969/70 Field Results

Months	Mar	Apr	May	Jun	Jly	Aug	Sep	Nov	Dec	May	Jly	Aug	Oct
Session	1	2	3	4	5	6	7	8	9	10	11	12	13
A.sylvaticus													
Catch	6	3	8	8	7	16	6	0	6	13	20	12	5
Individuals	6	3	6	6	6	12	5	0	6	9	18	11	5
Known alive	6	5	7	10	7	13	5	0	6	9	18	11	5
Estimated Pop.		6	7	18	7	13	5	0		5	14	10	
A.flav. Catch	0	0	2	3	1	1	0	0	0	2	6	0	0
Individuals	0	0	2	3	1	1	0	0	0	2	5	0	0
Known alive	0	0	2	3	1	1	0	0	0	2	5	0	0
Estimated pop.	not possible to calculate												
C.glareolus													
Catch	0	0	0	0	0	0	0	0	0	0	1	3	0

This species was not marked - no other estimates possible

Table 15 Population densities of *Apodemus* on the King Wood study area

Densities are given in mice per hectare and were obtained by averaging the Leslie and Chitty Estimates for the period in question and assuming that the area sampled was the area of the grid plus a 23m boundary strip.

Period Species	Year	Winter (Nov. - Feb.)	Summer (June - Aug.)
A.sylvaticus	1967	8.24	4.70
	1968	13.00	1.68
	1969	11.11	0.99
	1970	11.79	5.66
A.flavicollis	1967	2.60	0.31
	1968	3.52	2.48
	1969	5.34	0.31
	1970	1.22	4.90
Total *Apodemus*	1967	10.84	5.01
	1968	16.52	4.16
	1969	16.45	1.30
	1970	13.01	10.56

Corrected Winter densities for *Apodemus*, expressed in '*A.sylvaticus* equivalents'

1967	1968	1969	1970
12.04	18.14	18.91	13.92

Average winter density:

A.sylvaticus	11.04
A.flavicollis	3.16
Apodemus	14.20
'corrected' *Apodemus*	15.75
A.sylvaticus populations listed in table 8	20.17

Table 16 Disappearance rates of mice caught on the King Wood study area

Months after first capture	0	1	2	3	4	5	6	7	8	9	10	11	12	13
Female A.sylvaticus														
Number known alive	137	59	42	27	20	15	11	9	8	6	4	2	1	1
percentage	100	43	31	20	15	11	8	7	6	4	3	1	1	1
% of 'month 1' mice		100	71	47	34	25	19	15	13	10	7	3	2	2
Male A.sylvaticus														
Number known alive	206	90	61	43	29	16	13	9	5	3	2			
percentage	100	44	30	21	14	8	6	4	2	1	1			
% of 'month 1' mice		100	68	48	32	18	13	10	6	3	2			
Female A.flavicollis														
Number known alive	80	19	14	10	10	7	2	1	1					
percentage	100	24	18	13	13	9	3	1	1					
% of 'month 1' mice		100	68	52	52	36	10	5	5					
Male A.flavicollis														
Number known alive	88	22	19	14	7	2								
percentage	100	25	22	16	8	2								
% of 'month 1' mice		100	87	64	32	9								
All C.glareolus														
Number known alive	159	65	45	33	24	9	7	5	2	2				
percentage	100	41	28	21	16	6	5	4	1	1				
% of 'month 1' voles		100	68	50	36	13	11	8	3	3				

Table 17 Average weights of non-juvenile mice from both study grids

Note: Standard deviations are only given if sample size is greater than four.

Male A.sylvaticus

1967	Jan	Feb	Mar	Apr	May	Jun	Jly	Aug	Sep	Oct	Nov	Dec
Av. weight (g)	17.4	21.3	25.4	27.0	27.7		14.5	27.5		19.4	19.2	19.4
sample weighed	18	13	14	13	8	0	2	2	0	24	24	13
std deviation	2.7	3.1	2.7	1.6	2.5					4.0	2.8	1.4
1968												
Av. weight	17.6	20.7	21.2	23.5	24.4			19.0	18.0	17.7	18.7	
sample weighed	7	3	4	2	5	0	0	1	2	18	12	0
std deviation	1.5				1.5					3.3	3.0	
1969												
Av. weight	19.6	18.6	21.5	21.9	24.7	17.7	21.0	22.4	18.6	14.5	17.8	15.6
sample weighed	12	10	4	8	9	4	3	5	9	4	6	11
std deviation	2.2	2.6		2.7	2.6			1.5	3.5		3.2	2.9

Table 17 continued

Female A.sylvaticus

1967	Jan	Feb	Mar	Apr	May	Jun	Jly	Aug	Sep	Oct	Nov	Dec
Av. weight	13.8	16.5	17.8	19.5	20.0	24.7		25.0		19.0	16.7	16.4
sample weighed	21	18	13	12	5	4		1		12	18	5
std deviation	3.6	1.2	2.1	2.2	2.4					4.3	3.6	1.1
1968												
Av. weight	15.7	18.2	17.0	18.0		26.0		25.5	23.0	17.5	17.1	
sample weighed	8	4	3	1		1		2	3	11	7	
std deviation	2.3									4.6	3.0	
1969												
Av. weight	18.4	17.7	16.5	19.0	21.2	25.2	28.0	30.5	24.2	15.0	18.0	16.5
sample weighed	11	6	2	4	5	4	1	6	4	2	12	12
std deviation	3.2	2.1			1.5			5.8			4.6	3.3

Table 17 continued Male A.flavicollis

1967	Jan	Feb	Mar	Apr	May	Jun	Jly	Aug	Sep	Oct	Nov	Dec
Av. weight	23.0	29.0	25.0			40.0		20.0		36.0	26.1	
sample weighed	1	6	1			1		1		1	7	
std deviation		3.9									4.6	
1968												
Av. weight	25.7		30.0			32.0		25.0	22.5	27.4	29.3	
sample weighed	3		1			2		2	2	10	6	
std deviation										5.4	6.3	
1969												
Av. weight	34.5	32.6			41.0	24.0	29.0	16.0	25.3	20.0	24.2	28.0
sample weighed	4	5			1	1	1	1	3	1	4	1
std deviation		4.7										

Table 17 continued

Female *A.flavicollis*

1967	Jan	Feb	Mar	Apr	May	Jun	Jly	Aug	Sep	Oct	Nov	Dec
Av. weight	23.7	23.2	27.0	26.0	30.0	30.0				24.0	21.3	
sample weighed	3	4	1	3	3	1				2	7	
std deviation											5.5	
1968												
Av. weight	25.8		28.0	24.0	30.0	35.0		30.0	25.0	26.0	21.0	
sample weighed	5		1	1	1	2		4	1	3	1	
std deviation	3.6											
1969												
Av. weight	27.8	29.7			34.0	33.5			31.5		22.0	
sample weighed	5	3			1	2			2		1	
std deviation	3.7											

Table 18 Breeding condition of non-juvenile mice from both study grids

Note: figures are given thus: number classed as in breeding condition / number not so classed.

Male A.sylvaticus	Jan	Feb	Mar	Apr	May	Jun	Jly	Aug	Sep	Oct	Nov	Dec
1967	3/23	10/10	15/0	15/0	13/0	1/0	1/1	3/0		8/28	0/60	0/16
1968	0/13	1/8	3/6	6/0	8/0		0/1	2/0	12/0	7/12	3/16	1/22
1969	1/20	4/9	2/2	12/0	14/0	6/0	3/0	5/0	7/2	5/6	0/9	1/26
1970 (Jan 1971)	(0/16)		4/0		3/0		7/0	15/7				
Male A.flavicollis												
1967	0/7	3/4	0/1	1/1	3/0	2/0		1/0		0/4	0/13	
1968	0/5		1/0			5/0	2/0	4/0	7/11	4/8	0/6	0/5
1969	0/6	1/4			1/0	1/0	1/0	1/0	2/1	0/2	0/4	0/2
1970 (Jan 1971)	(0/3)		3/0		1/0		1/0	13/3				

Table 18 continued

Female A.sylvaticus	Jan	Feb	Mar	Apr	May	Jun	Jly	Aug	Sep	Oct	Nov	Dec
1967	0/28	0/25	3/17	16/3	8/0	8/0		2/0		8/12	7/19	0/8
1968	2/9	0/5	0/6	0/3	0/1	2 30		2/0	2/1	5/8	1/7	0/14
1969	0/11	0/7	0/2	0/4	2/4	8/0	1/0	5/1	4/0	3/1	3/11	0/20
1970 (Jan 1971)	(0/9)		3/2		3/0		9/1	10/8		0/4		
Female A.flavicollis												
1967	0/6	0/5	0/1	0/3	3/1	1/0				4/0	1/10	
1968	1/4		0/2	1/0	2/1	0/2		4/1	5/1	2/1	0/1	1/6
1969	0/7	0/4			1/1	2/0			1/1		0/1	0/1
1970 (Jan 1971)	(1/3)		0/2				3/0	12/4				

Table 19 A.sylvaticus / A.flavicollis weight ratios

	Jan	Feb	Mar	Apr	May	Jun	Jly	Aug	Sep	Oct	Nov	Dec
Female A.sylvaticus												
Av. weight	15.5	17.1	17.6	19.3	20.6	25.1	28.0	28.8	23.7	18.0	17.2	16.5
sample size	40	28	18	17	10	9	1	9	7	25	37	17
Female A.flavicollis												
Av. weight	26.1	26.0	27.5	25.5	30.8	33.4		30.0	29.3	25.7	21.2	
sample size	13	7	2	4	5	5		4	3	5	8	
syl./flav. wt ratio	1.69	1.52	1.57	1.32	1.50	1.33		1.04	1.24	1.42	1.23	
Male A.sylvaticus												
Av. weight	18.1	20.2	23.4	24.9	25.7	17.7	18.4	23.2	18.4	18.3	19.0	17.7
sample size	37	26	22	23	22	4	5	8	11	46	58	24
Male A.flavicollis												
Av. weight	29.8	30.6	27.5		41.0	32.0	29.0	21.5	24.2	27.5	26.8	28.0
sample size	8	11	2		1	6	1	4	5	12	17	1
syl. /flav. wt ratio	1.64	1.52	1.16		1.59	1.50	1.58	0.92	1.31	1.50	1.41	1.59

Table 20 Captures of juvenile *Apodemus* on the two study areas

	Woodland *A.sylvaticus*					Woodland *A.flavicollis*					Field *A.sylvat.*			Field *A.flavic.*		
Month	1967	1968	1969	1970	Total	1967	1968	1969	1970	Total	1969	1970	Total	1969	1970	Total
Jan	1				1											
Feb																
Mar																
Apr																
May						1		1		2		3	3			
Jun	3				3		1	1		2				1		1
Jul	2		1		3						2	2	4		3	3
Aug	3		2	11	16		5		10	15	3	4	7	1		1
Sep		1	1		2		1			1	1		1			
Oct	4			1	5	3			3							
Nov	5		3		8		1		1							
Dec											1		1			
Totals	18	1	7	12	38	4	8	2	10	24	7	9	16	2	3	5

Table 21 Average distance moved and the calculated boundary strip sizes for the King Wood study area

	Av. dist. moved	Number of movements	Range		Boundary strip (short - term)				Boundary strip (life movements)			
			from	to	A	F	Z	B	A'	F'	Z'	B'
A.flavicollis												
males	42.7	27	15.0	120.9	30	26	27	46.5	3	6	18	184.1
females	47.4	9	15.0	109.2	31	24	9	20.2	8	5	13	92.1
A.sylvaticus												
males	41.6	92	15.0	108.2	155	94	92	37.0	35	24	45	70.9
females	37.7	43	15.0	105.0	74	107	43	26.1	20	21	23	53.3
C.glareolus												
both sexes	48.0	49	15.0	109.2	99	63	49	31.5	29	14	27	59.4

Note: See section 3.9 for a description of the methods of calculation and an explanation of the symbols used in this table. All real numbers are distances in metres, all integer values are numbers of observations.

Table 22 The distribution of rodent captures between the three main habitats on the King Wodd study area

Note: The 'expected' number of captures is calculated from the total captures on the hypothesis of no habitat selection being shown. The chi-squared value is for the comparison between the observed and expected results, there being two degrees of freedom. The grid of 100 squares consisted of 52 Open Coppice; 29 Bramble ground cover and 19 Bracken ground cover. The expected values are rounded down to the nearest whole number but values accurate to six figures were used in the original calculations.

Species / Sex	From	To	Coppice		Bramble		Bracken		Chi-sq	Probability (%)
			Obs	Exp	Obs	Exp	Obs	Exp		
All A.sylvaticus	Jan 67	Jan 71	376	489	363	272	202	178	59.0	<0.1
All A.flavicollis	Jan 67	Jan 71	167	157	82	87	54	57	1.17	$95 > P > 10$
All C.glareolus	Jan 67	Jan 71	125	274	265	152	137	100	177.0	<0.1
Male A.sylvaticus	Jan 67	Jan 71	178	266	226	148	108	97	70.9	<0.1
Female A.sylvaticus	Jan 67	Jan 71	157	178	105	99	81	65	6.71	4 apprx.
Male A.flavicollis	Jan 67	Jan 71	79	79	48	44	26	29	0.62	97.5 apprx.
Female A.flavicollis	Jan 67	Jan 71	75	66	27	36	25	24	3.87	$95 > P > 10$

Table 22 continued

Species / Sex	From	To	Coppice Obs	Coppice Exp	Bramble Obs	Bramble Exp	Bracken Obs	Bracken Exp	Chi-sq	Probability (%)
All *A.sylvaticus*	Jan 67	Mar 67	72	83	54	46	34	30	3.17	$95 > P > 10$
	Apr 67	Oct 67	57	77	64	43	28	28	15.4	<0.1
	Nov 67	Mar 68	109	105	61	58	32	38	1.30	$95 > P > 10$
	Apr 68	Oct 68	19	39	41	21	15	14	27.3	<0.1
	Nov 68	Mar 69	35	62	52	35	34	22	25.8	<0.1
	Apr 69	Oct 69	17	33	33	18	15	12	19.5	<0.1
	Nov 69	Mar 70	34	47	37	26	21	17	8.70	1.5 approx.
	Apr 70	Jan 71	33	40	21	22	23	14	6.10	5 approx.
All *A.flavicollis*	Jan 67	Mar 67	16	15	9	8	5	5	0.10	95
	Apr 67	Oct 67	21	16	6	9	5	6	2.49	$95 > P > 10$
	Nov 67	Mar 68	25	22	9	12	9	8	1.36	ditto
	Apr 68	Oct 68	42	39	22	21	11	14	0.97	ditto
	Nov 68	Mar 69	19	22	17	12	7	8	2.31	ditto
	Apr 69	Oct 69	8	6	2	3	3	2	1.17	ditto
	Nov 69	Mar 70	5	7	6	4	3	2	1.68	ditto
	Apr 70	Jan 71	31	27	11	15	11	10	1.75	ditto

Table 22 continued

Species / Sex	From	To	Coppice Obs	Coppice Exp	Bramble Obs	Bramble Exp	Bracken Obs	Bracken Exp	Chi-sq	Probability
All *C.glareolus*	Jan 67	Mar 67	19	58	65	32	29	21	61.2	<0.1
	Apr 67	Oct 67	32	65	59	36	34	23	35.5	ditto
	Nov 67	Mar 68	29	68	65	37	37	24	47.6	ditto
	Apr 68	Oct 68	4	13	14	7	8	4	14.1	ditto
	Nov 68	Mar 69	4	5	3	2	3	1	0.91	95> P >10
	Apr 69	Oct 69	15	34	32	19	19	12	22.8	<0.1
	Nov 69	Mar 70	5	3	2	2	0	1	1.83	95> P >10
	Apr 70	Jan 71	17	25	25	14	7	9	11.6	<0.5

Table 22 continued

Species / Sex	From	To	Coppice		Bramble		Bracken		Chi-sq	Probability
			Obs	Exp	Obs	Exp	Obs	Exp		
Male A.sylvaticus	Jan 67	Mar 67	28	32	25	17	9	11	3.95	95> P> 10
	Apr 67	Oct 67	30	42	39	23	12	15	14.5	<0.1
	Nov 67	Mar 68	54	59	45	33	16	21	6.19	5> P> 2.5
	Apr 68	Oct 68	7	23	33	13	6	8	41.8	<0.1
	Nov 68	Mar 69	19	40	33	22	25	14	23.5	ditto
	Apr 69	Nov 69	10	20	18	11	12	7	11.7	<0.5
	Nov 69	Mar 70	12	22	18	12	14	8	11.1	ditto
	Apr 70	Jan 71	18	24	15	13	14	8	4.71	10> P> 5
Female A.sylvaticus	Jan 67	Mar 67	30	37	20	20	22	13	6.57	5> P> 2.5
	Apr 67	Oct 67	24	30	22	16	12	11	2.94	95> P> 10
	Nov 67	Mar 68	39	32	9	17	14	11	6.32	5> P> 2.5
	Apr 68	Oct 68	11	11	5	6	7	4	2.07	95> P> 10
	Nov 68	Mar 69	15	20	16	11	9	7	3.54	ditto
	Apr 69	Oct 69	7	10	11	6	3	3	5.61	10> P> 5
	Nov 69	Mar 70	17	20	17	11	6	7	3.54	95> P> 10
	Apr 70	Jan 71	14	14	5	7	8	5	2.62	ditto

Table 22 continued

Species / Sex	From	To	Coppice Obs	Coppice Exp	Bramble Obs	Bramble Exp	Bracken Obs	Bracken Exp	Chi-sq	Probability
Male *A.flavicollis*	Jan 67	Mar 67	9	7	5	4	1	2	1.48	<5
	Apr 67	Oct 67	11	6	1	3	1	2	5.56	ditto
	Nov 67	Mar 68	7	9	7	5	5	3	1.77	ditto
	Apr 68	Oct 68	22	22	16	12	6	8	1.52	ditto
	Nov 68	Mar 69	10	11	8	6	4	4	0.60	ditto
	Apr 69	Oct 69	3	3	1	2	3	1	2.73	ditto
	Nov 69	Mar 70	3	4	5	2	1	1	3.08	ditto
	Apr 70	Jan 71	14	12	5	6	5	4	0.77	ditto
Female *A.flavicollis*	Jan 67	Mar 67	5	6	4	3	3	2	0.55	ditto
	Apr 67	Oct 67	7	7	5	4	3	2	0.18	ditto
	Nov 67	Mar 68	14	9	1	5	3	3	5.76	5 approx.
	Apr 68	Oct 68	16	12	3	6	5	4	3.28	<5
	Nov 68	Mar 69	9	10	8	5	3	3	1.19	ditto
	Apr 69	Oct 69	5	2	0	1	0	0	4.61	ditto
	Nov 69	Mar 70	2	2	1	1	2	0	1.43	ditto
	Apr 70	Jan 71	17	14	5	8	6	5	1.69	ditto

Table 23 Sex ratios of *Apodemus* captured in various habitats

Species	Habitat	Males	Femls	M/F
A.sylvaticus individuals	Whole wood	206	137	1.50
A.sylvaticus total capts.	Whole wood	485	327	1.48
A.flavicollis individuals	Whole wood	88	80	1.11
A.flavicollis total capts.	Whole wood	143	131	1.09
A.sylvaticus captures	Open coppice	178	157	1.13
A.sylvaticus captures	Bramble	226	105	2.15
A.sylvaticus captures	Bracken	81	65	1.25
A.flavicollis captures	Open coppice	79	75	1.05
A.flavicollis captures	Bramble	48	27	1.78
A.flavicollis captures	Bracken	26	29	0.90
A.sylvaticus individuals	Field	35	34	1.03
A.sylvaticus captures	Field	49	48	1.02
A.flavicollis individuals	Field	6	8	0.75
A.flavicollis captures	Field	6	9	0.67

Table 24 Numbers of rodents caught on each square of the King Wood grid between 1967 and 1971.

Note. The top decile of squares for each group are outlined in heavy lines. To facilitate comparisons the envelope at the end of the thesis contains transparent overlays of this table and the habitat types from figure 12.

All Rodents

	1	2	3	4	5	6	7	8	9	10
A	26	24	11	28	9	10	25	12	9	14
B	3	31	20	18	15	18	22	8	22	21
C	15	25	20	22	11	28	16	22	7	16
D	25	**35**	21	**35**	10	6	12	6	4	15
E	20	29	**43**	**57**	**32**	16	12	27	21	18
F	18	25	**50**	**40**	**32**	10	13	9	2	23
G	24	17	28	**35**	9	16	12	12	4	14
H	25	**32**	21	10	15	19	16	13	11	16
I	24	17	10	10	22	10	9	9	9	10
J	12	12	9	10	4	9	14	9	8	10

Table 24 continued

A.sylvaticus

	1	2	3	4	5	6	7	8	9	10
A	11	10	9	19	5	7	14	8	3	10
B	1	17	15	6	6	9	12	1	8	11
C	5	8	8	8	7	13	7	11	5	14
D	16	16	4	18	6	2	2	5	2	15
E	14	17	21	34	17	7	3	8	9	14
F	9	15	20	24	17	6	5	4	2	10
G	7	9	19	24	6	12	3	8	4	7
H	8	10	12	8	13	12	9	10	5	9
I	10	9	9	6	18	7	5	4	6	5
J	10	7	5	6	2	5	9	4	5	4

A.flavicollis

	1	2	3	4	5	6	7	8	9	10
A	2	2	1	2	2	0	2	0	4	3
B	1	1	0	4	5	5	1	4	4	5
C	2	1	4	4	0	2	1	7	2	1
D	2	6	6	3	3	2	5	0	1	0
E	1	4	6	4	3	7	4	10	10	1
F	4	5	12	3	8	1	0	3	0	10
G	1	0	2	3	1	1	5	2	0	5
H	2	1	2	2	1	4	5	2	4	4
I	1	4	0	2	4	2	4	4	3	3
J	2	5	3	4	2	4	2	3	3	6

Table 24 continued

A.sylvaticus
males

	1	2	3	4	5	6	7	8	9	10
A	4	5	6	12	3	5	8	6	1	1
B	0	11	13	4	2	5	7	1	2	7
C	3	2	6	8	5	10	5	4	3	5
D	9	12	2	10	4	2	0	1	1	9
E	9	8	14	20	14	6	1	3	5	6
F	5	7	15	14	10	1	5	3	1	3
G	6	3	10	10	3	8	2	5	3	3
H	6	7	9	6	5	7	4	4	1	3
I	7	3	3	3	4	3	3	1	4	2
J	3	3	0	1	0	0	5	2	3	3

A.sylvaticus
females

	1	2	3	4	5	6	7	8	9	10
A	4	5	1	7	1	2	3	1	2	8
B	1	4	1	0	3	3	4	0	5	4
C	2	6	2	0	2	3	1	7	2	8
D	5	3	1	7	1	0	2	3	0	4
E	5	7	6	11	2	1	2	3	3	5
F	3	8	3	7	2	5	0	1	1	5
G	1	5	9	12	2	4	0	2	0	4
H	1	2	3	2	8	4	4	5	4	6
I	3	5	5	2	11	4	2	3	1	2
J	6	4	5	4	0	3	3	2	1	1

Table 24 continued

<u>A.flavicollis</u>
males

	1	2	3	4	5	6	7	8	9	10
A	0	2	0	0	0	0	2	0	2	1
B	1	1	0	2	5	0	1	1	3	4
C	0	0	2	4	0	0	0	4	0	1
D	0	3	5	2	1	2	3	0	0	0
E	1	3	3	3	3	2	2	5	5	0
F	2	4	6	1	6	1	0	2	0	5
G	0	0	0	2	0	1	4	0	0	2
H	1	0	0	2	0	1	3	1	2	2
J	1	5	0	2	1	1	0	1	3	3

<u>A.flavicollis</u>
females

	1	2	3	4	5	6	7	8	9	10
A	1	0	1	2	2	0	0	0	1	2
B	0	0	0	2	0	4	0	2	1	1
C	2	1	2	0	0	1	0	1	2	0
D	2	2	1	1	2	0	1	0	1	0
E	0	0	2	0	0	5	1	5	5	1
F	2	1	5	2	1	0	0	1	0	5
G	1	0	2	1	1	0	1	2	0	2
H	1	1	2	0	1	3	2	1	1	1
I	1	3	0	2	2	2	2	3	1	0
J	1	0	2	1	0	3	2	2	0	3

Table 24 continued

Apodemus

	1	2	3	4	5	6	7	8	9	10
A	13	12	10	21	7	7	10	8	7	13
B	2	18	15	10	11	14	13	5	12	16
C	7	9	12	12	7	15	8	18	7	15
D	18	22	10	21	9	4	7	5	3	15
E	15	20	27	38	20	14	7	18	19	15
F	13	20	32	27	25	7	5	7	2	20
G	8	9	21	27	7	13	8	10	4	12
H	10	11	14	10	14	16	14	12	9	13
I	11	13	9	8	22	9	9	8	9	8
J	12	12	8	10	4	9	11	7	8	10

Clethrionomys

	1	2	3	4	5	6	7	8	9	10
A	13	12	1	7	2	3	9	4	2	1
B	1	13	5	8	4	4	9	3	10	5
C	8	16	8	10	4	13	8	4	0	1
D	7	13	11	14	1	2	5	1	1	0
E	5	9	16	19	12	2	5	9	2	3
F	5	5	18	13	7	4	8	2	0	2
G	16	8	7	8	2	3	4	2	0	3
H	15	21	7	0	1	3	2	1	2	3
I	13	4	1	2	0	1	0	1	0	2
J	0	0	1	0	0	0	3	2	0	0

Table 24 continued

	1	2	3	4	5	6	7	8	9	10
A	R	R	0	R	0	0	0	0	0	0
B	R	R	R	R	0	0	R	0	0	0
C	R	R	R	R	R	R	R	0	0	R
D	R	R	R	R	R	R	0	0	0	0
E	P	P	R	R	R	0	0	0	0	0
F	P	P	P	R	R	0	0	0	0	0
G	P	P	P	R	R	0	0	0	0	0
H	P	P	P	0	0	0	0	0	0	0
I	P	P	P	P	0	0	0	0	0	0
J	P	P	P	P	0	0	0	0	0	0

Grid habitats

Key:-

P = *Pteridium* (Bracken)

R = *Rubus* (Bramble)

0 = Open Coppice

see fig. 12

Table 25 An analysis of the factors related to the degree of habitat selection shown by *A.sylvaticus*

Notes:

H_s is an index of habitat selection obtained by expressing the captures of *A.sylvaticus* in the open coppice habitat as a fraction of the total captures. If there is no selection against the open habitat the value of H_s is 0.52. The populations of *A.sylvaticus* (A.s), *A.flavicollis* (A.f) and *C.glareolus* (C.g) are the average population estimates for the period. They are classified 'high' or 'low' depending on whether they are above or below the average for the species.

Period	H_s value	A.s.pop.	A.f. pop.	C.g.pop.
Jan 67 - Mar 67	0.48 (none)	24.8 (high)	7.8 (low)	21.9 (high)
Apr 67 - Oct 67	0.38 (weak)	22.5 (low)	3.8 (low)	20.1 (high)
Nov 67 - Mar 68	0.54 (none)	37.6 (high)	9.7 (high)	22.7 (high)
Apr 68 - Oct 68	0.25 (strong)	9.1 (low)	11.7 (high)	5.2 (low)
Nov 68 - Mar 69	0.29 (strong)	36.3 (high)	17.5 (high)	5.7 (low)
Apr 69 - Oct 69	0.26 (strong)	9.3 (low)	1.7 (low)	11.5 (low)
Nov 69 - Mar 70	0.37 (weak)	29.0 (high)	4.3 (low)	2.3 (low)
Apr 70 - Oct 70	0.43 (weak)	18.5 (low)	16.0 (high)	13.0 (high)

A multiple regression analysis was carried out using the figures in the above table and also including the period of the year (scored +1 for winter, -1 for summer).

The results given over leaf indicate that a high proportion of the observed variation in H_s can be accounted for by variation in the rodent populations. Variation in the *C.glareolus* and *A.sylvaticus* populations being the two most important.

Table 25 continued

Variances of:

A.s. pop.	A.f. pop.	C.g. pop.	Summer/Winter score
118.5	33.3	64.8	1.14

Variance of H_s	0.01105
Variance accounted for by above four factors	0.00826
Residual variance	0.00279

Regression coefficients for:

A.s. value	A.f. value	C.g. value	Summer/Winter value
0.00159	0.00156	0.00928	0.02683
Variances of above:			
0.0001	0.0001	0.00005	0.02683

The high value for C.g. with its low variance indicates that this is important. The values for A.s and A.f. are similar and of lesser importance. The summer/winter value is unimportant.

Table 26 The distribution of captures on the field study grid with respect to the proximity of woodland

Notes:

The total captures in row 1 (10 grid squares) near the woodland; row 2 (10 squares) 15m further into the field and rows 3 - 10 (80 squares) are compared with the expected value assuming a random distribution.

The expected capture values are rounded down to the nearest whole number in the table but accurate values were used in the original calculations.

Species	Row 1		Row 2		Rows 3/10		chi-sq	P
	Obs	Exp	Obs	Exp	Obs	Exp		
A.flavicollis	7	1	2	1	6	12	23.33	0.1%
A.sylvaticus	18	10	7	10	77	81	7.22	3%

The figures are for both sexes, all captures between 1969 and 1970 inclusive.

Table 27 Disappearance rates of mice caught on the Field C study area

Months after first capture	0	1	2	3	4	5	6	7	8	9
Female A.sylvaticus										
Number known alive	34	7	5	3	2	2	2	1		
Percentage	100	21	15	9	6	6	6	3		
Male A.sylvaticus										
Number known alive	35	8	5	2						
Percentage	100	23	14	6						
Female A.flavicollis										
Number known alive	8	-	-							
Percentage	100	-	-							
Male A.flavicollis										
Number known alive	6	-	-							
Percentage	100	-	-							

Table 28 Recorded movements between the two study grids by *A.sylvaticus*

Ref No.	Sex	Position before move	Position after move	Number capts before move	Number capts after move	Dates of captures either side of movement Last Before	First After	Time-lag Wood-Field	Time-lag Field-Wood
357	M	Wood A5	Field N3	1	1	6.9.68	25.5.69	8.6 months	Average 1.5 months
412	M	Wood I1	Field N2	1	1	11.11.68	2.3.69	3.8 months	
423	M	Wood E1	Field N5	6	2	3.4.69	24.4.69	0.8 months	
428	F	Wood J7	Field K9	1	3	17.12.68	17.6.69	6.0 months	
431	F	Wood B2	Field M6	7	2	16.6.69	17.6.69	0.0 months	
450	F	Wood B7	Field Q10	1	1	26.1.69	16.8.69	6.8 months	
482	M	Wood E4	Field O5	1	2	16.6.69	17.6.69	0.0 months	
608	M	Field R10	Wood D1	1	1	16.8.69	17.9.69		1.0 months
723	F	Wood D1	Field R6	1	2	10.3.70	3.5.70	2.5 months	
723	F	Field Q7	Wood H5	2	1	12.7.70	6.8.70		0.8 months
723	F	Wood H5	Field Q6	1	1	6.8.70	9.8.70	0.1 months	
727	M	Wood E4	Field L10	1	1	10.3.70	12.7.70	4.0 months	
765	M	Field M2	Wood F1	1	2	12.7.70	6.8.70	Average 3.3 months	0.8 months
801	M	Field M2	Wood H2	1	1	9.8.70	26.8.70		0.5 months
802	M	Field L3	Wood D5	1	1	9.8.70	30.8.70		0.5 months
880	F	Field N5	Wood I3	1	1	12.10.70	31.1.71		3.5 months
883	F	Field M1	Wood G3	1	1	12.10.70	31.1.71		3.5 months

Table 29 Fluctuations in *Apodemus* catches on the King Wood study area

Note: These figures are derived in the same way as those in tables 6 and 7 with which they should be compared.

	Jan	Feb	Mar	Apr	May	Jun	Jly	Aug	Sep	Oct	Nov	Dec	Variance
A.sylvaticus													
1967 catch	25½	19½	15	11½	8	5	3	8	(31½)	55	43	24	
percentages	10.2	7.8	6.0	4.6	3.2	2.0	1.2	3.2	12.6	22.1	17.3	9.6	41.42
1968 catch	23	13	10	4	2½	1	½	4	14	29	27	35	
percentages	14.1	8.0	6.1	2.5	1.5	0.6	0.3	2.5	8.6	17.8	16.6	21.5	55.22
1969 catch	30	17	(13)	9	8	4	1	3	10	14	24	38	
percentages	17.5	9.9	7.6	5.3	4.7	2.3	0.6	1.8	5.8	8.2	14.0	22.2	43.77
Average %	14.0	8.6	6.6	4.1	3.1	1.7	0.7	2.4	9.0	16.0	16.0	17.8	38.47
A.flavicollis													
1967 catch	5½	4½	1	2½	4	1	0	1	(6)	11	10	0	
percentages	11.8	9.7	2.1	5.4	8.6	2.1	0.0	2.1	12.9	23.7	21.5	0.0	64.18
1968 catch	8	0	1½	1	1½	3½	1	11	21	14	7	11	
percentages	9.9	0.0	1.9	1.2	1.9	4.3	1.2	13.7	26.1	17.4	8.7	13.7	66.03
1969 catch	12	10	(5)	0	2	2	0	1	5	2	5	3	
percentages	25.5	21.3	10.6	0.0	4.3	4.3	0.0	2.1	10.6	4.3	10.6	6.4	64.60
Average %	15.8	10.3	4.9	1.8	4.9	3.2	0.4	6.0	16.5	15.1	13.6	6.7	31.93

<u>Table 30</u> Summary of the three major (2,000+ trap-night) surveys

The following habitats were trapped:

King Wood (TL6603), 9,900 trap-nights Jan 1967 - Jan 1971.
A mixed wood, mainly deciduous with coppice and some bracken and bramble undergrowth.

Coptfold Field (TL6603), 2,500 trap-nights March 1969 - Oct 1970.
An arable field adjacent to King Wood

Rumsey's Nursery (TQ3797), 2,352 trap-nights July-Sept 1970.
An area of waste ground colonised by tall grasses, nettles and *Epilobium hirsutum*.

	King Wood		Coptfold Field		Rumsey's Nursery	
Species	catch	%	catch	%	catch	%
S.araneus	63	3.4	2	1.7	33	7.4
S.minutus	5	0.3	0	0.0	6	1.3
N.fodiens	2	0.1	0	0.0	0	0.0
M.minutus	0	0.0	0	0.0	2	0.5
A.sylvaticus	941	51.0	100	82.7	153	34.3
A.flavicollis	303	16.4	15	12.4	0	0.0
M.musculus	2	0.1	0	0.0	22	5.0
C.glareolus	527	26.6	4	3.3	222	50.0
M.agrestis	1	0.1	0	0.0	7	1.6

Table 31 Summary of five 'bottle-hunt' small mammal collections from Essex

Note: Only in 1968 were the Apodemus remains identified to species. Of the 46 skulls, 2 were unidentifiable, 1 was *A.flavicollis* and the remaining 43 *A.sylvaticus*.

Date of collection	18.9.66		12.3.67		24.3.67		26.10.69		12.3.72	
Species	No.	%	No.	%	No.	%	No.	%	No.	%
S.araneus	102	56.7	133	46.8	160	50.2	81	61.8	50	42.7
S.minutus	5	2.8	6	2.1	20	6.3	6	4.6	1	0.9
N.fodiens	2	1.1	10	3.3	5	1.8	6	4.6	9	7.7
Apodemus spp	22	12.5	46	16.2	46	14.4	13	10.0	27	23.1
M.musculus	1	0.6	3	1.0	-	-	-	-	-	-
M.minutus	-	-	-	-	1	0.3	-	-	-	-
C.glareolus	43	23.9	77	27.1	82	25.7	23	17.6	29	24.8
M.agrestis	5	2.8	9	3.1	5	1.5	2	1.5	1	0.9

Table 32 Small mammal remains found in Owl pellets collected in Essex between 1959 and 1969

Type of Owl indicated thus: *Tyto alba* (Barn);
Strix aluco (Tawny); *Asio flammeus* (S.Ear); *Asio otus* (L.Ear)

Locality	Grid Ref	Owl	No. Pellets	S.araneus	S.minutus	N.fodiens	M.minutus	Apodemus spp	M.musculus	C.glareolus	M.agrestis
Flatford		Barn & Tawny	26+	28	23		4	11	2	16	110
Leigh Marsh	TQ8285	S.Ear	11					1			15
N.Fambridge	TQ8596	Barn	5	1	3			1		2	16
New England	TQ9889	S.Ear	2								3
Jerry Wood	TQ9990	Barn	36+	35	20		2	12			162
Fox's Farm	TR0192	Barn	91	71	15	1	2	17			186
Paglesham	TQ9593	L.Ear & Barn or S.Ear	16					5	1	2	16
Purdey's Farm	TQ8890	Barn	11+	4	2		3	7	1		9
Roper's Farm	TQ9290	Barn	2								6
Hullbridge	TQ8295	L.Ear	20+								26
Havengore Isl	TQ9889	S.Ear	6	3	1						9
Ardleigh		Barn	170	87	13	9	7	124	10	33	201

Table 33 A comparison of the results from four small mammal sampling methods

See Table:-	35		30		31		32	
Species	Survey trapping		Coptfold trapping		Bottle-hunts		Owl pellets	
	No.	%	No.	%	No.	%	No.	%
S.araneus	181	20.9	65	3.3	526	51.0	229	17.1
S.minutus	16	1.9	5	0.3	38	3.7	77	5.8
N.fodiens	3	0.4	2	0.1	32	3.1	10	0.8
M.minutus	16	1.8	0	0.0	1	0.1	18	1.0
Apodemus spp	436	50.4	1359	69.2	154	15.1	178	13.3
A.sylvaticus	423	48.7	1041	53.0				
A.flavicollis	13	1.5	318	16.2				
M.musculus	37	4.3	2	0.1	4	0.4	14	1.1
C.glareolus	128	14.4	531	27.0	254	24.6	53	4.0
M.agrestis	51	5.9	1	0.1	22	2.1	759	56.7

Table 34 Distribution and abundance of small mammals in Essex

A comparison of the percentage of localities sampled in which the species was found; and the total catch in those areas where the species was definitely present. In the live trapping 67 localities were sampled but from only 52 of these was sufficient information available to calculate the 'percentage catch', see table 35. The bottles were collected from 155 localities although from only 33 localities were the *Apodemus* remains identified to species.

	percentage of localities		percentage of catch in these localities	
Species	Traps	Bottles	Traps	Bottles
S.araneus	61.2	75.5	25.2	54.6
S.minutus	11.9	14.8	5.2	14.9
N.fodiens	4.5	12.3	1.5	11.1
M.minutus	9.0	0.7	9.0	6.0
Apodemus spp	89.6	46.5	49.9	22.3
A.sylvaticus	88.1	60.6	51.2	18.2
A.flavicollis	23.9	3.0	12.4	7.7
M.musculus	13.4	1.9	9.6	9.8
C.glareolus	74.6	61.9	17.7	30.0
M.agrestis	34.4	11.0	9.0	12.5

Table 35 Results of the extensive trapping survey in Essex, 1960 - 72

Notes:

1. The trappings are listed in chronological order of the first trapping at a particular locality.
2. The traps were set in the afternoon or evening and collected the following day. No period of prebaiting was used.
3. Each trap-site was consigned to one of the following habitat types:

   A. Urban gardens, allotments or other areas within a 'grey' area on an Ordnance ($\frac{1}{4}$") map.

   B. Woodland in which the nearest non-woodland habitat was more than 400m away.

   C. Any rural habitat within 400m of arable land.

   D. Any rural habitat other than B or C.

No more precise habitat details can be given as the traps were set in as wide a variety of habitats as occurred in the trapping area.

4. In those cases where the exact number of animals caught was not recorded the presence of a species is indicated thus: +.
5. The trappings included in this table are all those carried out by the author or those which were part of the Essex Field Club surveys and meetings. The intensive surveys detailed in tables 12 and 30 are not included.

Table 35 continued

Date	Locality	Habitat	Grid Ref	Trap-nights	S.araneus	S.minutus	N.fodiens	M.minutus	A.sylvaticus	A.flavicollis	M.musculus	C.glareolus	M.agrestis
18.4.60	Marsh House	C	TM2223	24	+				3			+	
20.3.60	Skippers Isl.	D	TM2124	24					3				+
18.2.61	Quintin Hill	C	TQ3999	24					11			+	+
26.2.61	Netherhouse	C	TQ3897	24	+				4			+	
19.3.61	Theydon Garn.	C	TQ4699	24					13			+	
8.4.61	Easton Lodge	C	TL5924	24					5	1		+	
4.6.67				100	4				8			8	
23.5.61	Hill Farm	C	TQ4798	15	+				4	4		+	
18.6.61	Piggots Farm	C	TQ4597	60	+				5	1		+	
Jun. 61	McEntee Sch.	A	TQ3691	?									+
7.8.61	Bower Farm	C	TQ5093	24					7	1		+	
29.10.61	Norsey Wood	D	TQ6895	6					1	3		+	
23.2.69				67					5			1	
April 63	Fingringhoe	D	TM0419	?					+			+	
6.9.64				63	6				12			6	2
29.9.64				74	9		1		10		2	8	7
Feb + June 65				80	2				15			12	2
20.9.70				50	5				3		1		
7.4.63	Alder Wood	C	TQ4796	30					2			1	
1963	Hawkswood	D	TQ3895	?	+				+			+	+
1964				185	4				9			4	3
11.4.64	Loughton	B	TQ4297						+			+	
1965	Broomfield	C	TL7010	?	+				+	+	+	+	
18.6.66	Woodford	A	TQ3991	24					4			1	1
16.10.66	Little Leighs	C	TL7117	?					+	+	+	+	+
2.2.67	The Mores	C	TQ5696	25	2				3			1	
2.2.67	Beachet Wood	C	TL4901	25	1				3	1		2	
8.2.67	Blakes Wood	C	TL7706	25					3			2	

Table 35 continued

Date	Locality	H	Grid Ref	TN	Sa	Sm	Nf	Mi	As	Af	Mu	Cg	Ma
26.2.67	Deer Park	C	TL4103	15					1			2	
1967	Galley Hill	C	TL3903	45	1				6	3		2	
28.2.67	Parsons Spring	C	TL6202	71					13	1		1	
23.4.67	Doneyland	D	TM0120	45	+				4			+	1
Aug.67	Lt.Claydons	C	TL7401	60					10	2		+	
21.4.68	Peveralls	C	TL5535	180	3				4			4	
14.9.68	Birch Hall	C	TQ4499	100	3				10	3		4	
21.9.68	Tillingham	D	TL9904	40	8				5			2	1
27.10.68	Romford Sewage	A	TQ5184	48					40				1
27.10.68	Damyns	D	TQ5583	40	1				7			1	
29.12.68	Epping Long G.	C	TL4305	20	1							5	
29.12.68	Latton Park	C	TL4707	40	1				4			3	2
23.2.69	Hankins Wood	C	TQ6899	54					14	2		3	
27.4.69	Mersea Island	D	TM0514	74	6				2			6	
27.4.69	Spratts Marsh	D	TL9829	67					5			1	
17.5.69	Poors Piece	C	TL7806	47					1			2	
27.7.69	Lit.Wakering	D	TQ9288	30	4							1	
27.7.69	Wakering 2	D	TQ9088	20	3								
28.6.69	Pond Rd	A	TQ4182	26					1				
28.6.69	N.Outfall	A	TQ4182	26	4								2
28.6.69	St.Mary	A	TQ4382	40	1								
28.6.69	Wanstead Park	A	TQ4188	46	1				2				
28.6.69	Suburban Gdn	A	TQ4498	20					1				
1.9.69	Great Wood	C	TQ4896	20		1				1		2	
2.9.69	Claybury	C	TQ4391	30		1			1				
Sept.69	Bennets Farm	D	TQ5693	100	6				2			1	
Sept. 69	Lea Gravel Pt	D	TQ3798	280	9	4		8	35				3
Jan. 70				44	2				2				
July 70				487	17				19		5		2
17.9.70				47	1			1	5			2	

Table 35 continued

Date	Locality	H	Grid Ref	TN	Sa	Sm	Nf	Mi	As	Af	Mu	Cg	Ma
8.8.71	Lea Gravel Pt	D	TQ3798	40	4			1	2				
26.8.71				75	3							3	1
11.9.69	Hainault	C	TQ4691	50							3		
Sept.69	Chingford	C	TQ3898	42		1			9		2		
July 70				350	9				3		8		2
14.9.69	Chingford	C	TQ3997	40	2				2			1	1
15.9.69	Collier Row	C	TQ4891	50	2	2			5		2		2
Sept.69	Hainault	C	TQ4891	60	2	2			1		4		1
25.1.70	Quendon	C	TL5230	119					7	1		1	
1.2.70	Thundersley	D	TQ7887	80					17			1	
5.4.70	Colchester	C	TL9622	18	1				3				
5.4.70	Colchester	C	TL9422	18					3			1	
24.5.70	Shadwell Wood	C	TL5741	124					3			1	
July 70	Sewardstone	D	TQ3797	134	3				10				2
24.9.70				25	2		1					1	
7.8.71				30	1	1							
8.8.71				40	6	1			5				
31.7.70	Hackney Marsh	D	TQ3587	60					2				
18.9.70				50	2				7				
25.10.70	Grays Chalk P	D	TQ6078	160	3				8			13	
16.5.71	Colne Point	D	TM0912	120					3				1
3.1.71	Westley Hts	C	TQ6785	84	3				19			2	
23.1.72	Sawbridgeworth	D	TL4915	110	+				+			+	+
12.9.71	Bowers Marsh	C	TQ7586	117	8	2		2	4		5	2	3
Oct. 71				270	12	1	1	2	11			5	6
5.3.72	Gt Holland	C	TM2019	119	3			1	28			4	1
12.3.72	Vicarage Wood	D	TQ5793	160					12	1		3	

Table 36 A comparison of the proportion of the small rodent species in the total rodent catch in the four types of survey

This table is based on the surveys summarised in table 33.

Species	Survey trapping		Coptfold trapping		Bottle-hunts		Owl pellets	
	No.	%	No.	%	No.	%	No.	%
Apodemus spp	436	63.5	1359	71.8	154	35.4	148	23.6
Mus	37	5.5	2	0.1	4	0.9	13	2.1
Clethrionomys	128	19.2	531	28.1	254	58.4	53	8.5
Microtus	51	7.6	1	0.1	22	5.0	399	63.6
Micromys	16	2.4	0	0.0	1	0.2	14	2.2

Table 37 Captures of *Apodemus* in relation to habitat in the Essex survey

Based on the results of the extensive Essex survey, see table 35 for details. The table gives the total captures for each habitat type.

Habitat type	'C' Arable	'D' Non-arable	Totals
Species			
A.sylvaticus	231	212	443
A.flavicollis	21	4	25
Totals	252	216	468

A '2 x 2 ' contingency test using Yates correction gives a chi-squared value of 10.59 which has an associated probability factor of less than 1%. It is therefore highly probable that the two species of mice show differences in their preferences for habitat types 'C' and 'D'.

Table 38 A comparison of the abundance of *A.flavicollis* in King Wood with the results from the extensive Essex survey

i) King Wood results

Month	Catch per night of 100 trap-nights *A.sylvaticus*	*A.flavicollis*	*A.flavicollis* / *Apodemus* ratio
Jan.	15.55	4.77	0.23
Feb.	11.88	3.00	0.20
Mar.	8.11	1.22	0.13
Apr.	6.55	0.66	0.19
May	5.00	1.33	0.21
Jun.	2.36	1.45	0.38
Jul.	0.80	0.40	0.33
Aug.	6.60	6.20	0.48
Sep.	7.25	8.75	0.55
Oct.	18.66	5.16	0.22
Nov.	19.50	4.87	0.20
Dec.	20.00	2.83	0.12

ii) Extensive survey results

See section 4.7 of text for explanation of estimates.

Area	Month	Trap -nights	A.syl. catch	A.flav. catch	Estimates a	b	c	d	e
Marsh House	Apr	24	3	0	0.85	0.75	1.57	0.16	0.28
Quintin Hill	Feb	24	11	0	0.48	0.08	2.85	0.72	2.21
Netherhouse	Feb	24	4	0	0.48	0.41	2.85	0.72	0.80
Theydon Garn.	Mar	24	13	0	0.74	0.16	1.95	0.29	1.70
Easton Lodge	Apr	24	5	1	0.85	0.56	1.57	0.16	0.55
Easton Lodge	Jun	100	8	0	0.23	0.02	2.36	1.45	3.05
Hill Farm	May	15	4	4	0.82	0.15	0.75	0.20	1.69
Piggots Farm	Jun	60	5	1	0.42	0.06	1.42	0.87	2.29
Bower Farm	Aug	24	7	1	0.22	0.01	1.58	1.49	3.87

Table 38 continued

Area	Month	Trap -nights	A.syl. catch	A.flav. catch	Estimates a	b	c	d	e
Norsey Wood	Oct	6	1	3	0.73	0.38	1.12	0.31	0.87
Norsey Wood	Feb	67	5	0	0.13	0.32	7.96	2.01	1.01
Alder Wood	Apr	30	2	0	0.82	0.82	1.97	0.20	0.18
The Mores	Feb	25	3	0	0.47	0.51	2.97	0.75	0.60
Beachet Wood	Feb	25	3	1	0.47	0.41	2.97	0.75	0.80
Blakes Wood	Feb	25	3	0	0.47	0.51	2.97	0.75	0.60
Deer Park Wood	Feb	15	1	0	0.63	0.80	1.78	0.45	0.20
Parsons Spring	Feb	71	13	1	0.12	0.04	8.44	2.13	2.81
Lt. Claydons	Aug	60	10	2	0.02	0.00	3.96	3.72	5.81
Peveralls Wood	Apr	180	4	0	0.30	0.68	11.80	1.20	0.37
Birch Hall	Sep	100	10	3	0.00	0.00	7.25	8.75	7.11
Damyns Wood	Oct	40	7	0	0.12	0.18	7.47	2.07	2.17
Latton Park	Dec	40	4	0	0.32	0.59	8.00	1.13	0.50
Hankins Wood	Feb	54	14	2	0.19	0.03	6.42	1.62	3.22
Poors Piece	May	47	1	0	0.53	0.79	2.35	0.62	0.21
Great Wood	Sep	20	0	1	0.16	0.45	1.45	1.75	0.48
Claybury	Sep	30	1	0	0.06	0.45	2.17	2.62	0.48
Bennets Farm	Sep	100	2	0	0.00	0.21	7.25	8.75	0.97
Hainault	Sep	50	0	0	0.01	0.00	3.65	4.37	0.00
Hainault	Sep	60	1	0	0.00	0.45	4.35	5.25	0.48
Quendon	Jan	119	7	1	0.00	0.12	18.51	5.68	1.88
Thundersley	Feb	80	17	0	0.09	0.02	9.51	2.40	3.42
Shadwell Wood	May	124	3	0	0.19	0.49	6.20	1.65	0.63
Gt Holland Pit	Mar	119	28	0	0.23	0.02	9.65	1.45	3.67
Vicarage Wood	Mar	160	12	1	0.14	0.16	12.98	1.96	1.70

Table 38 continued

Total number of areas		34
Number with *A.sylvaticus*		32
Number with *A.flavicollis*		13
Number which should have contained *A.flavicollis* if Null Hypothesis were true	(estimate a)	22.7
	(estimate b)	23.7
Total catch of *A.sylvaticus*		212
Expected catch of *A.sylvaticus*	(estimate c)	170
Total catch of *A.flavicollis*		22
Expected catch of *A.flavicollis*	(estimate d)	68
	(estimate e)	56

Table 39 A summary of the national survey of *Apodemus* captures

Habitat type:	woods with arable nearby	other woods	non-wood, non-garden	garden
Number of localities				
A.sylvaticus	17	27	29	18
A.flavicollis	6	12	1	9
Catch of *A.sylvaticus*	1760	328	858	340
Catch of *A.flavicollis*	131	39	1	32
Occurrence of *A.flavicollis* expressed as a percentage of *A.sylvaticus*:-				
1. Based on number of habitats	35%	39%	3%	31%
2. Based on total catch	7.4%	12%	0%	9%
3. Based on catch in areas where *A.flav*. was caught	12%	31%	-	49%
4. As (3) but excluding May/June results	6½	12%	-	49%

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* indicates a reference which I have not examined in the original but only in abstract.

Figure 1

see notes page 218

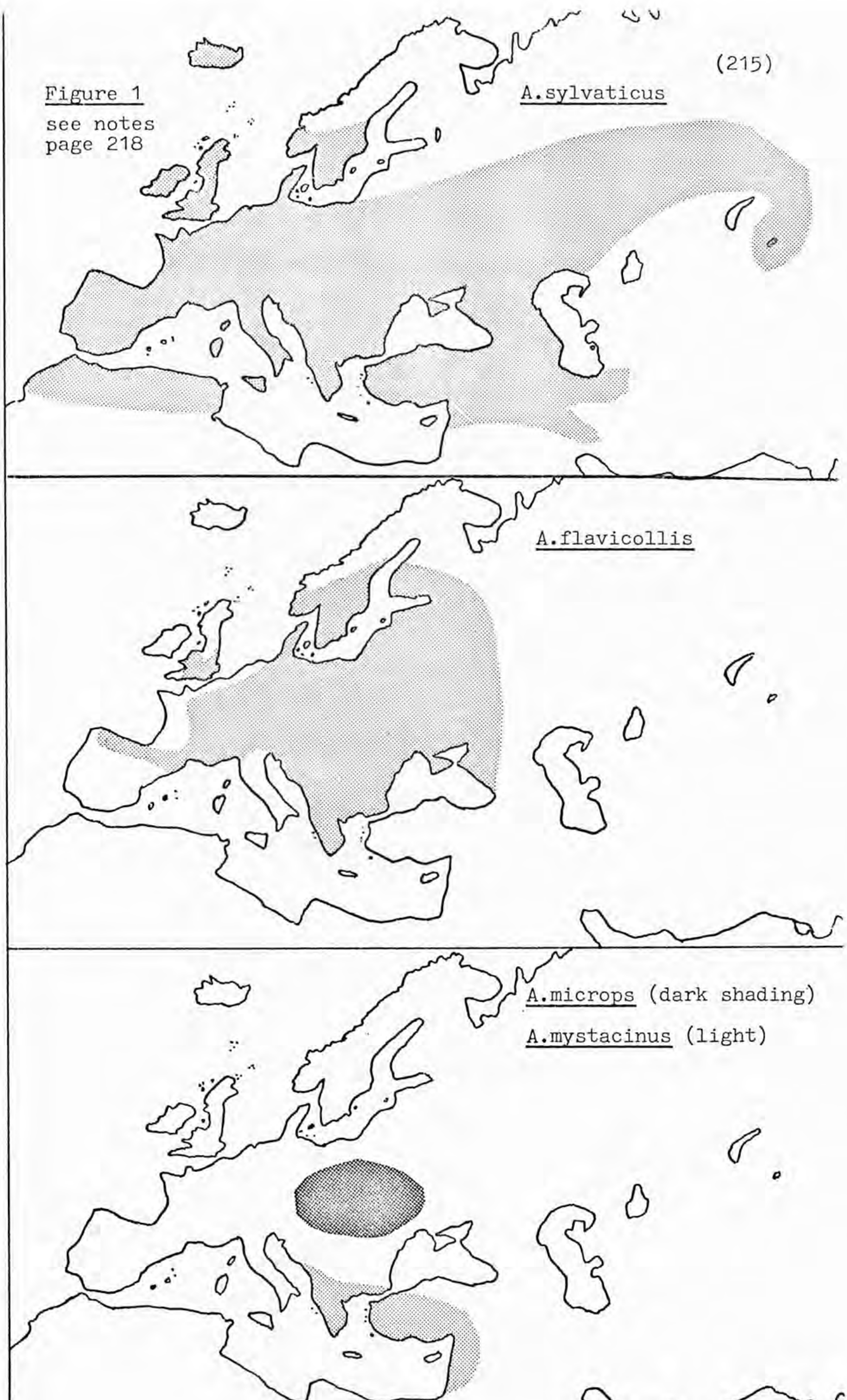


Figure 2

see notes on page 218

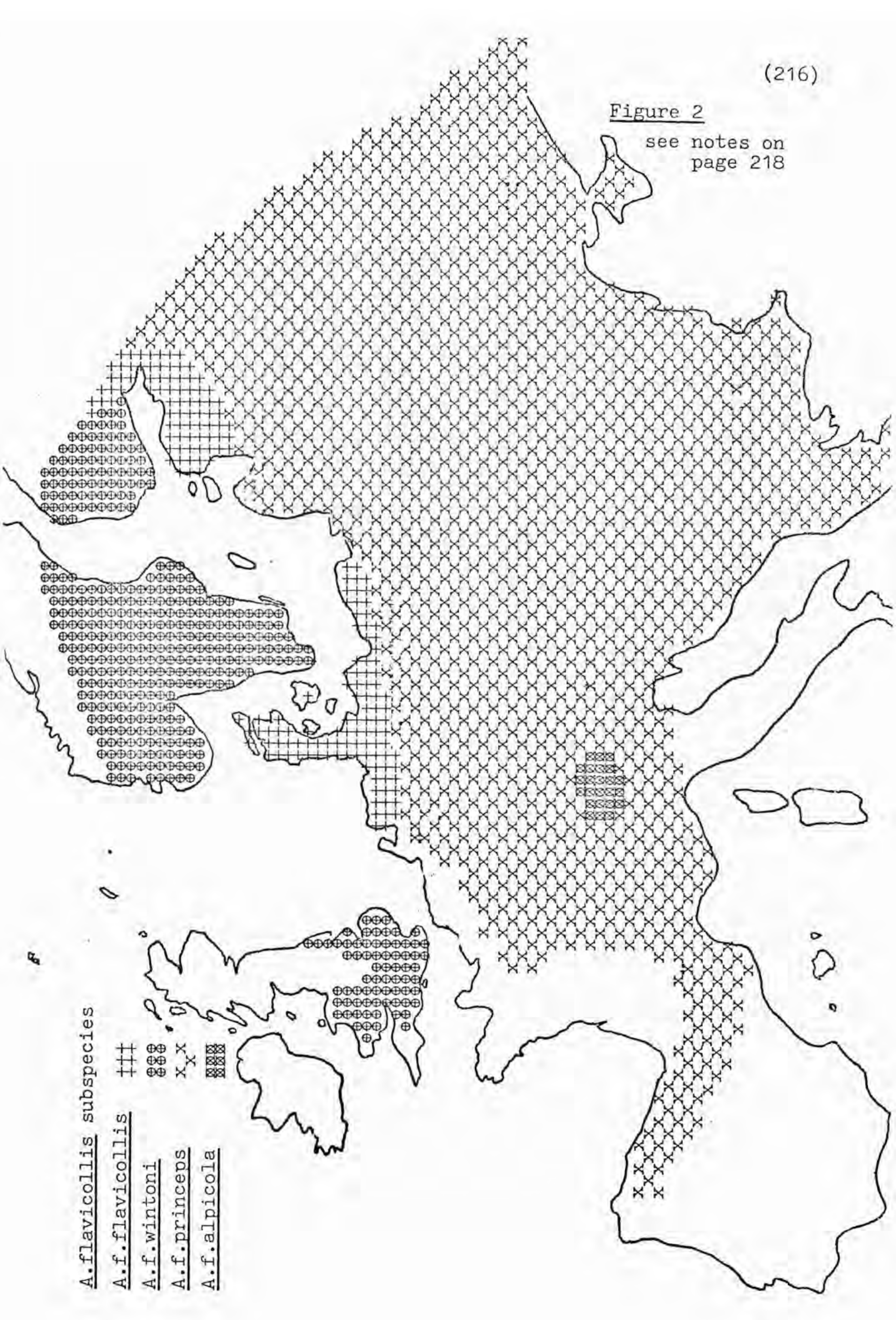
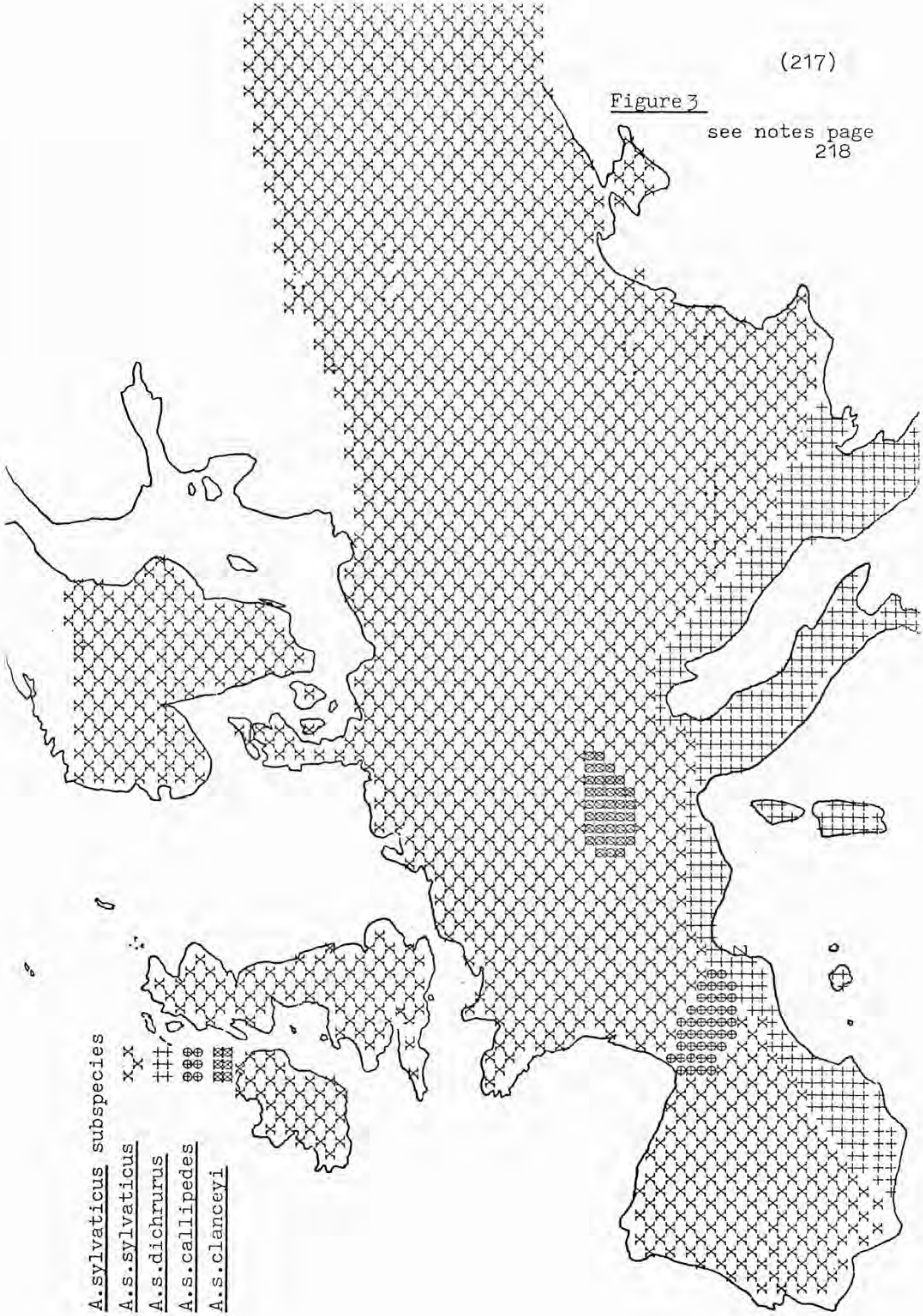


Figure 3

see notes page 218



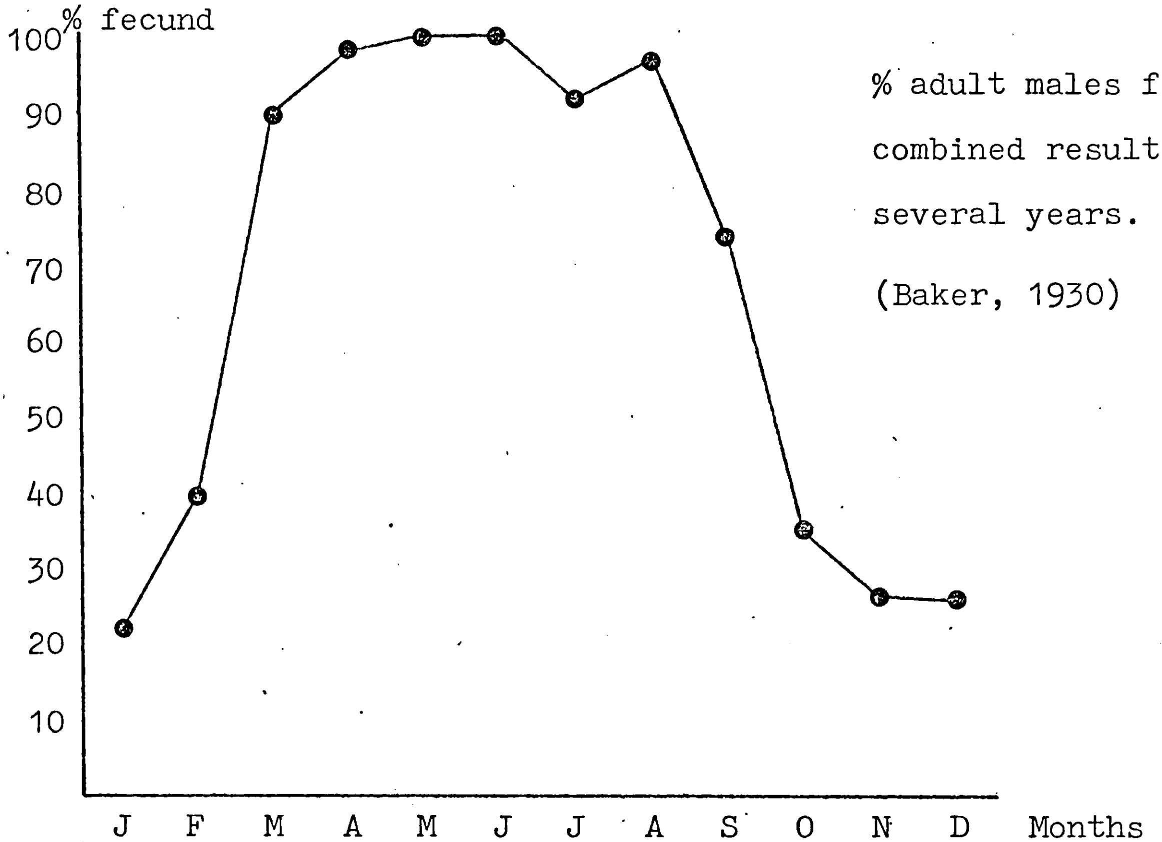
Notes on the distribution maps, figures 1 - 3.

These maps were compiled from information (sometimes conflicting) in the following works:

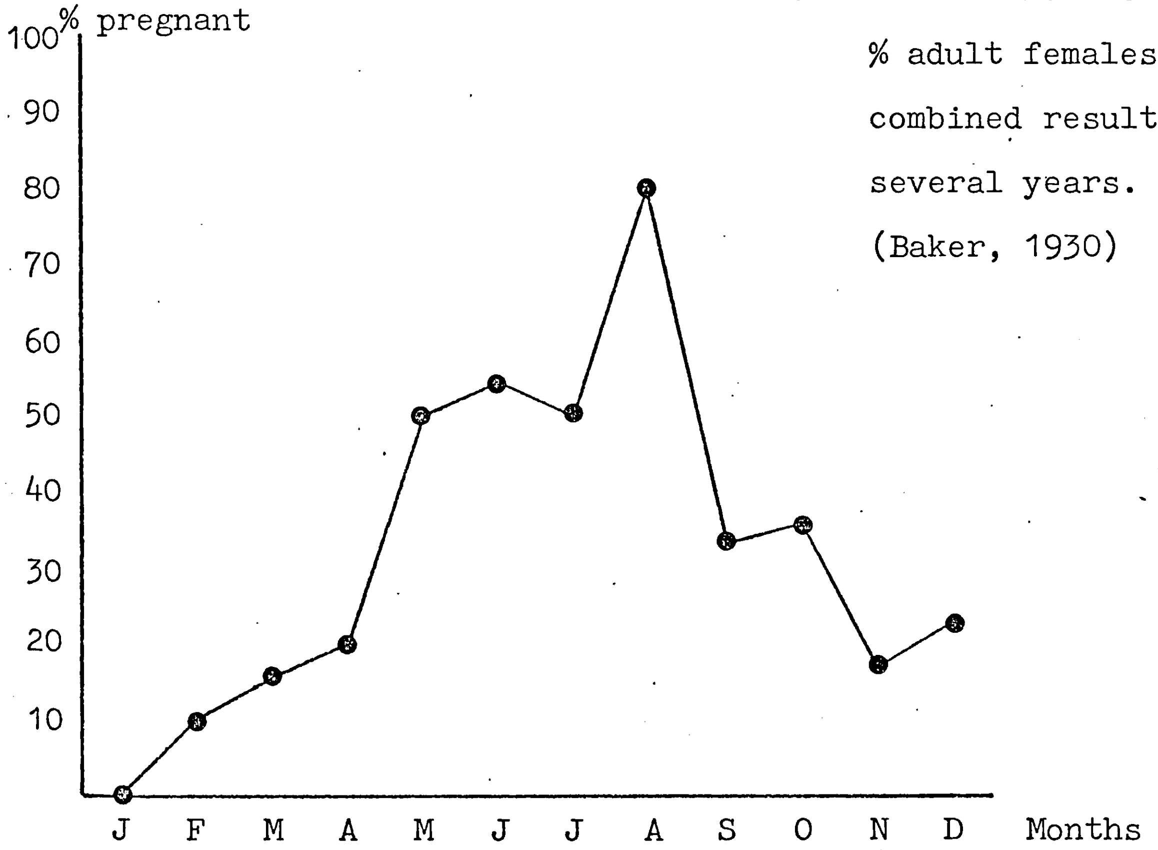
Corbet (1966)
Girons (1966-7)
Van den Brink (1967)
Ursin (1956)

The likely accuracy of the maps varies with the region of the range. The further from England, the fewer the records. The maps do not include information on small island populations. The subspecies maps include only the British and mainland Europe subspecies which, in my opinion, are possibly valid.

Figure 4 (i) Breeding cycle and weight changes in *A.sylvaticus*, from published sources.



% adult males fecund, combined results from several years.
(Baker, 1930)

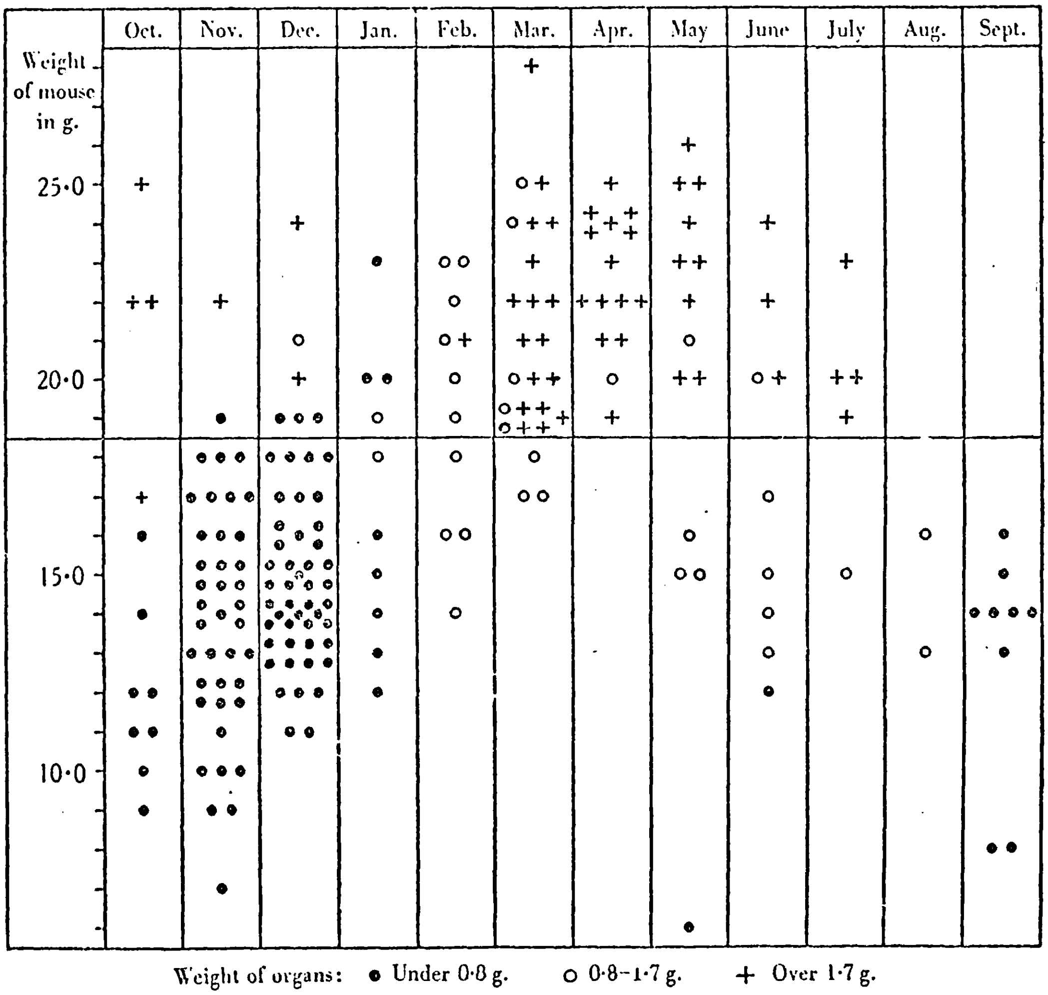


% adult females pregnant, combined results from several years.
(Baker, 1930)

Figure 4 (ii)

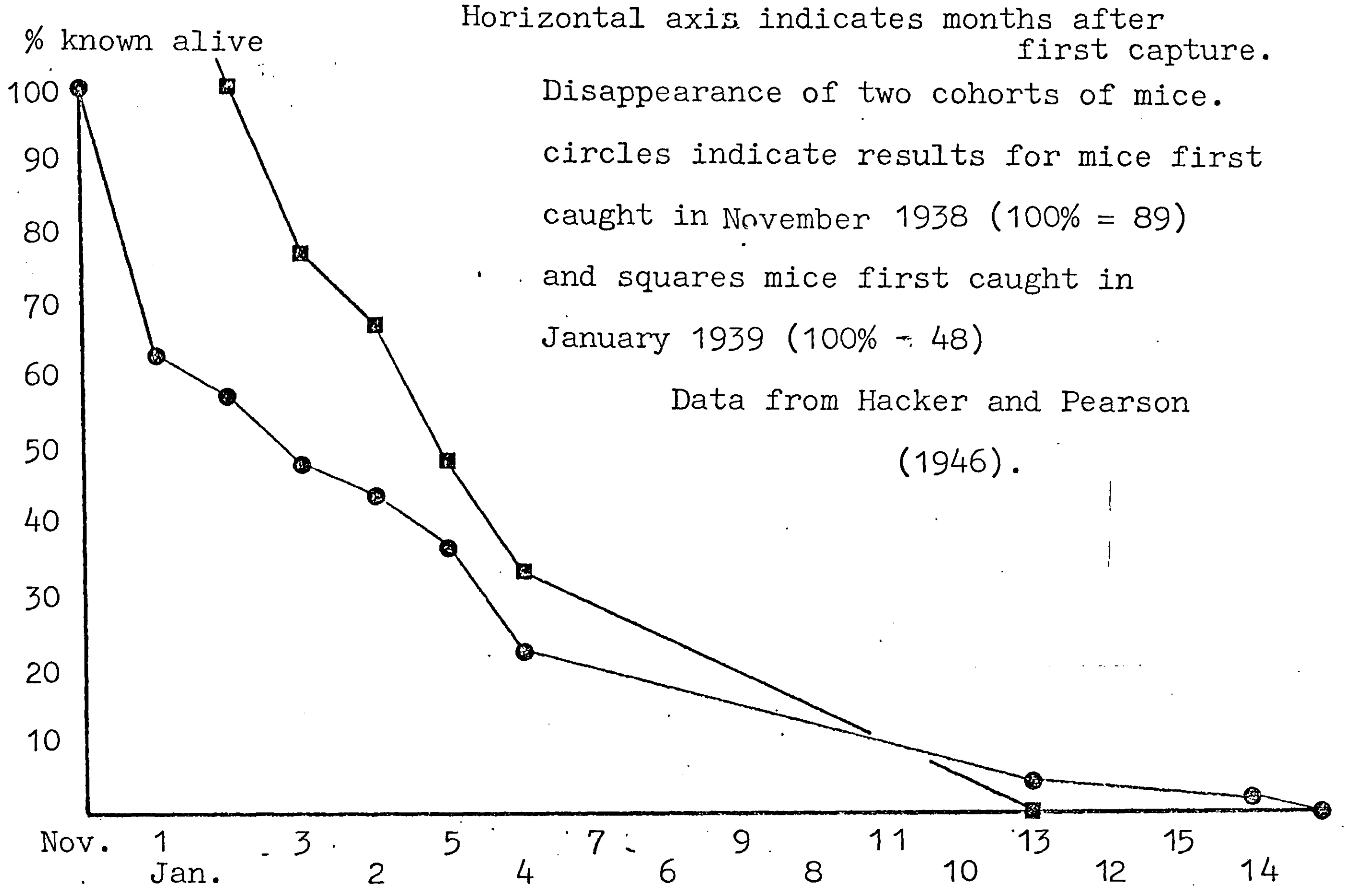
Weight and breeding condition of male A. sylvaticus.

Figure from Hacker and Pearson (1944).



Breeding condition was assessed from weight of testes under 0.8g - non-breeding mice.

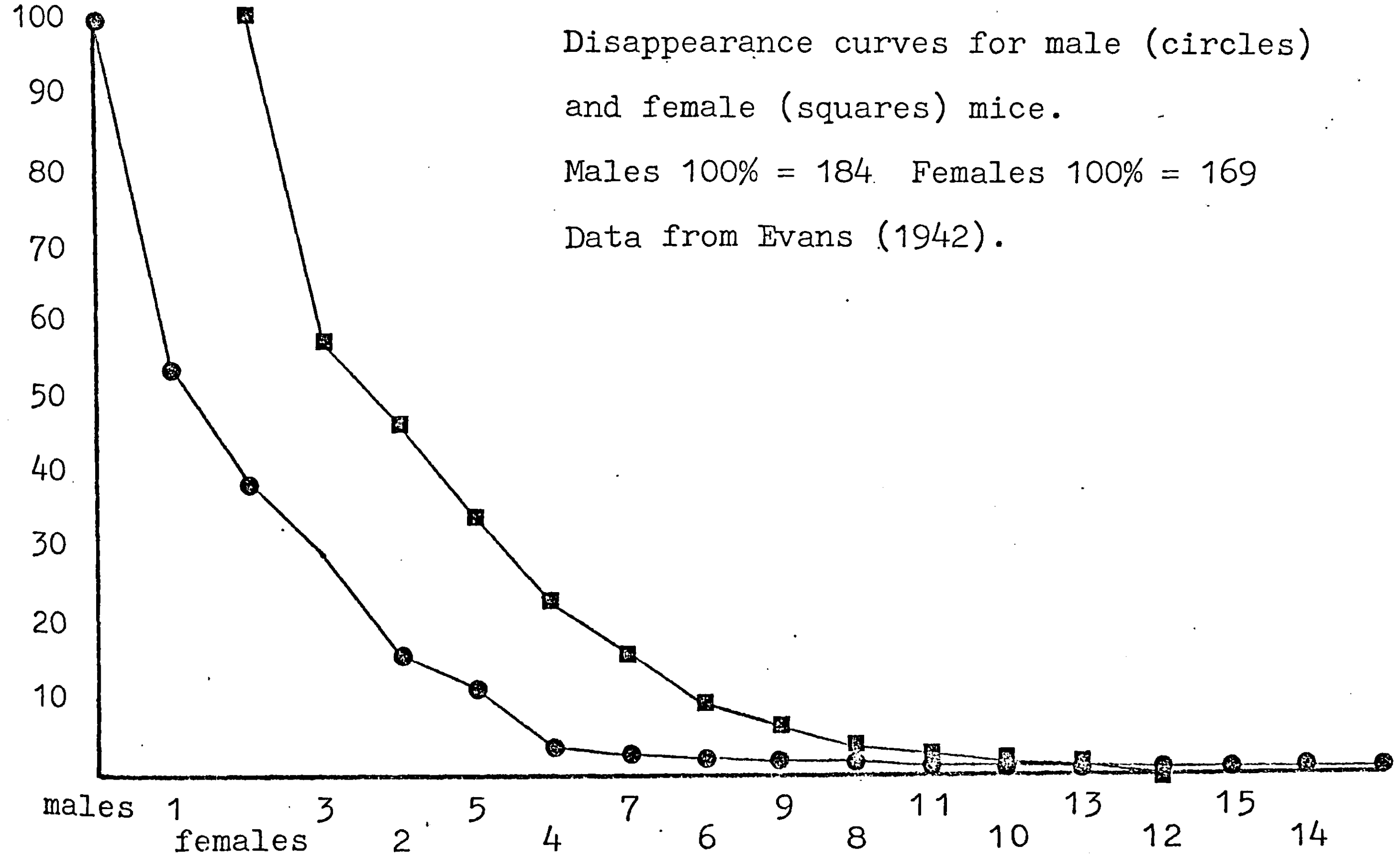
Figure 5 Disappearance curves for populations of *A.sylvaticus*, from published sources



Horizontal axis indicates months after first capture.

Disappearance of two cohorts of mice. circles indicate results for mice first caught in November 1938 (100% = 89) and squares mice first caught in January 1939 (100% = 48)

Data from Hacker and Pearson (1946).



Disappearance curves for male (circles) and female (squares) mice.

Males 100% = 184 Females 100% = 169

Data from Evans (1942).

Figure 6 (i) Population fluctuations in *A.sylvaticus*
See section 2.5 of text and table 6 for an explanation of how these results were obtained. The basic data are from published studies. The dates given are the years in which each set of results began and are not the years of publication.

Figure 6 (ii)

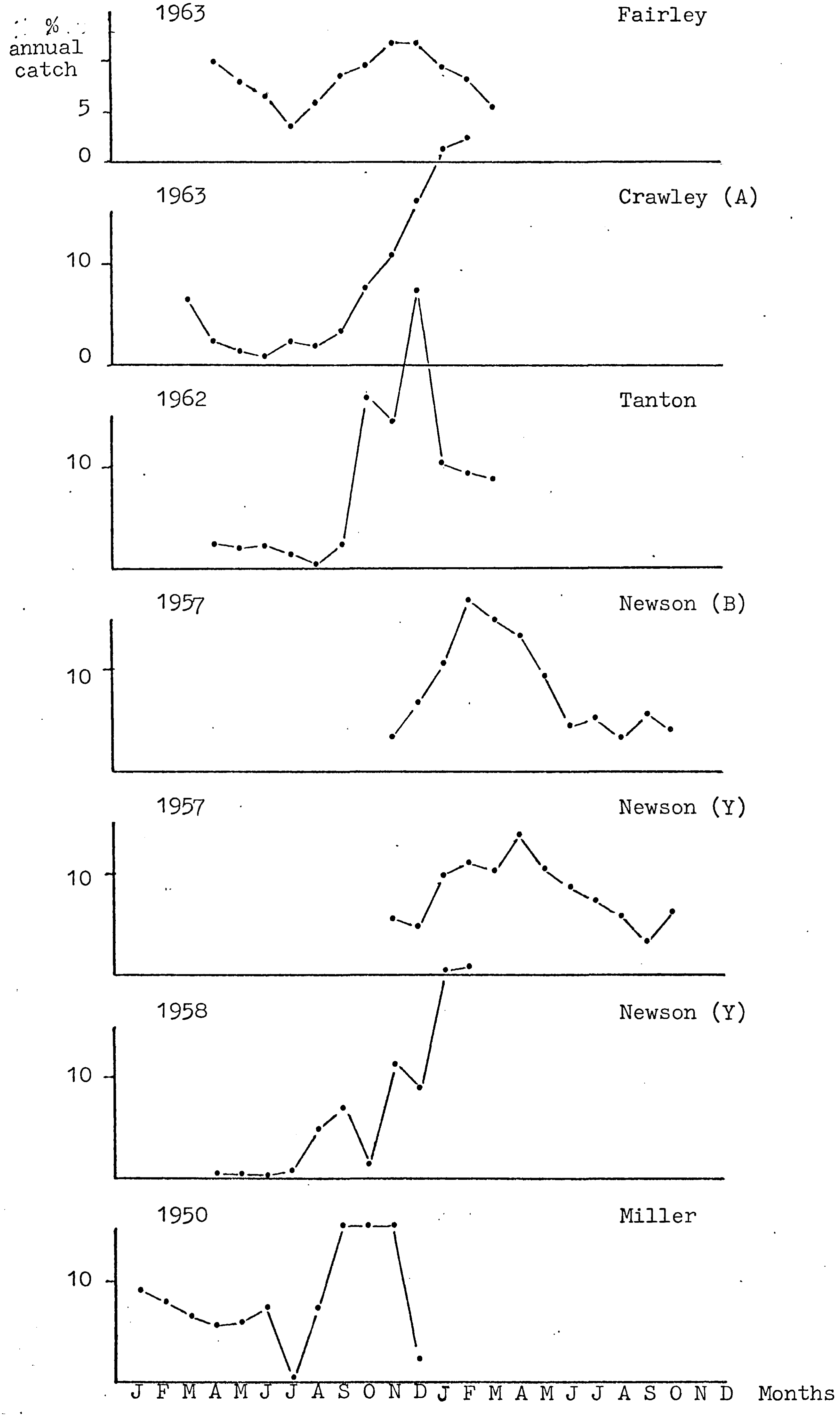
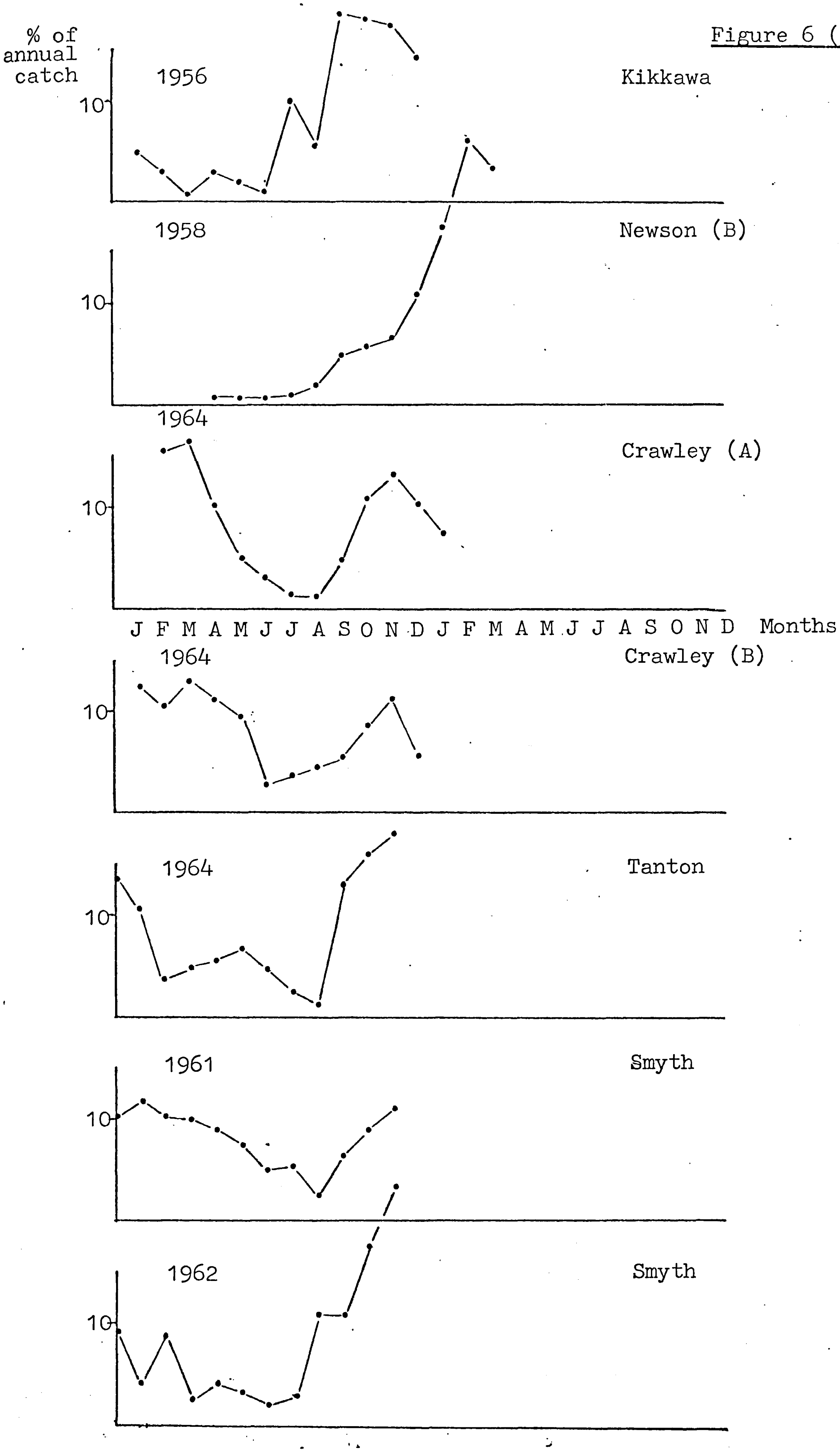

% annual catch
1963
Fairley
5
0
1963
Crawley (A)
10
0
1962
Tanton
10
1957
Newson (B)
10
1957
Newson (Y)
10
1958
Newson (Y)
10
1950
Miller
10
J F M A M J J A S O N D J F M A M J J A S O N D
Months

Figure 6 (iii)


% of annual catch
1956
Kikkawa
10
1958
Newson (B)
10
1964
Crawley (A)
10
J F M A M J J A S O N D J F M A M J J A S O N D Months
1964
Crawley (B)
10
1964
Tanton
10
1961
Smyth
10
1962
Smyth
10

<u>Figure 7</u> The average pattern of <u>A.sylvaticus</u> population fluctuation

The results shown here are the average of the 14 studies summarised in table 6 and figure 6.

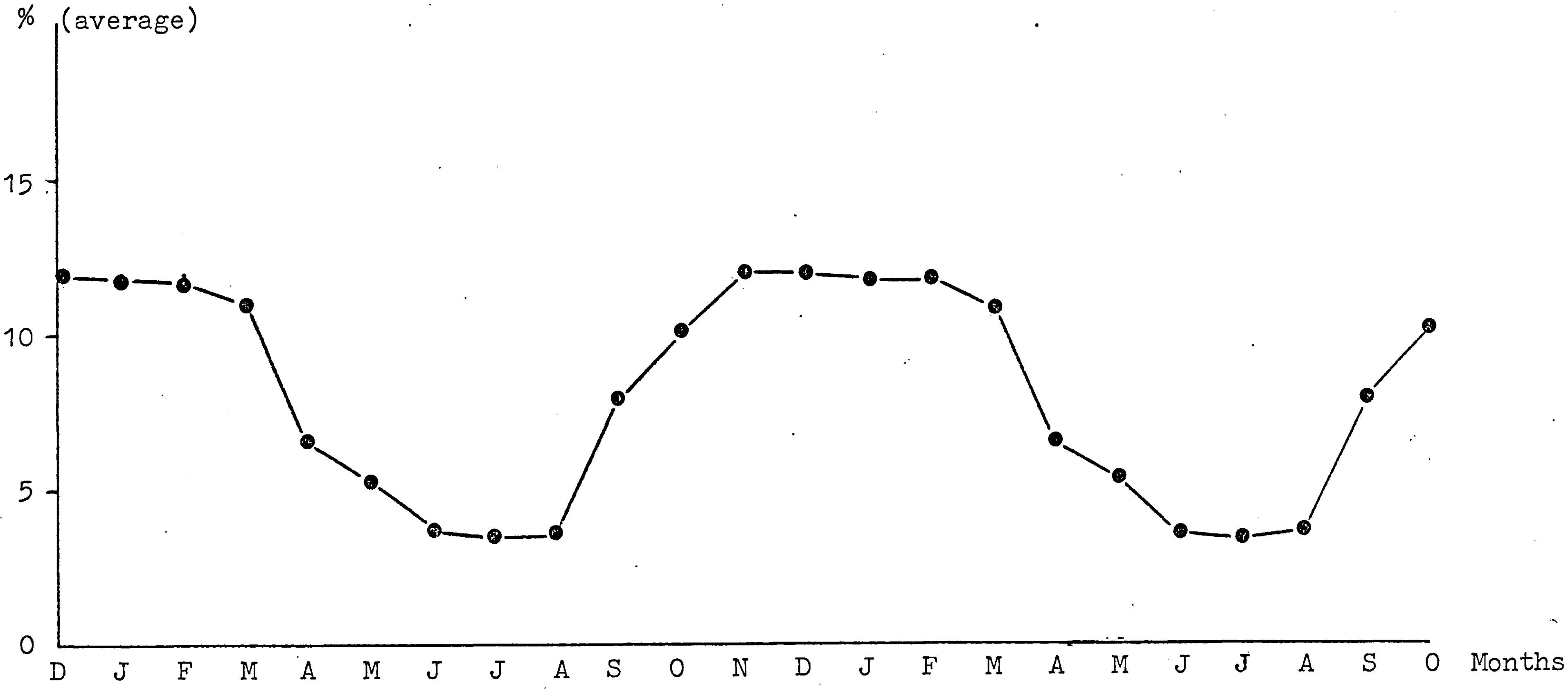
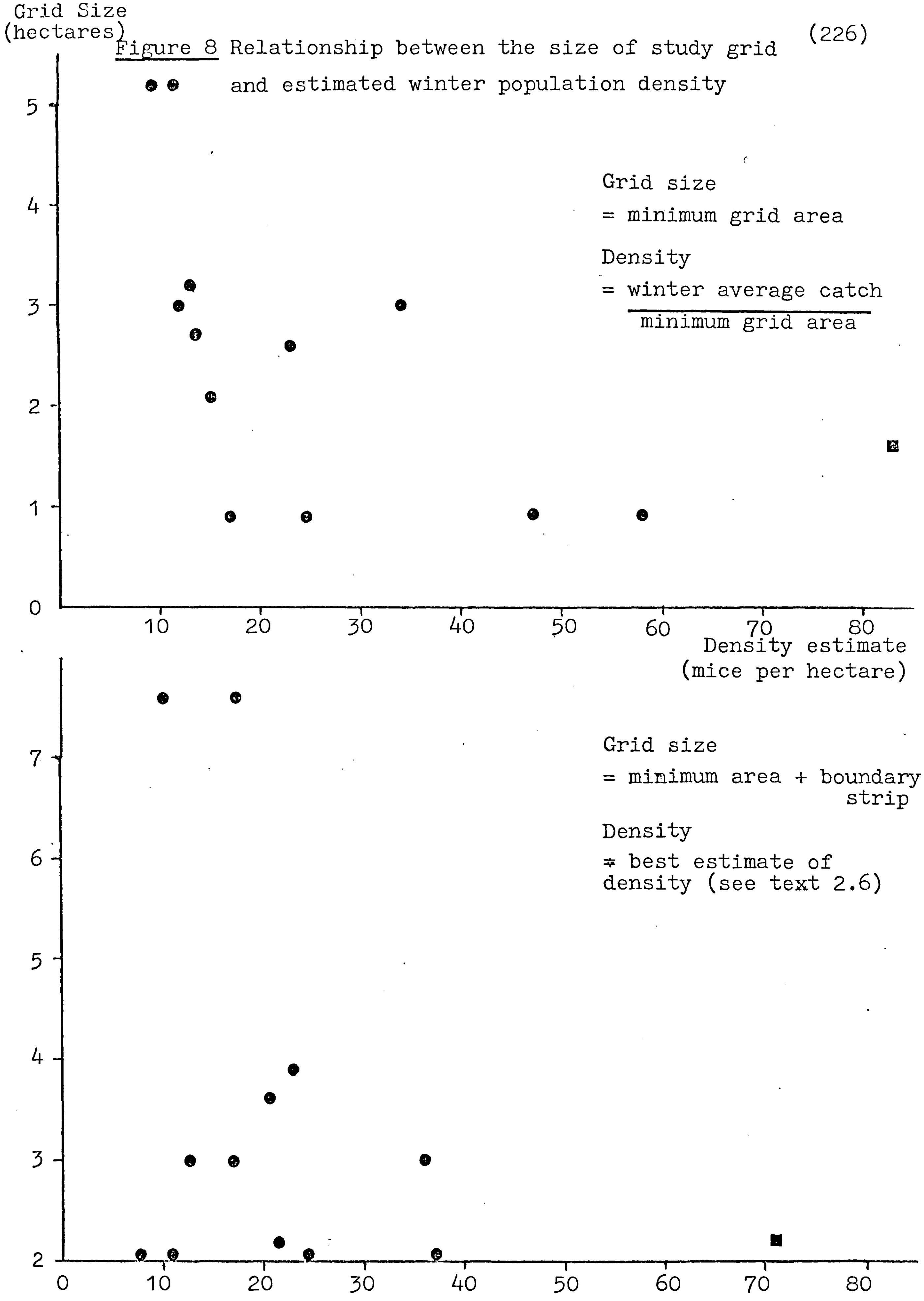


Figure 8 Relationship between the size of study grid and estimated winter population density



N.B. The aberrant results from Kikkawa's study are shown as square symbols.

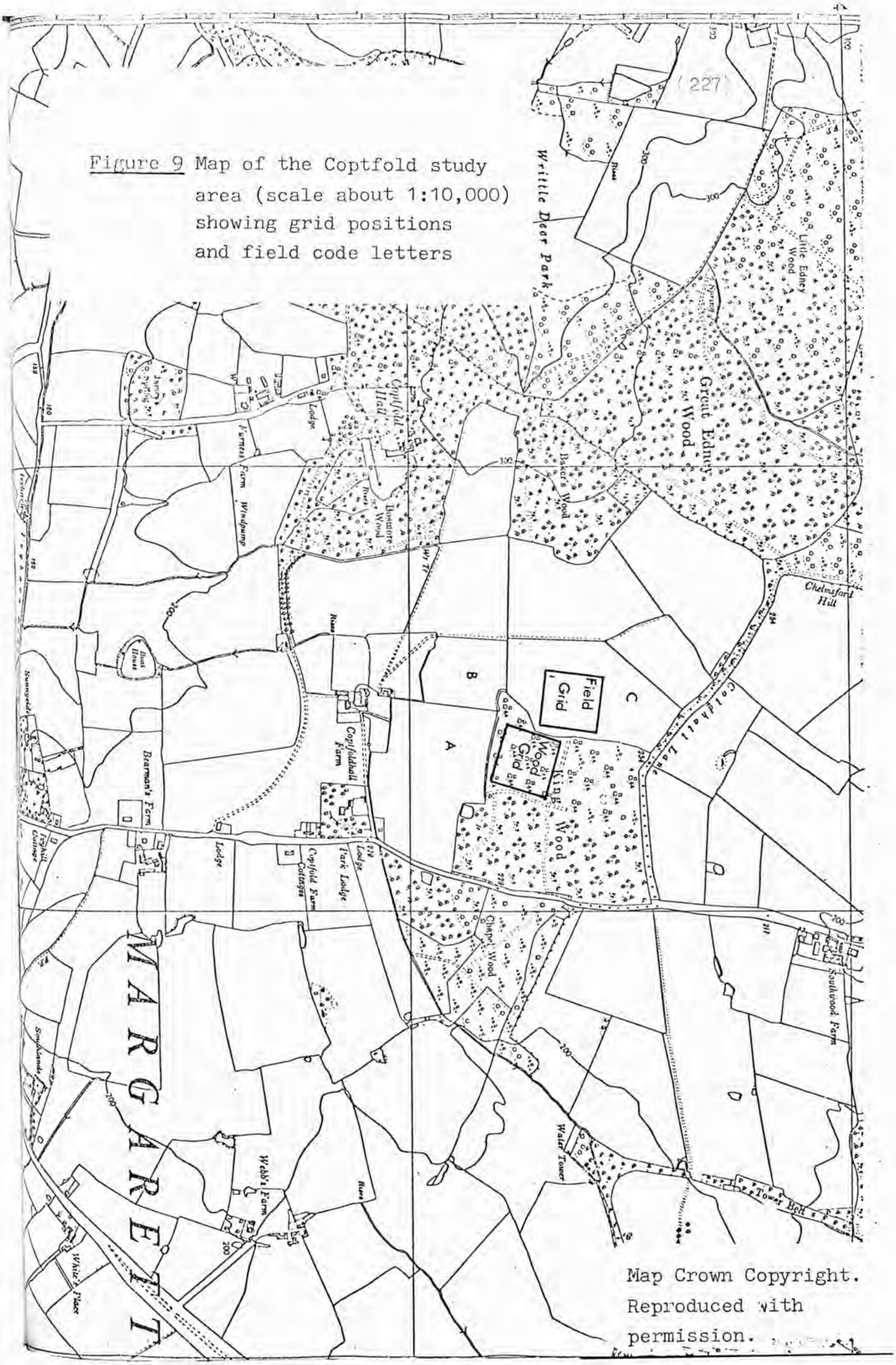


Figure 9 Map of the Coptfold study area (scale about 1:10,000) showing grid positions and field code letters

Map Crown Copyright. Reproduced with permission.

Figure 10 Aerial photograph of the Coptfold stud area

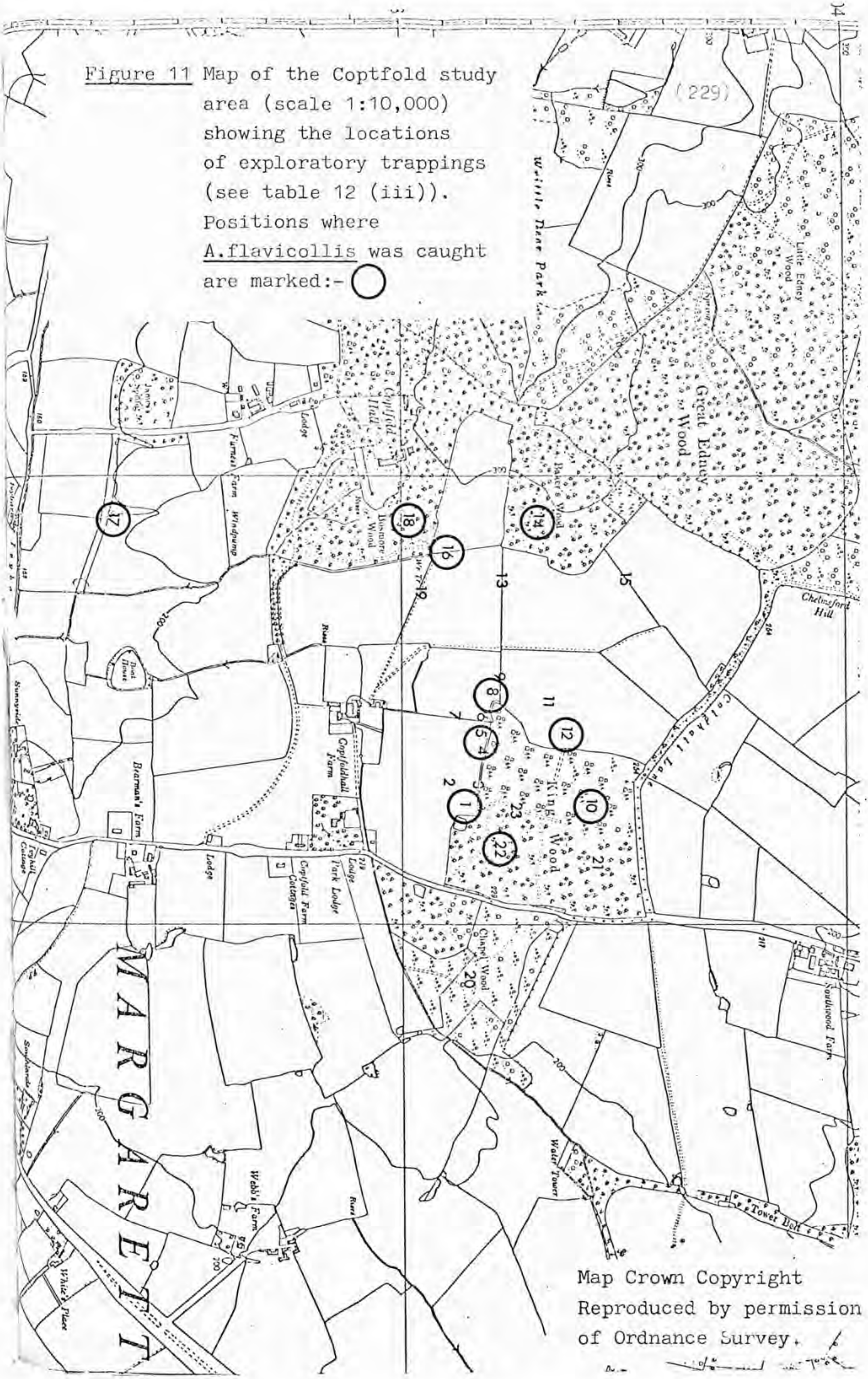


Figure 11 Map of the Coptfold study area (scale 1:10,000) showing the locations of exploratory trappings (see table 12 (iii)). Positions where *A.flavicollis* was caught are marked:- ○

Figure 12 Sketch map of the King Wood study grid and surrounding area.

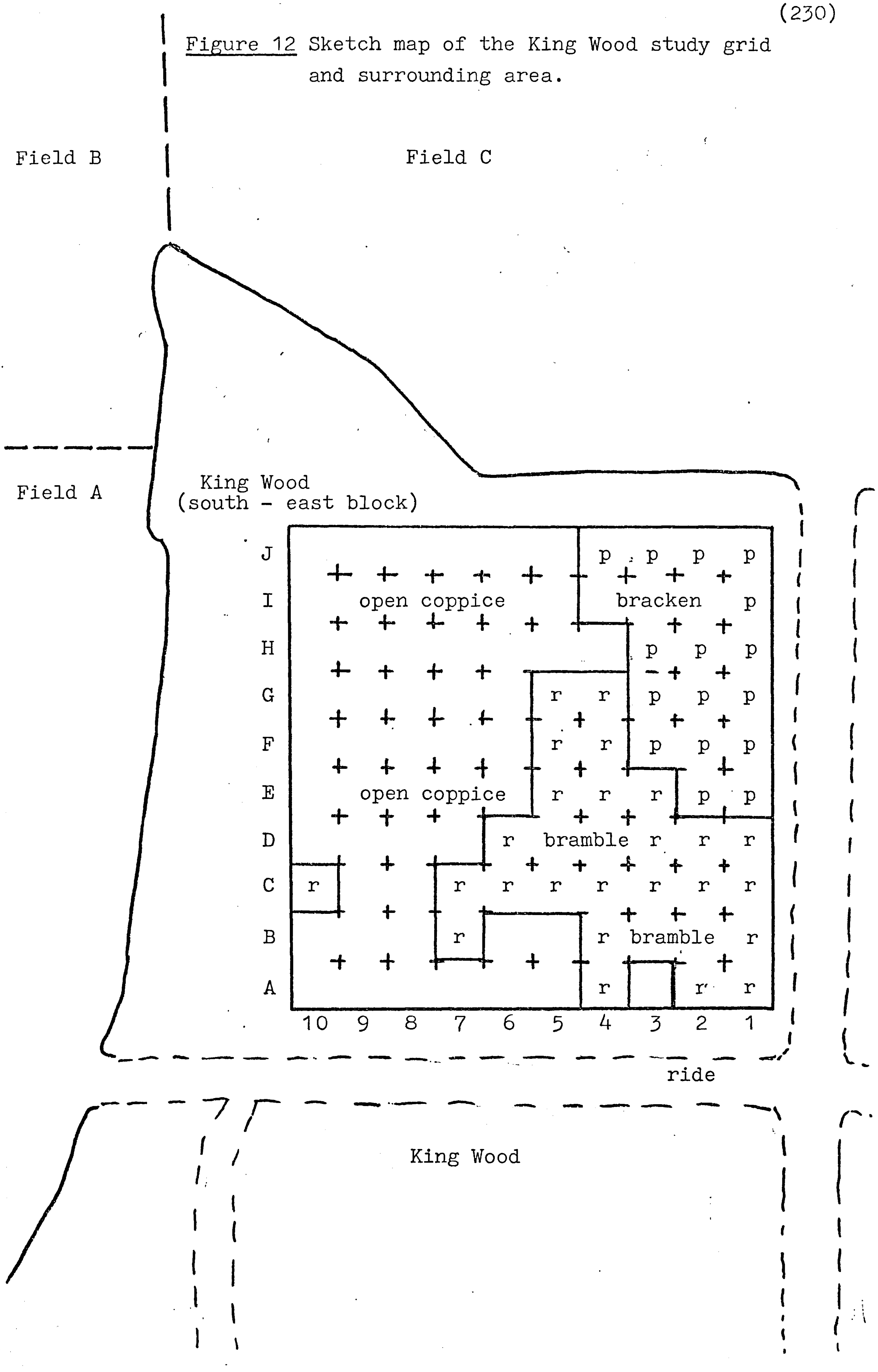


Figure 13 The open coppice area, grid position

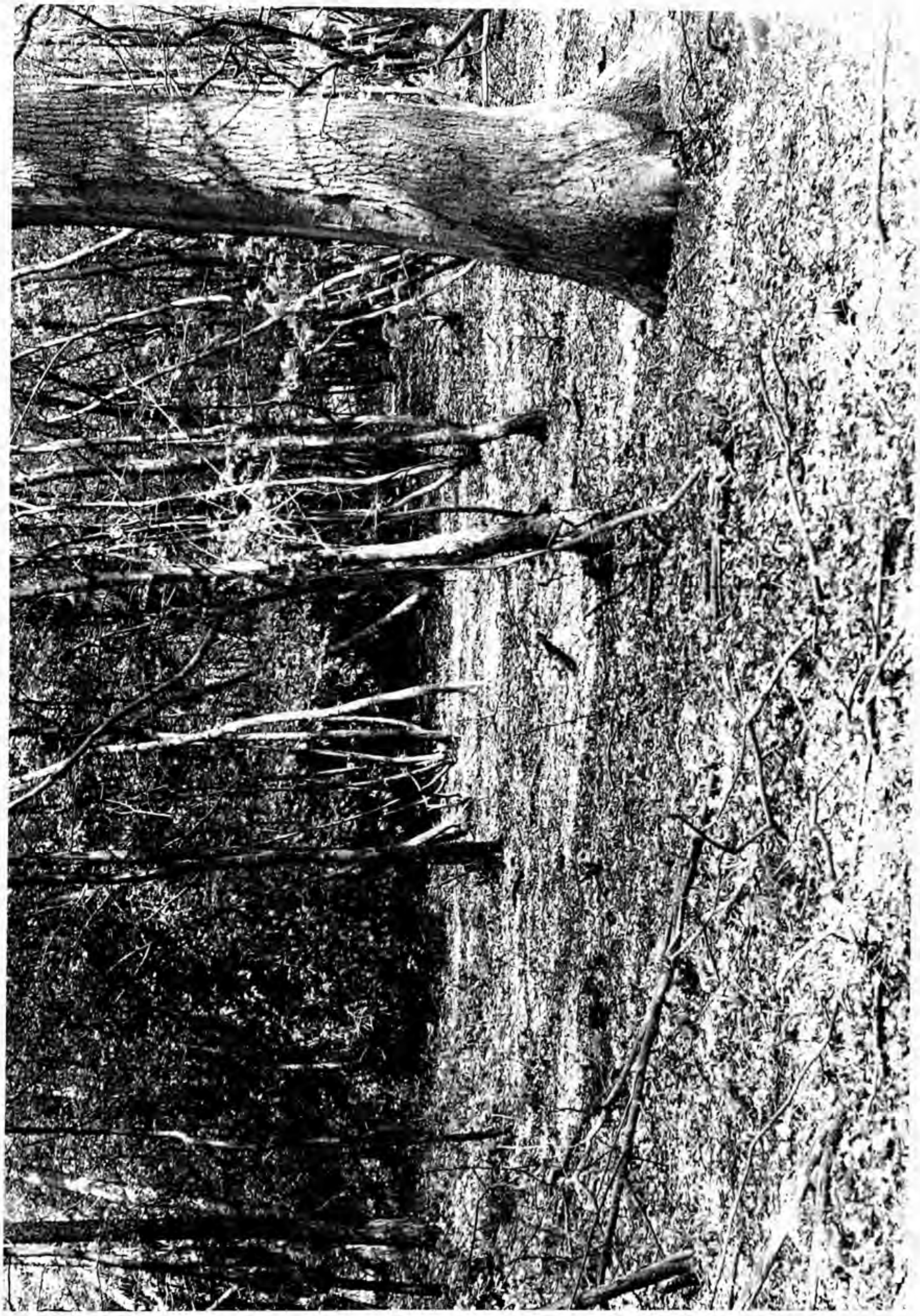


Figure 14 The open coppice habitat, grid position DF

Figure 15 The bracken area in the King Wood study grid

Figure 16 The Control area, grid position 13

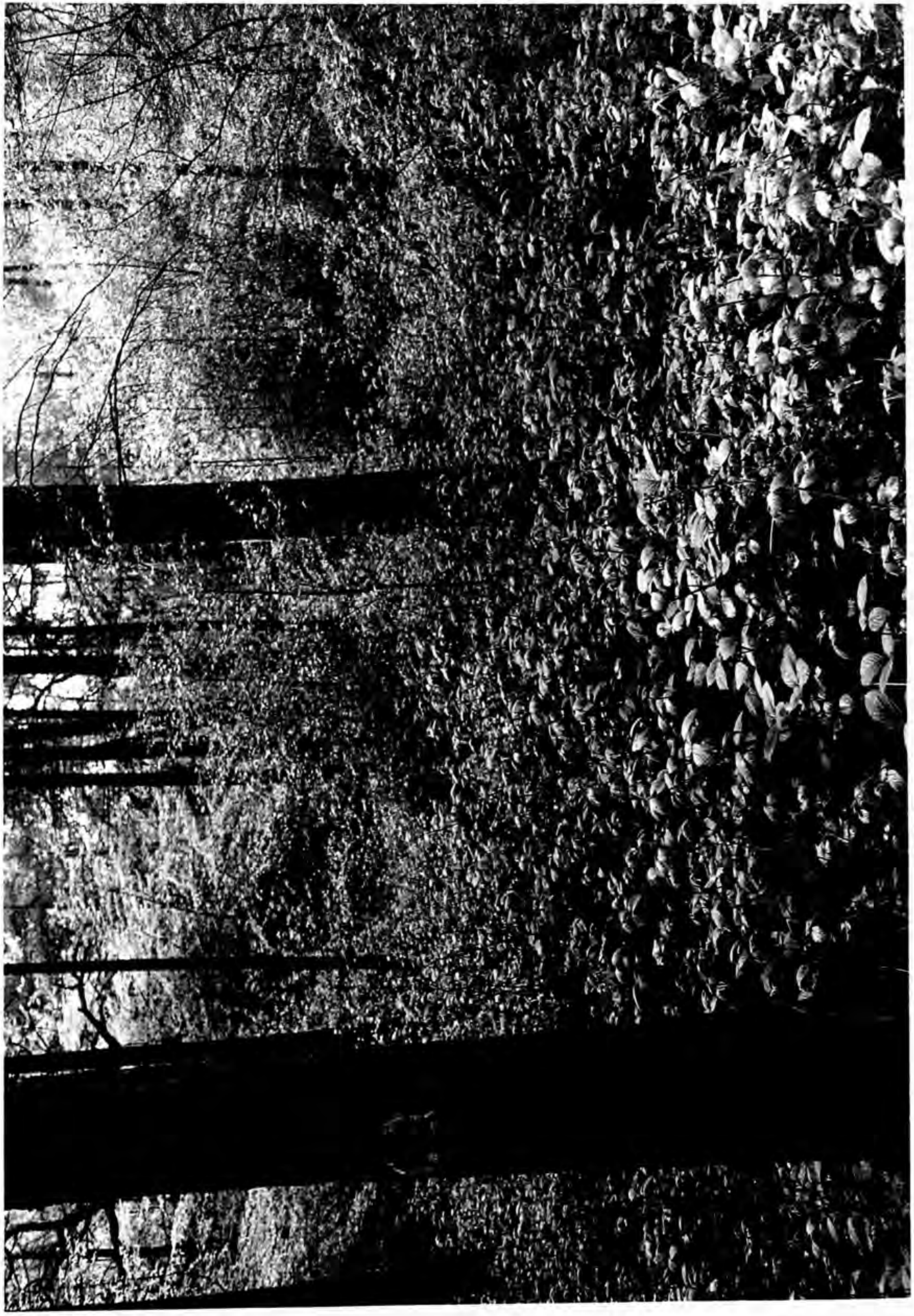


Figure 17 The [illegible] area, grid position [illegible]

Figure 14

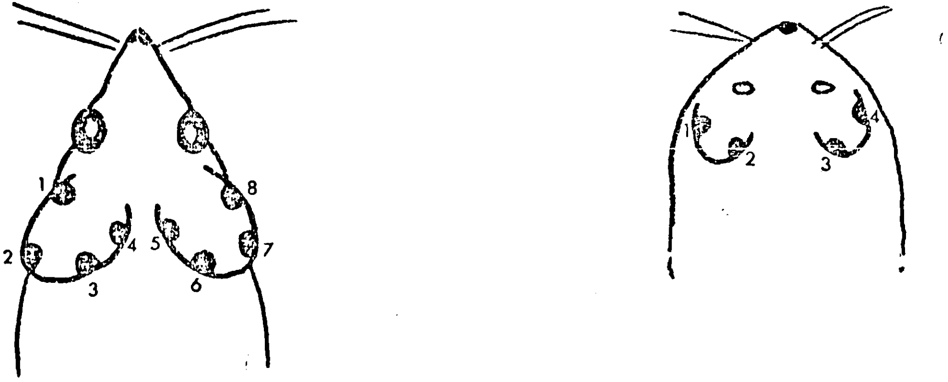
The ride which separates row 1 of the stud grid from the south-west block of King Wood.

Figure 19 The edge of King Wood where it adjoins the field 3 study area

Figure 26 The south edge of King Wood where it adjoins field A

Figure 21 Method of marking rodents and the marking codes.

Mice Ear notching Voles



The written Codes: The ear notch code (no notch = 0) is the first digit in a three digit code. The second two digits are the sum of the two toe clip codes (only one front and one hind toe being clipped on any individual). When toe '9' is clipped the front toe code is multiplied by ten.

Toe clipping
(Mice and Voles)

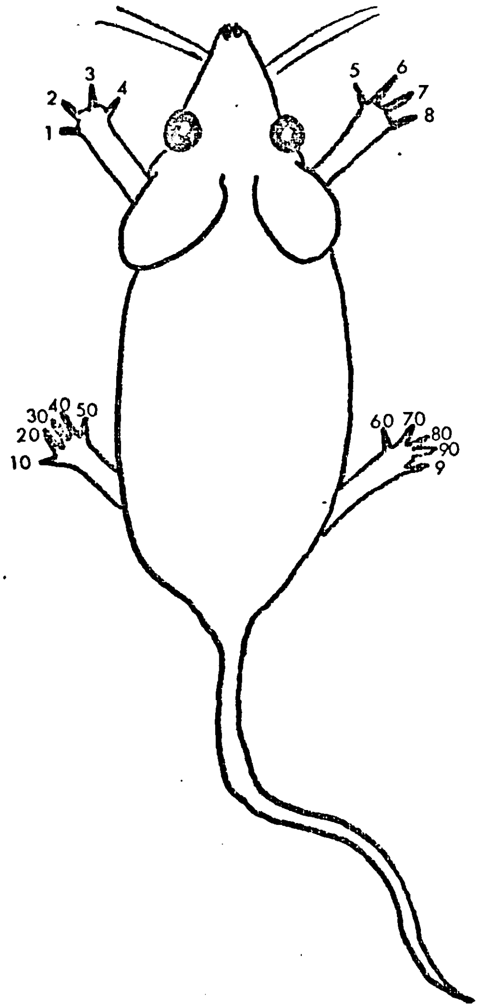


Figure 22 (i) Population estimates for the two *Apodemus* species in the two Coptfold study areas.

The solid symbols and solid lines indicate the population estimates based on the Leslie and Chitty method (see section 3.6 of text) where the data permitted this estimate to be calculated. The open symbols and dotted lines indicate the number of individual mice actually captured during the trapping periods (i.e. value C_t referred to in section 3.6 of text).

The Field Grid trappings began in 1969.

Figure 22 (ii) 1967

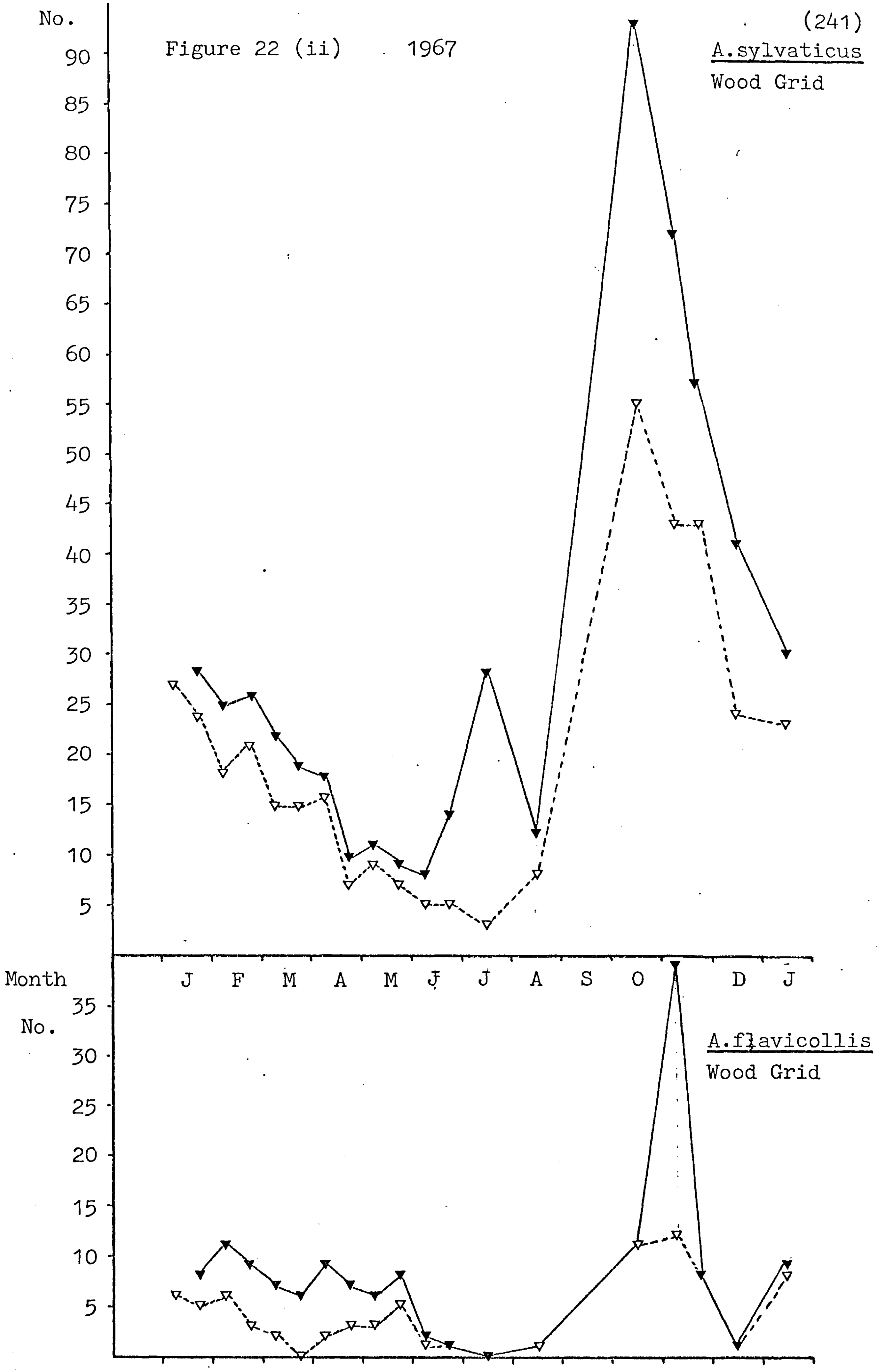


Figure 22 (iii) 1968

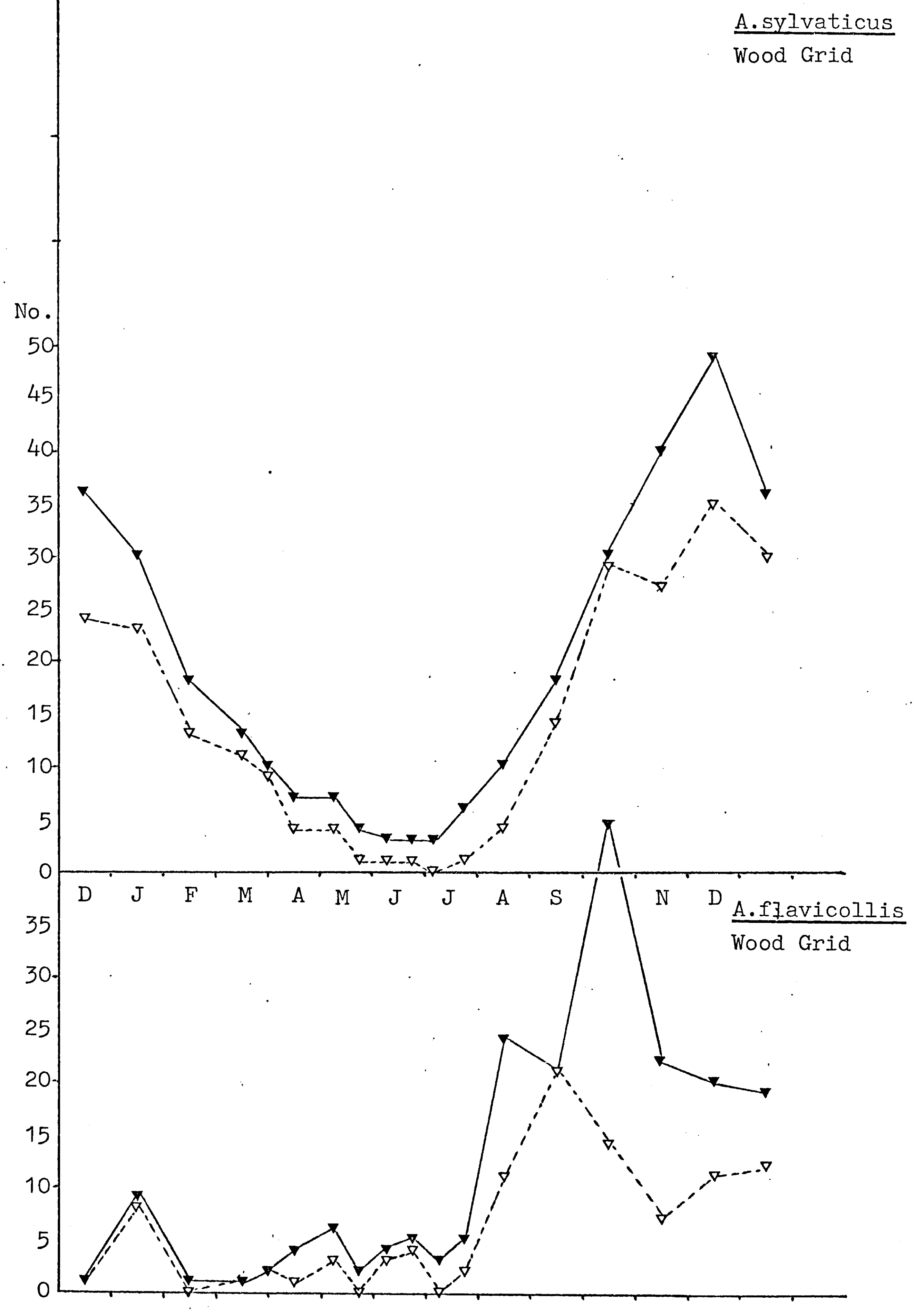
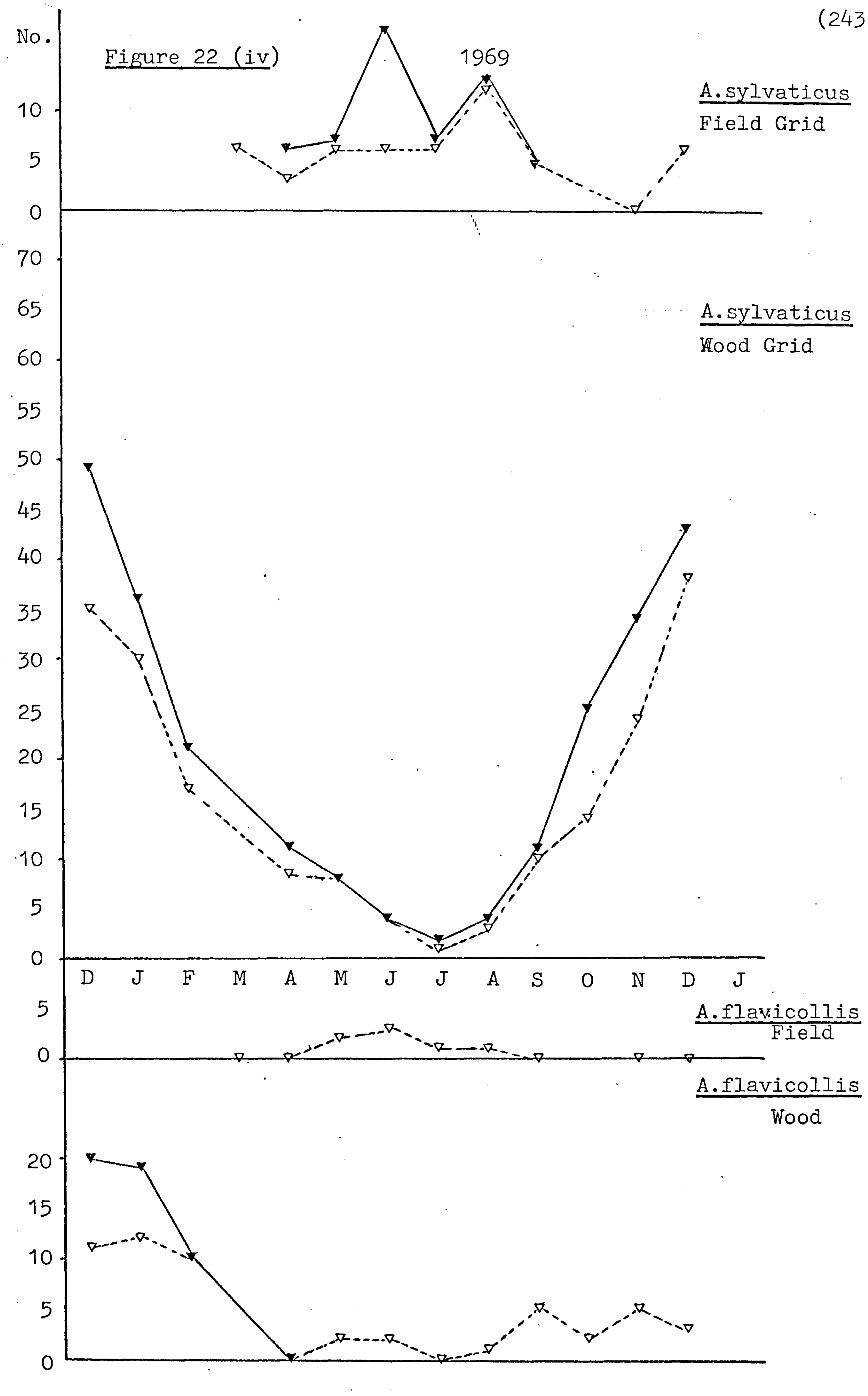


Figure 22 (iv)


No.
1969
A.sylvaticus
Field Grid
10
5
0
70
65
60
55
50
45
40
35
30
25
20
15
10
5
0
A.sylvaticus
Wood Grid
D
J
F
M
A
M
J
J
A
S
O
N
D
J
5
0
A.flavicollis
Field
A.flavicollis
Wood
20
15
10
5
0

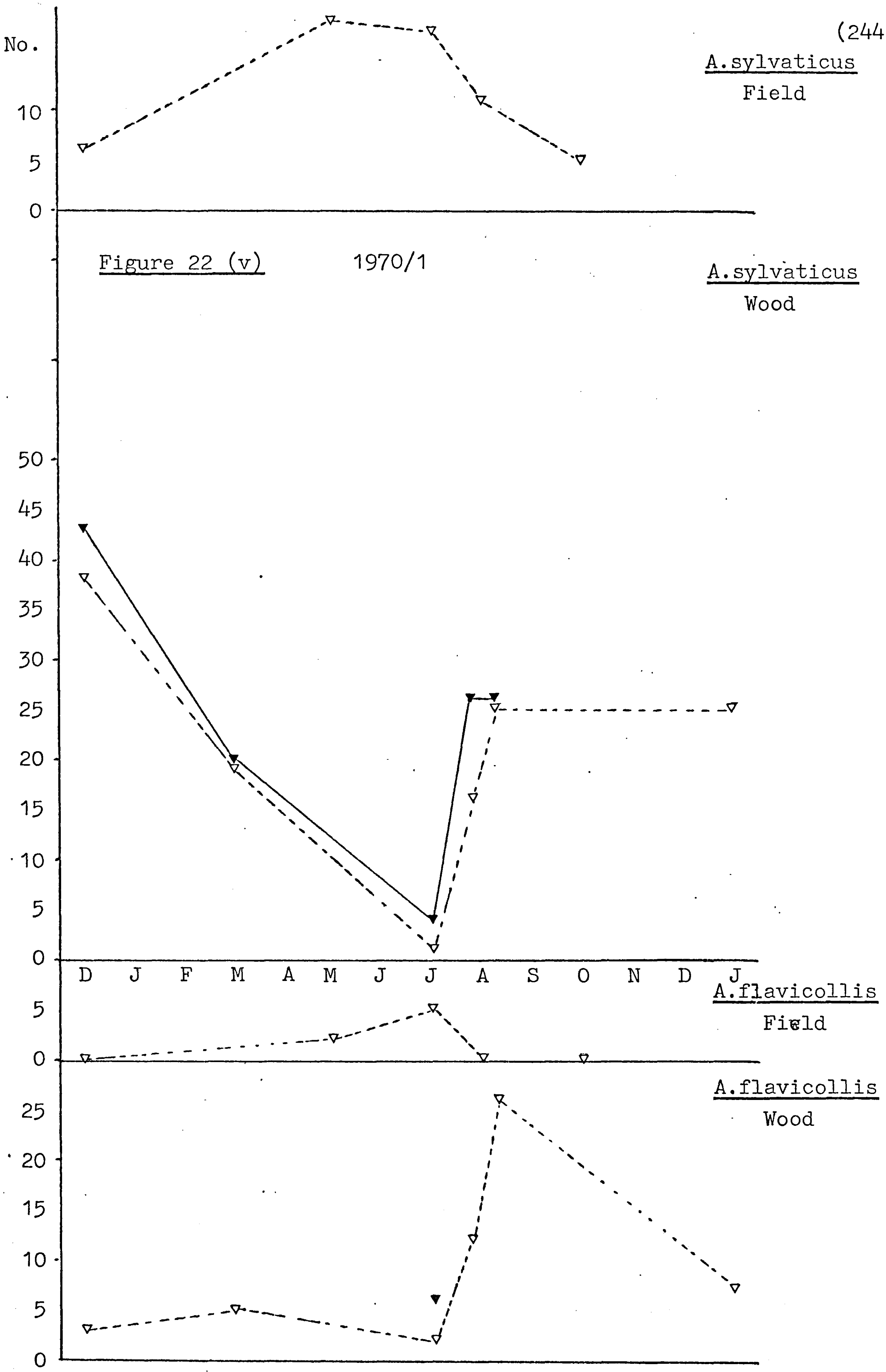


Figure 22 (v) 1970/1

Figure 23 Disappearance curves for *Apodemus* on the King Wood study grid.

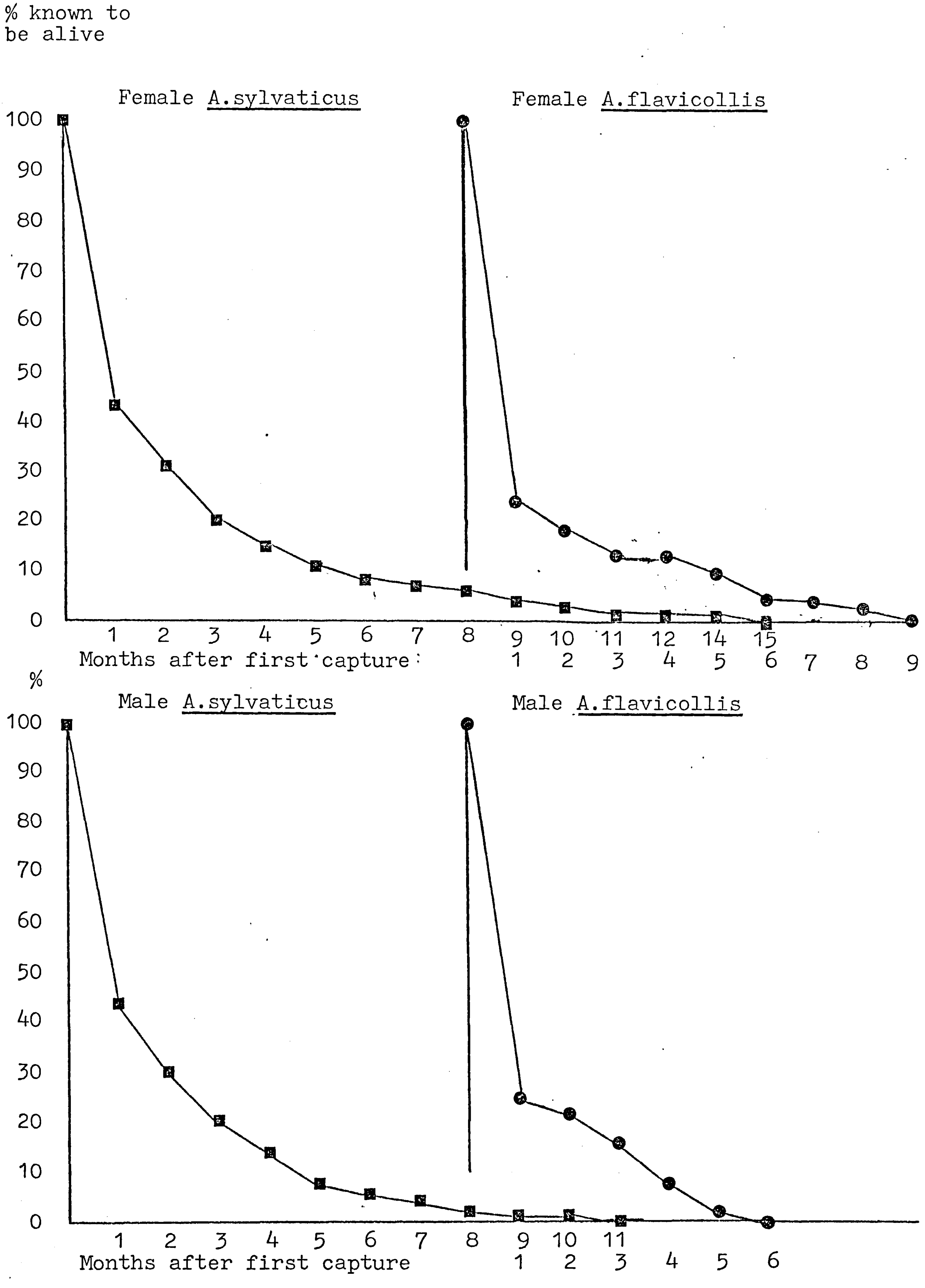
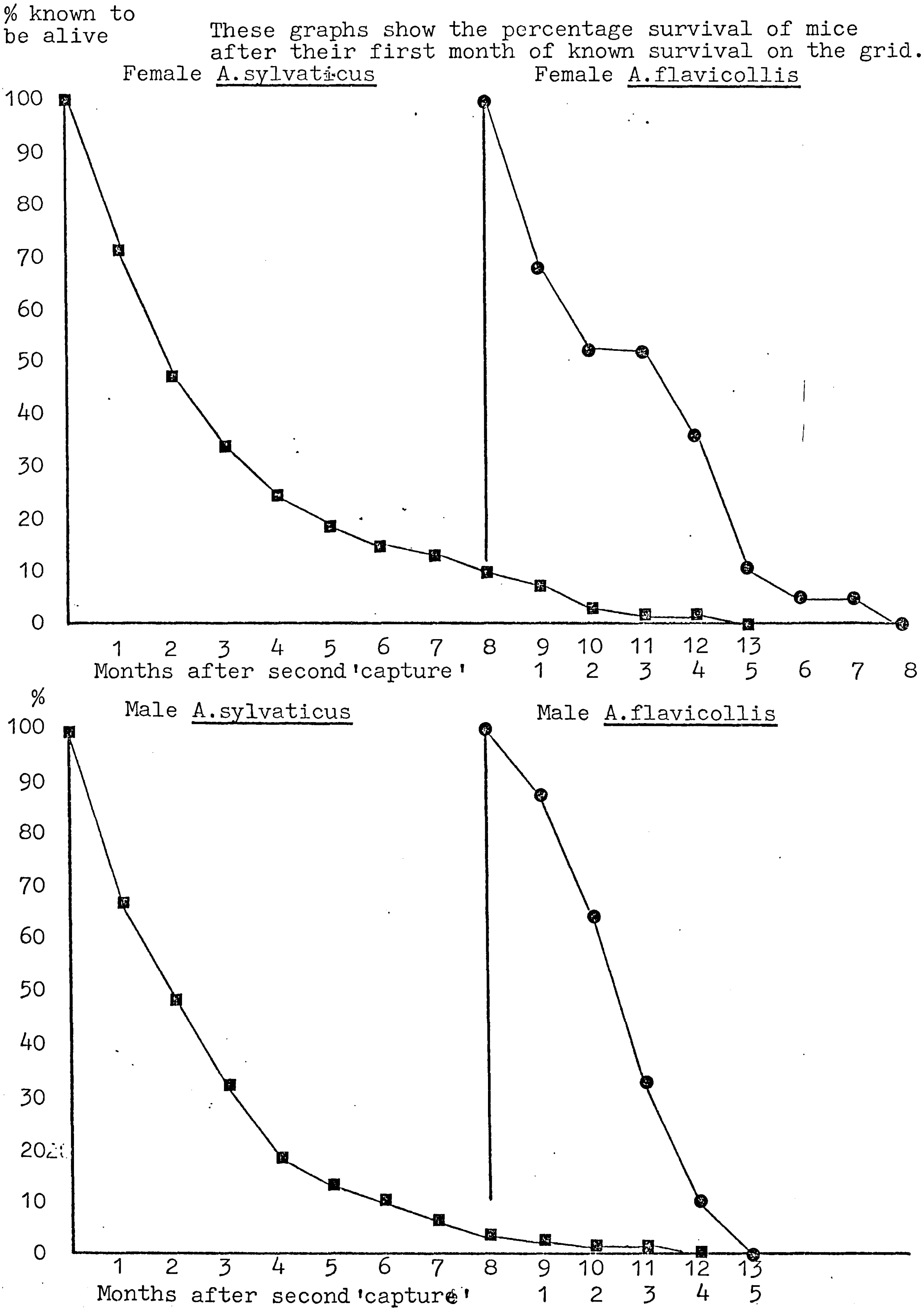


Figure 24 Disappearance curves for resident *Apodemus* on the King Wood study grid



These graphs show the percentage survival of mice after their first month of known survival on the grid.

Figure 25 Survival of monthly cohorts of mice on the King Wood (i) study area

Each block of the graph indicates the time of first capture of each cohort of mice and the time of the final disappearance from the trappable population of that cohort. Within each block, the vertical height of the block indicates the number of mice in that cohort known to be alive at that time. The upper line of the graph indicates the total number of mice known to be alive at that time (value K_t - see section 3.6 of text).

Figure 25 (ii)

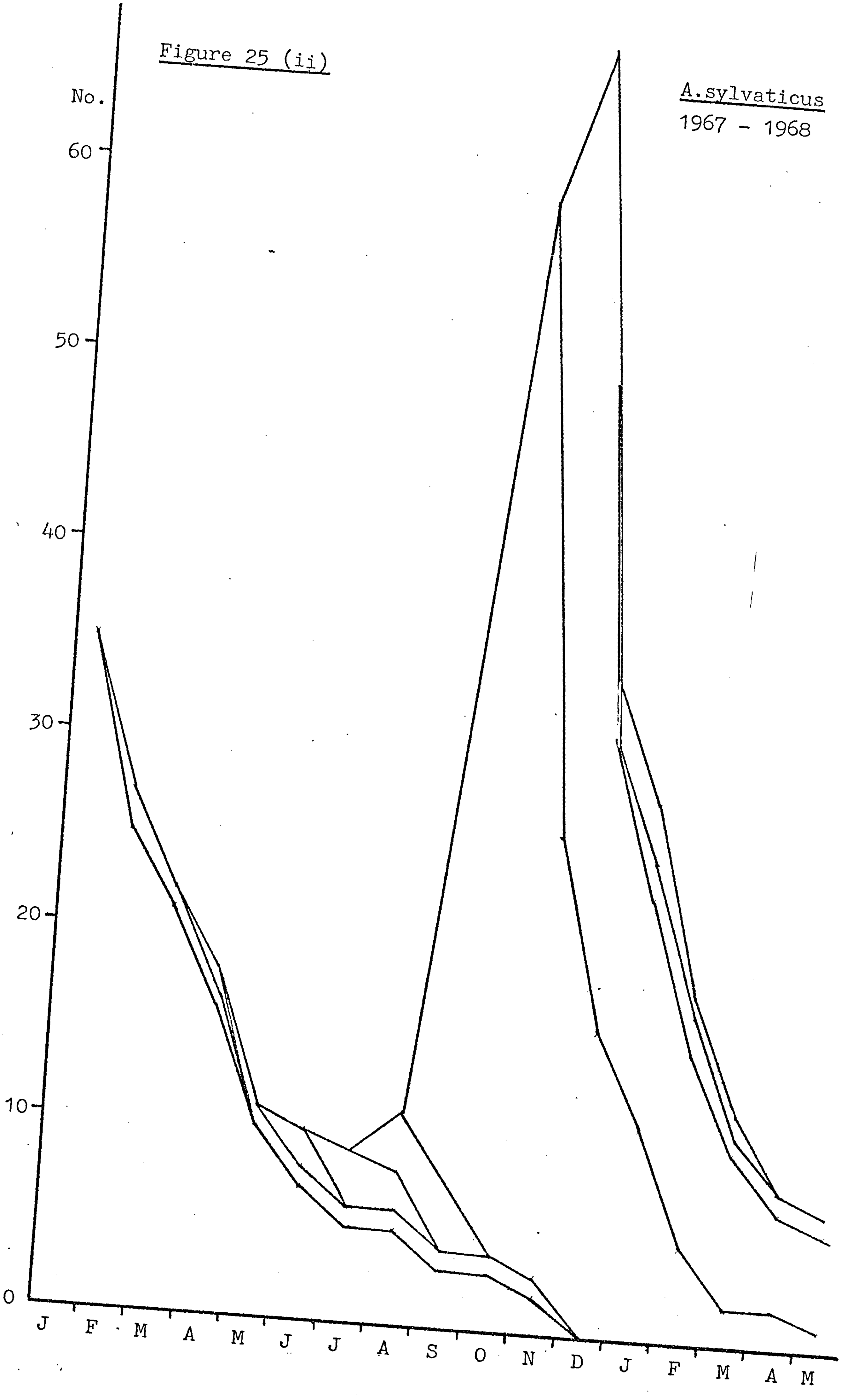

No.
60
50
40
30
20
10
0
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
A.sylvaticus
1967 - 1968

Figure 25 (iii)

A.sylvaticus
1968 - 1969

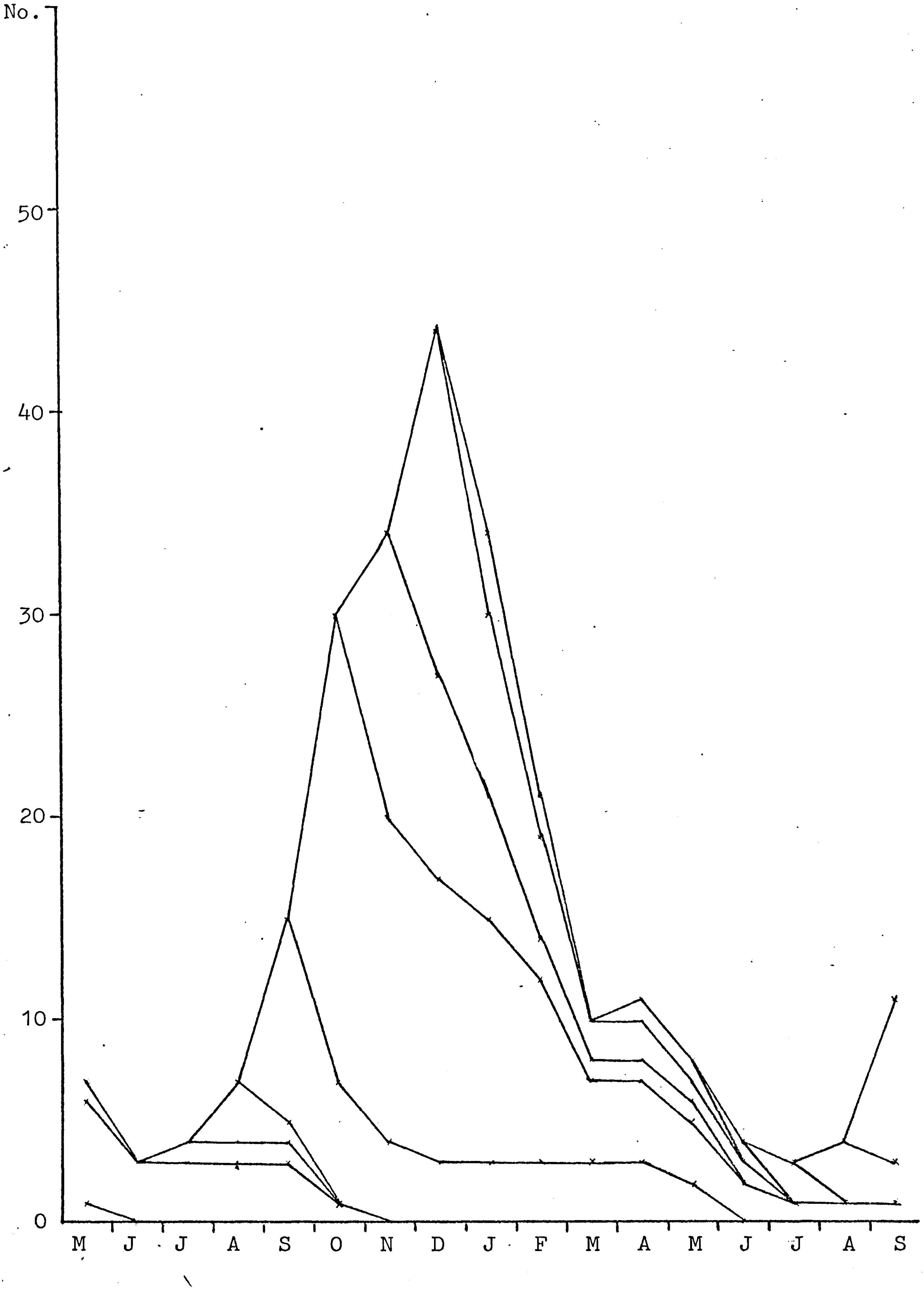


Figure 25 (iv)

A.sylvaticus
1969 - 1970

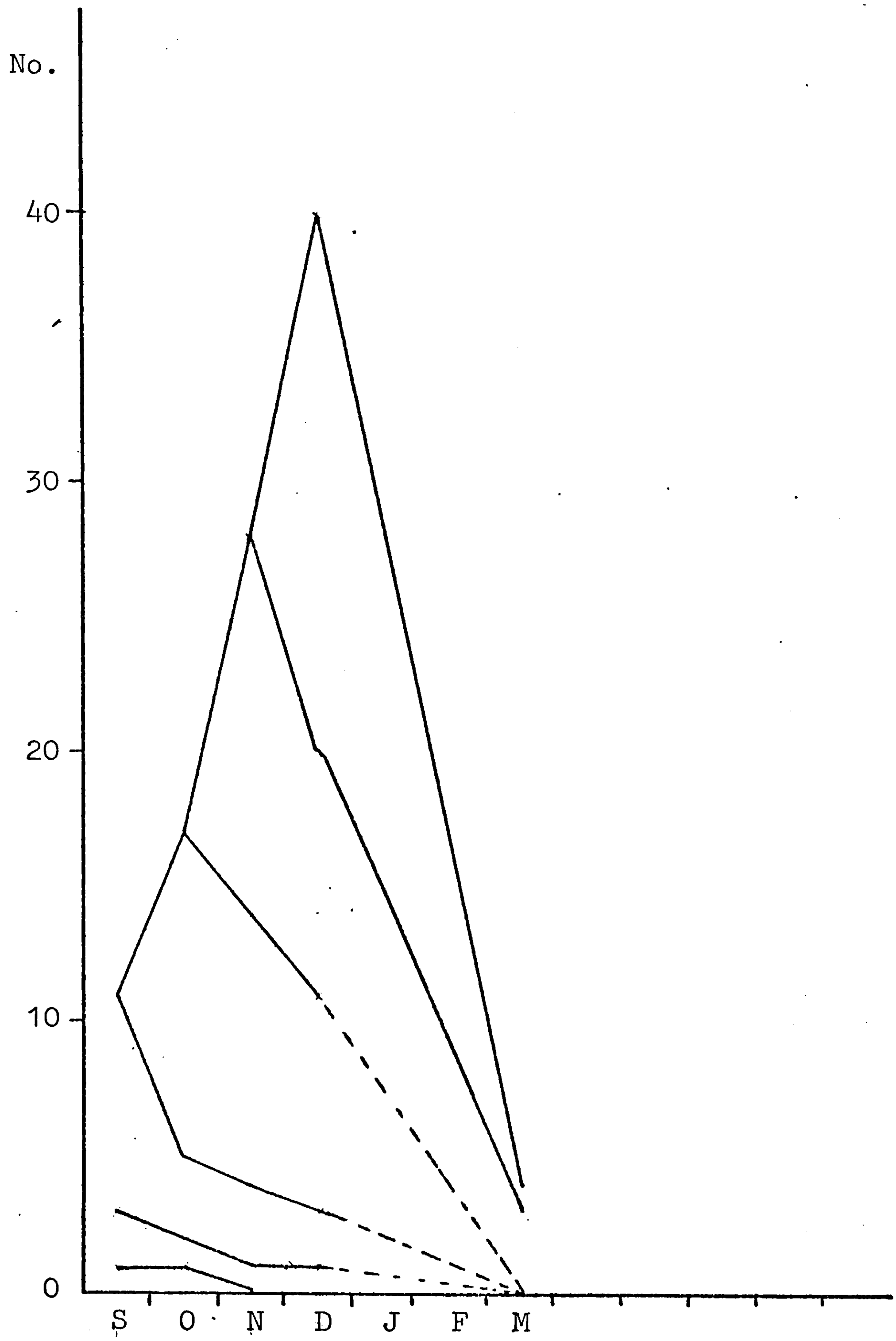


Figure 25 (v)

A.flavicollis

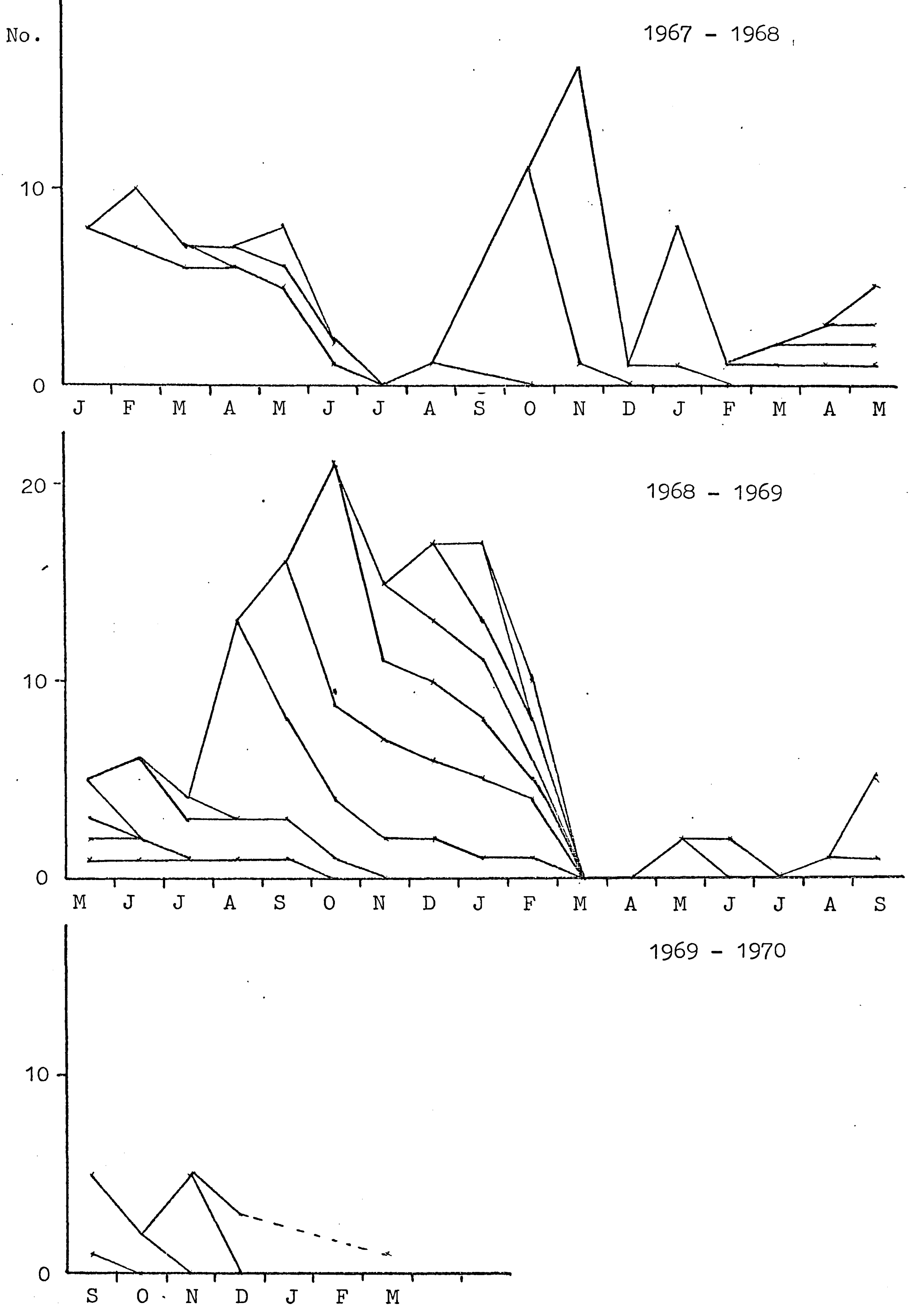


Figure 26 Seasonal changes in body weights of *Apodemus*

The body weight was recorded to the nearest gram and in the diagrams the mice are grouped in two gram weight classes. The width of the blocks indicates the percentage in that weight class during the month in question. Data from both main study grids and from all years of the study were grouped to prepare these figures. Where less than 5 mice were weighed in a month the dots indicate into which weight classes they fell.

Figure 26 (ii)

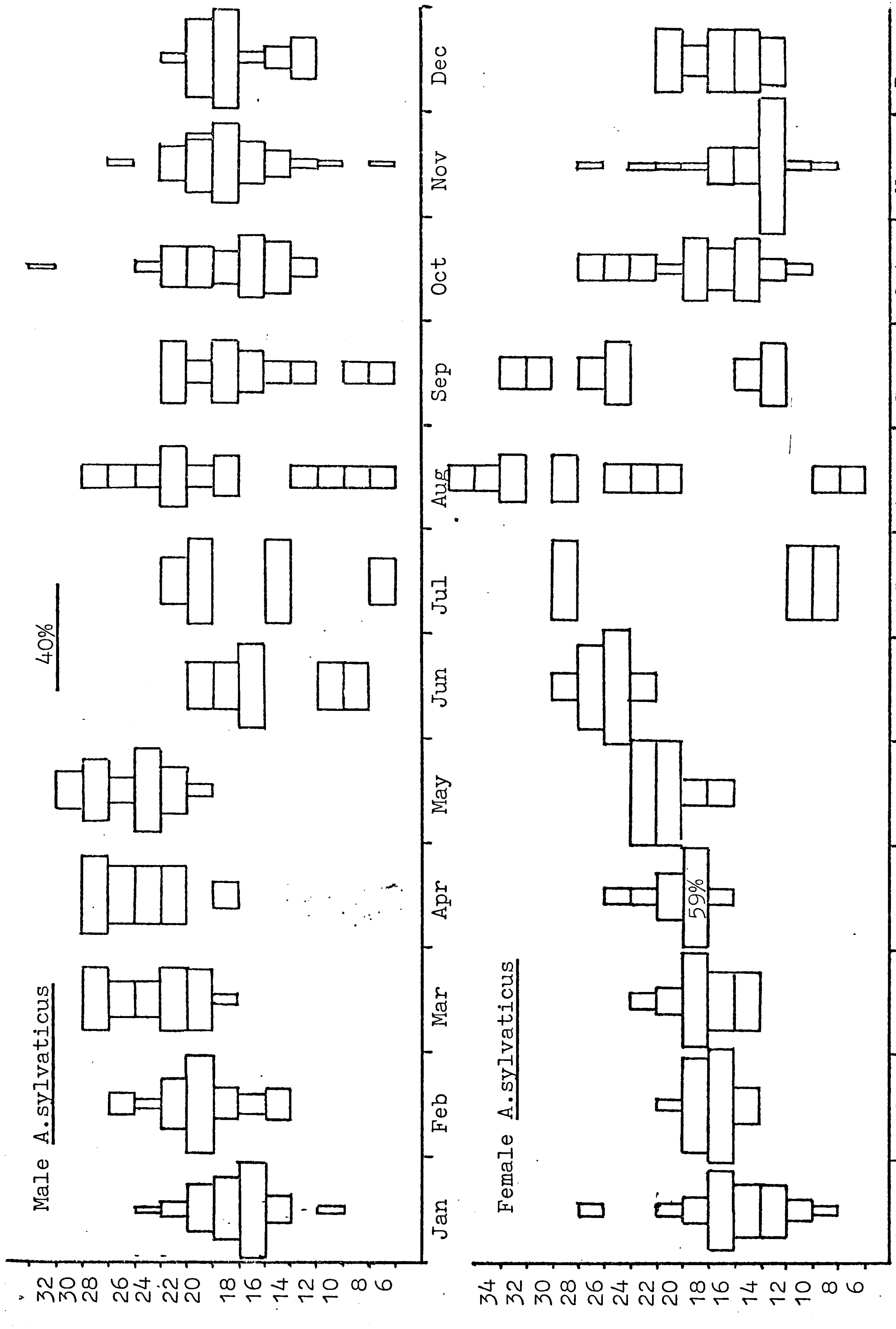

Male A.sylvaticus
40%
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
32
30
28
26
24
22
20
18
16
14
12
10
8
6
Female A.sylvaticus
59%
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6

Figure 26 (iii)

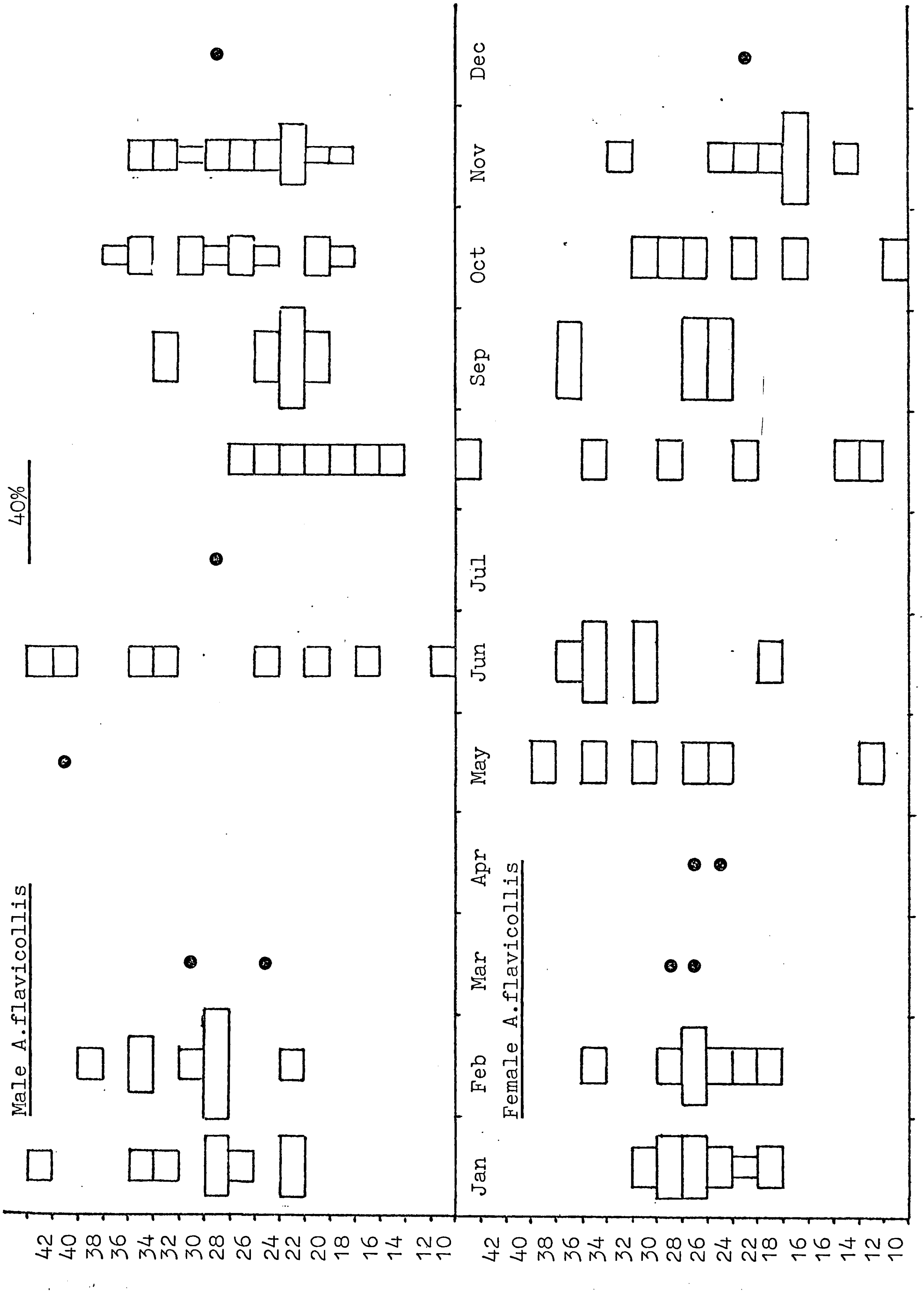
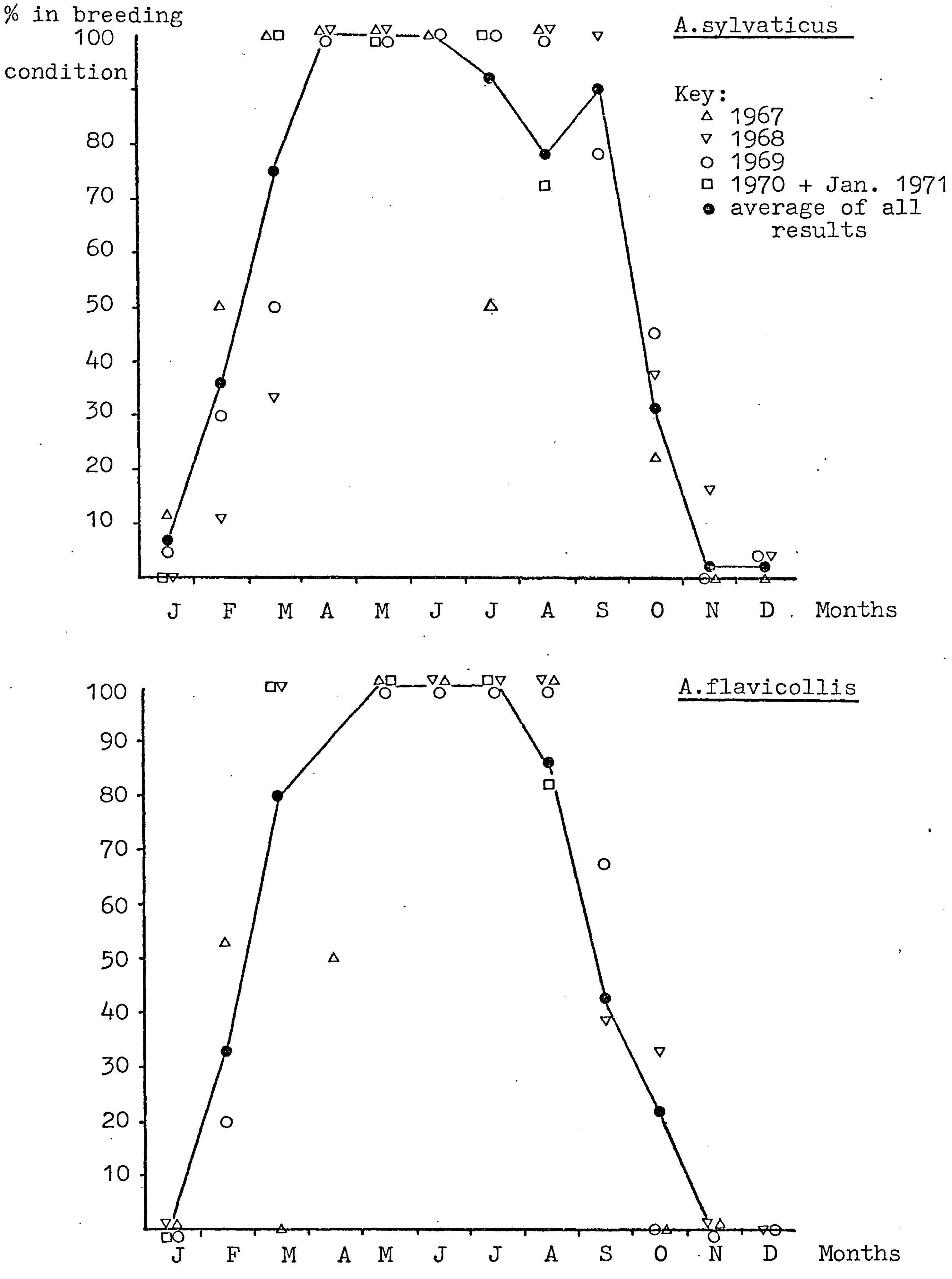
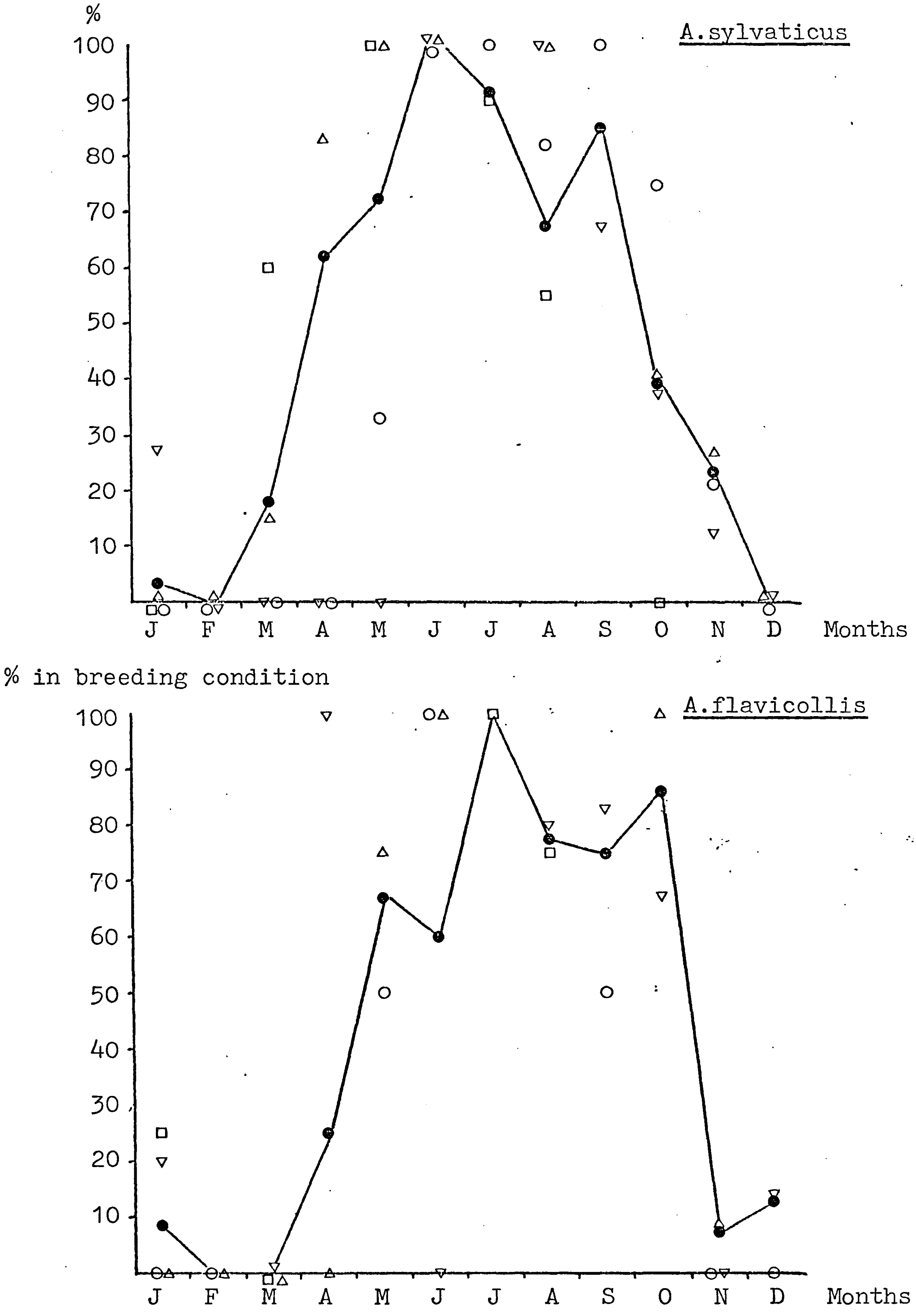


Figure 27 Breeding cycle of male *Apodemus*



See section 3.8.2 of text for method of identifying breeding condition. Only adult animals were counted.
Table 17 contains the figures from which these percentages were calculated.

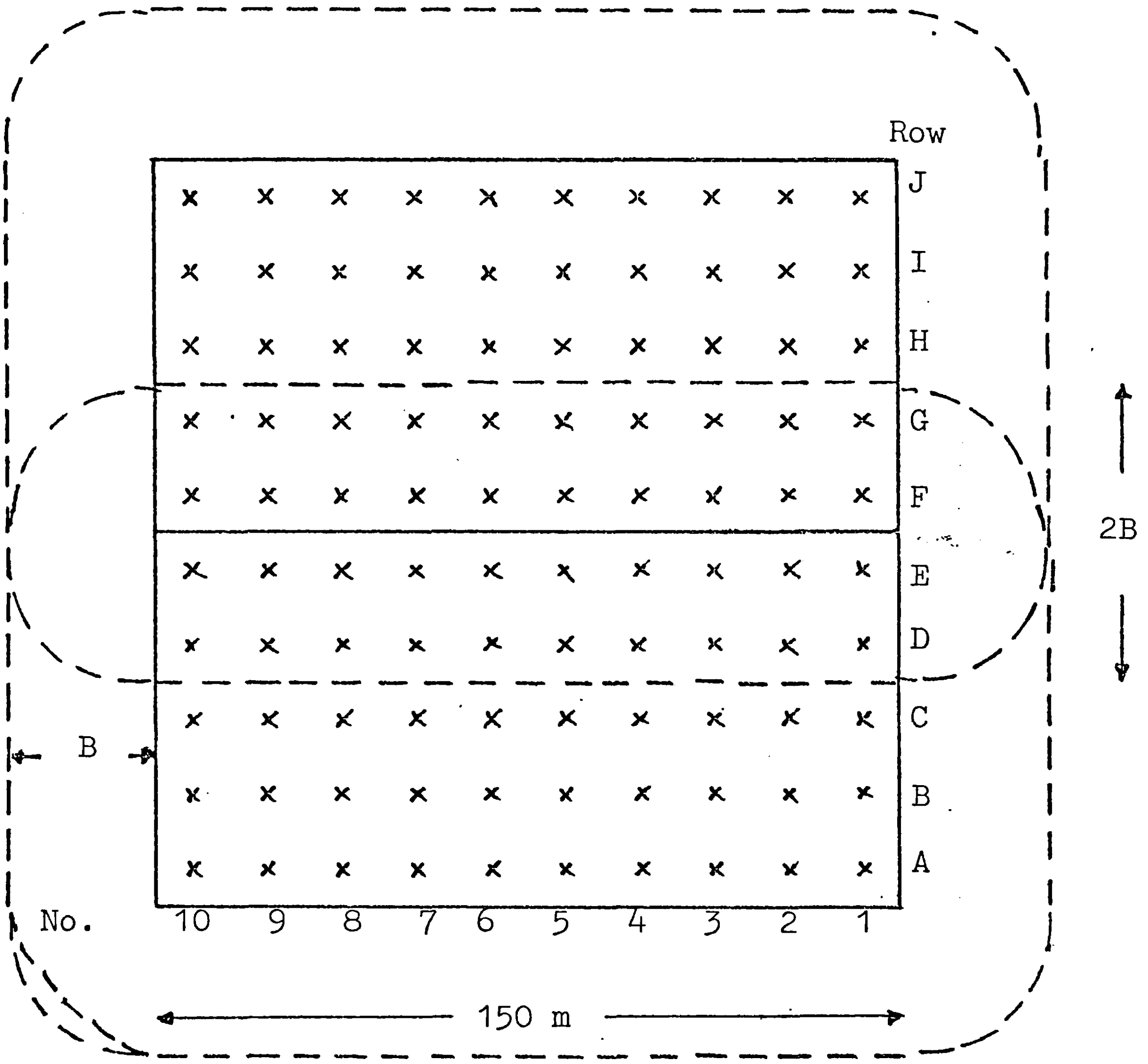
Figure 28 Breeding cycle of female Apodemus



See key and notes on figure 27

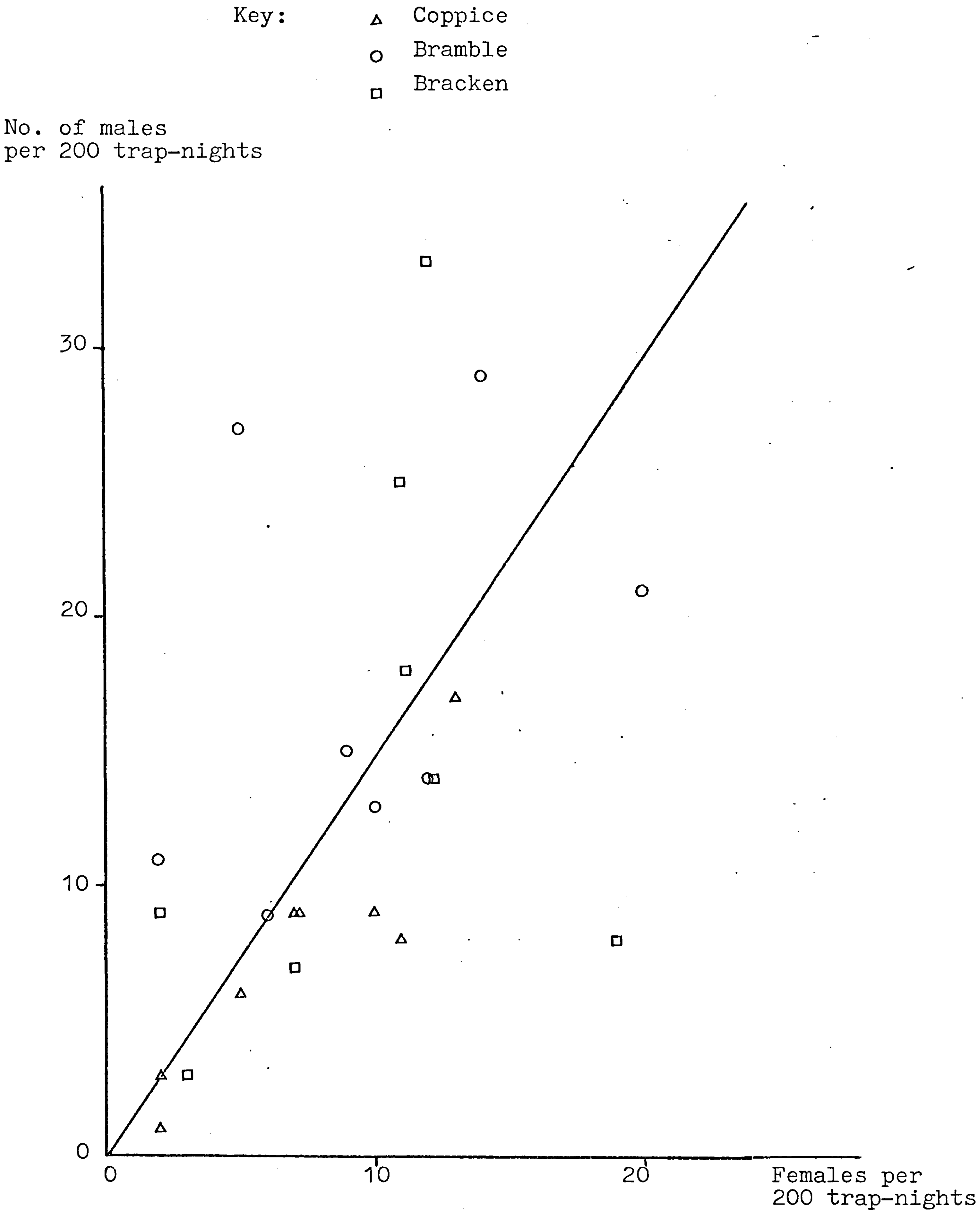
Figure 29 Method of calculating boundary strip size.

The trap-points (15m apart) are marked X
The two adjacent grid halves are outlined by solid lines
The area sampled by each grid half is outlined by interrupted lines



The method for the calculation of the value of 'B' is given in section 3.9.3 of the text.

Figure 30 Sex ratios in *A.sylvaticus* captures in the three King Wood habitat types.



Note: the data on which this graph is based is tabulated in table 22. Each point represents the captures during one of the six monthly periods on one of the habitat areas, transformed to a 'catch per 200 traps' basis. The line represents the overall sex ratio in King Wood captures.

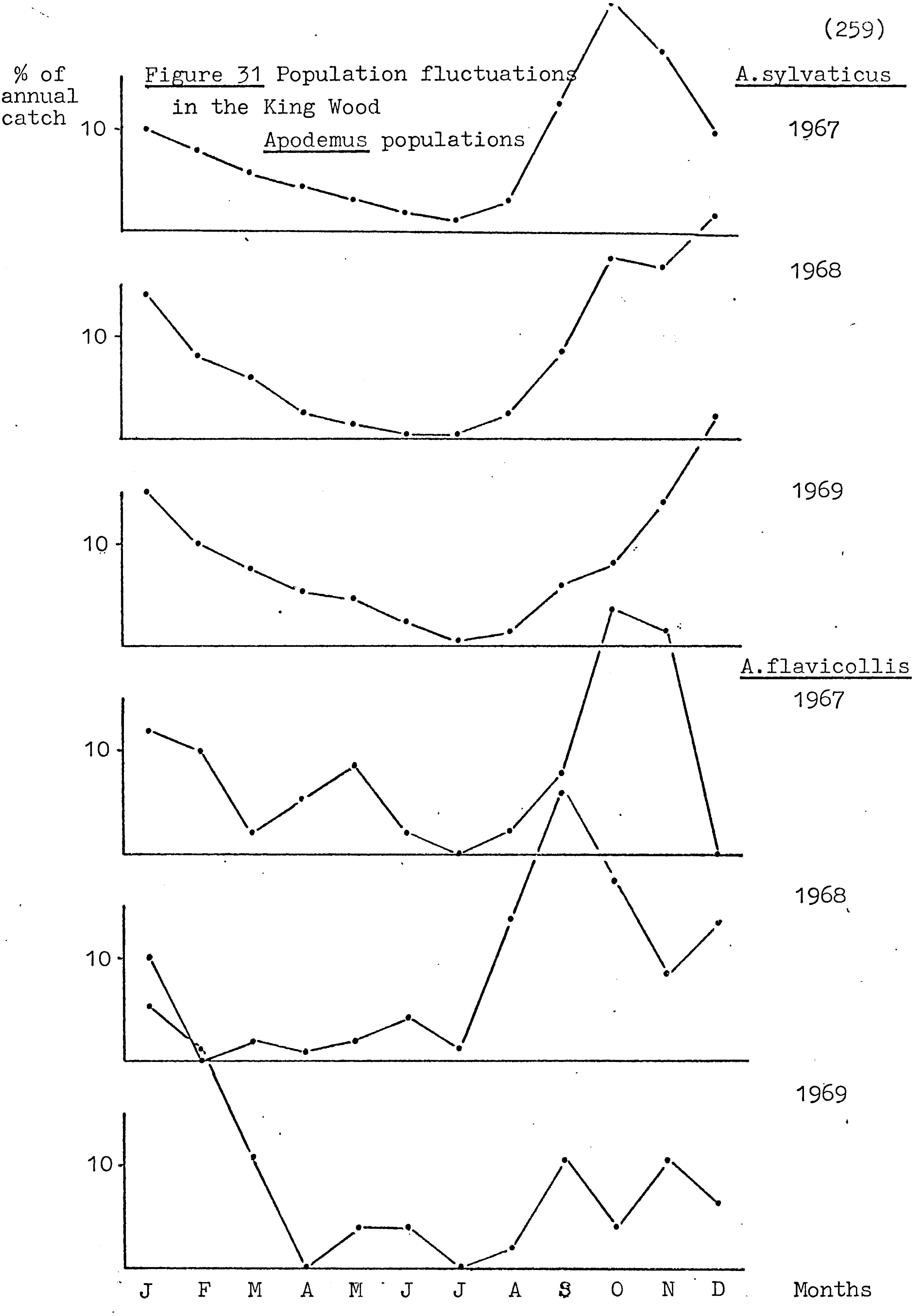


Figure 31 Population fluctuations in the King Wood *Apodemus* populations

Compare with the results from published sources - see figure 6.

See sections 2.5 and 3.12 of text for an explanation of the methods used in calculating these percentages.

Figure 31 (ii) Average pattern of fluctuation in King Wood *Apodemus* populations

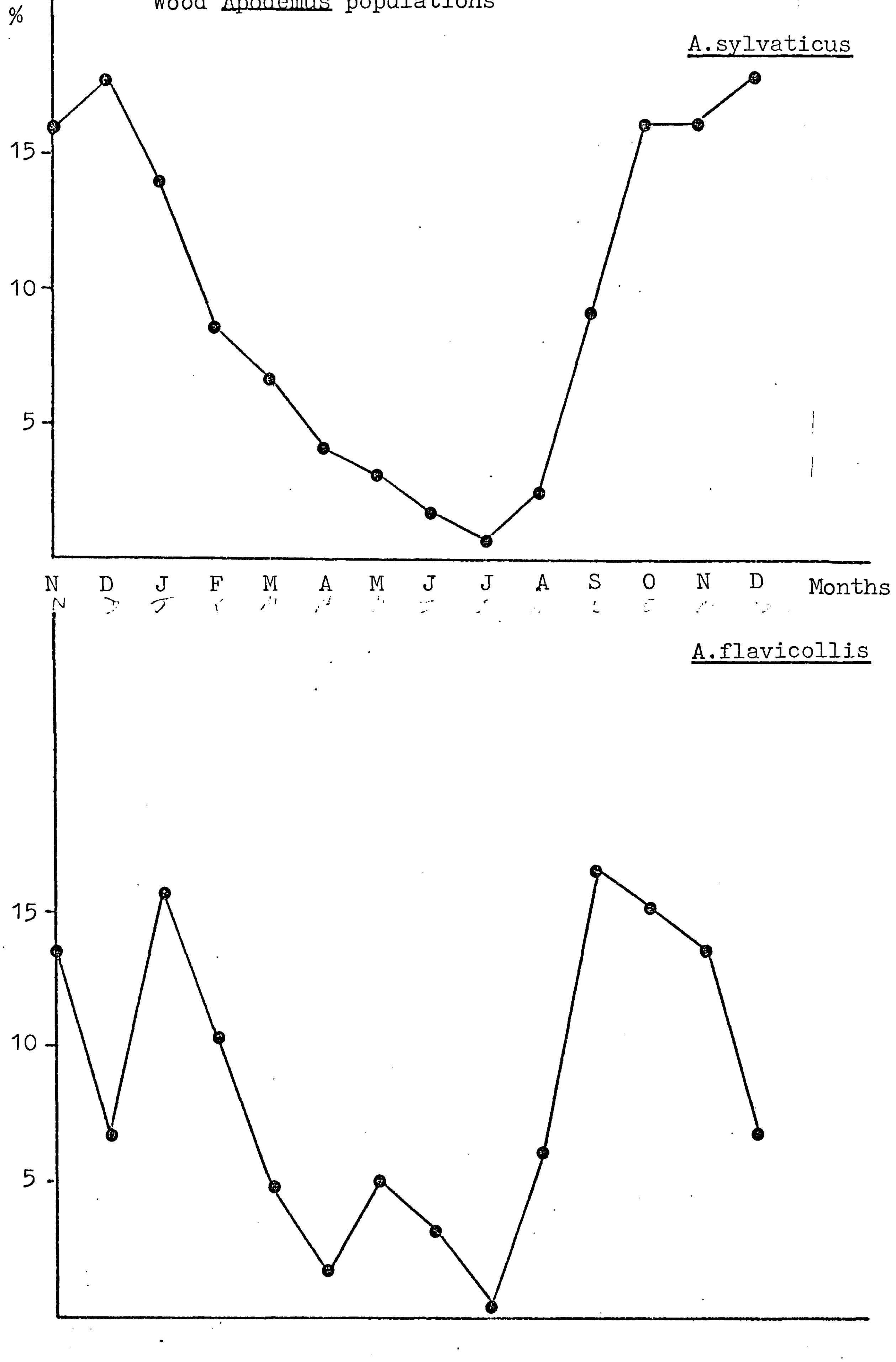


Figure 32 The distribution of *A.sylvaticus* in Essex

Key on page 264

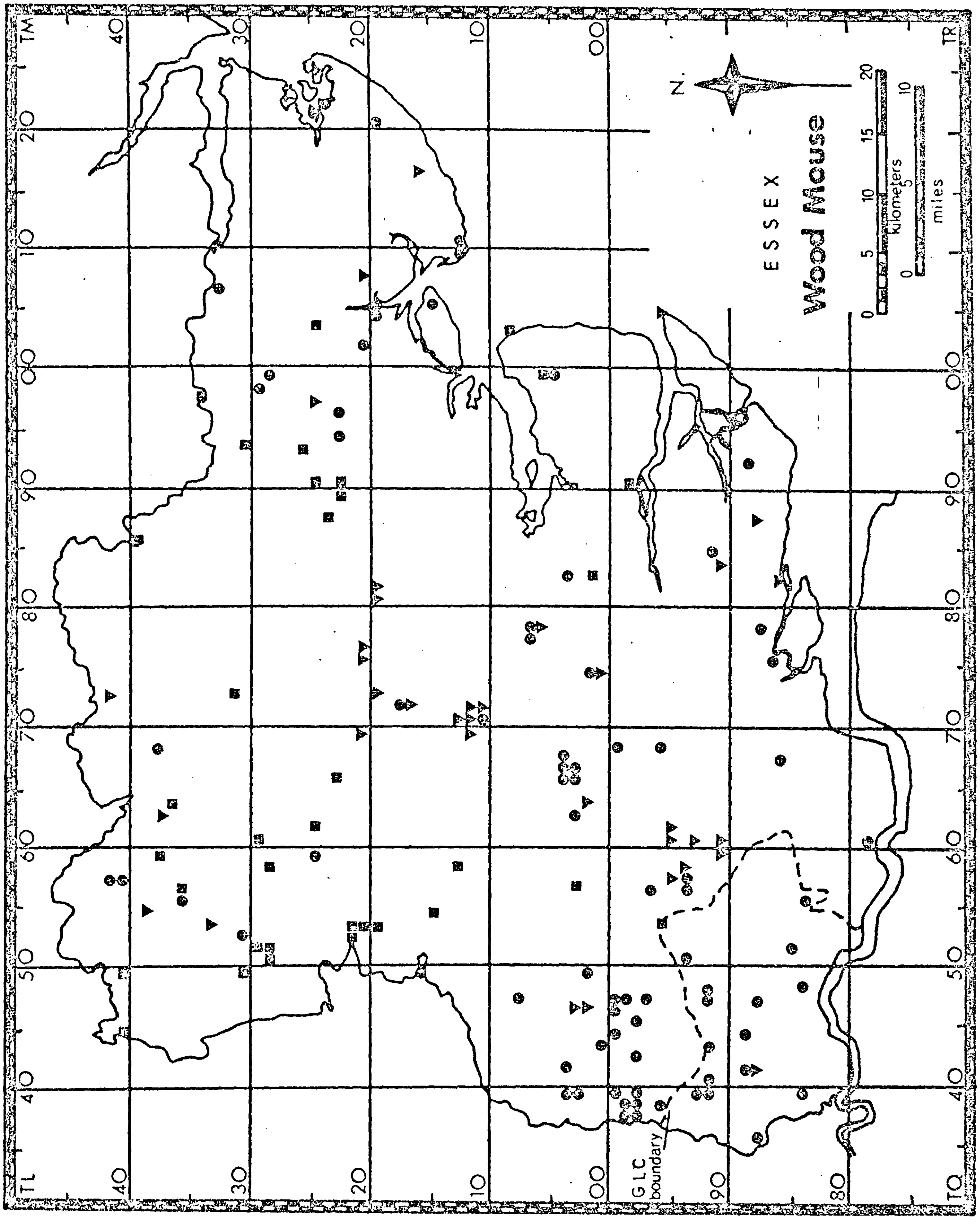


Figure 33 The distribution of A.flavicollis in Essex

Key on page 264

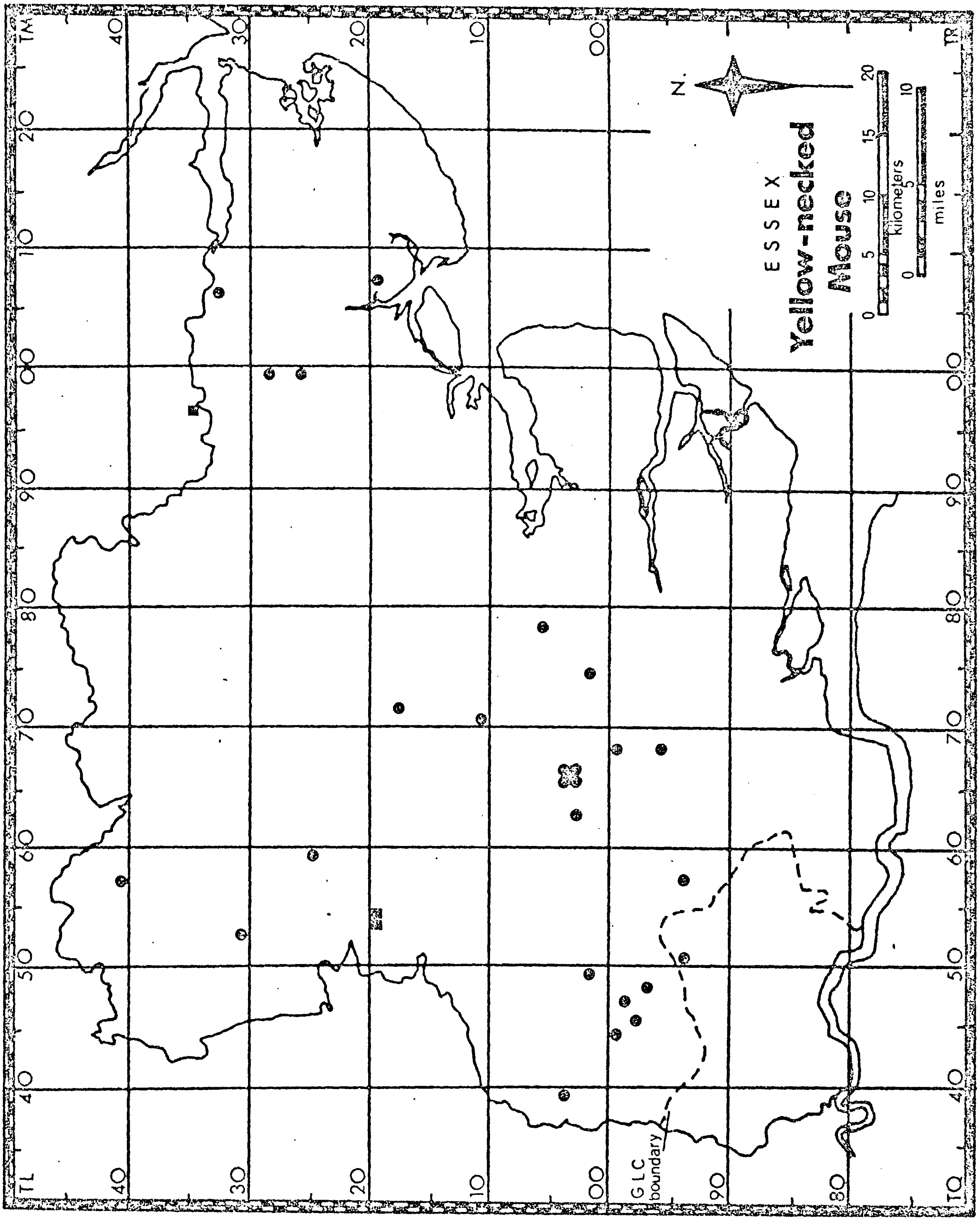
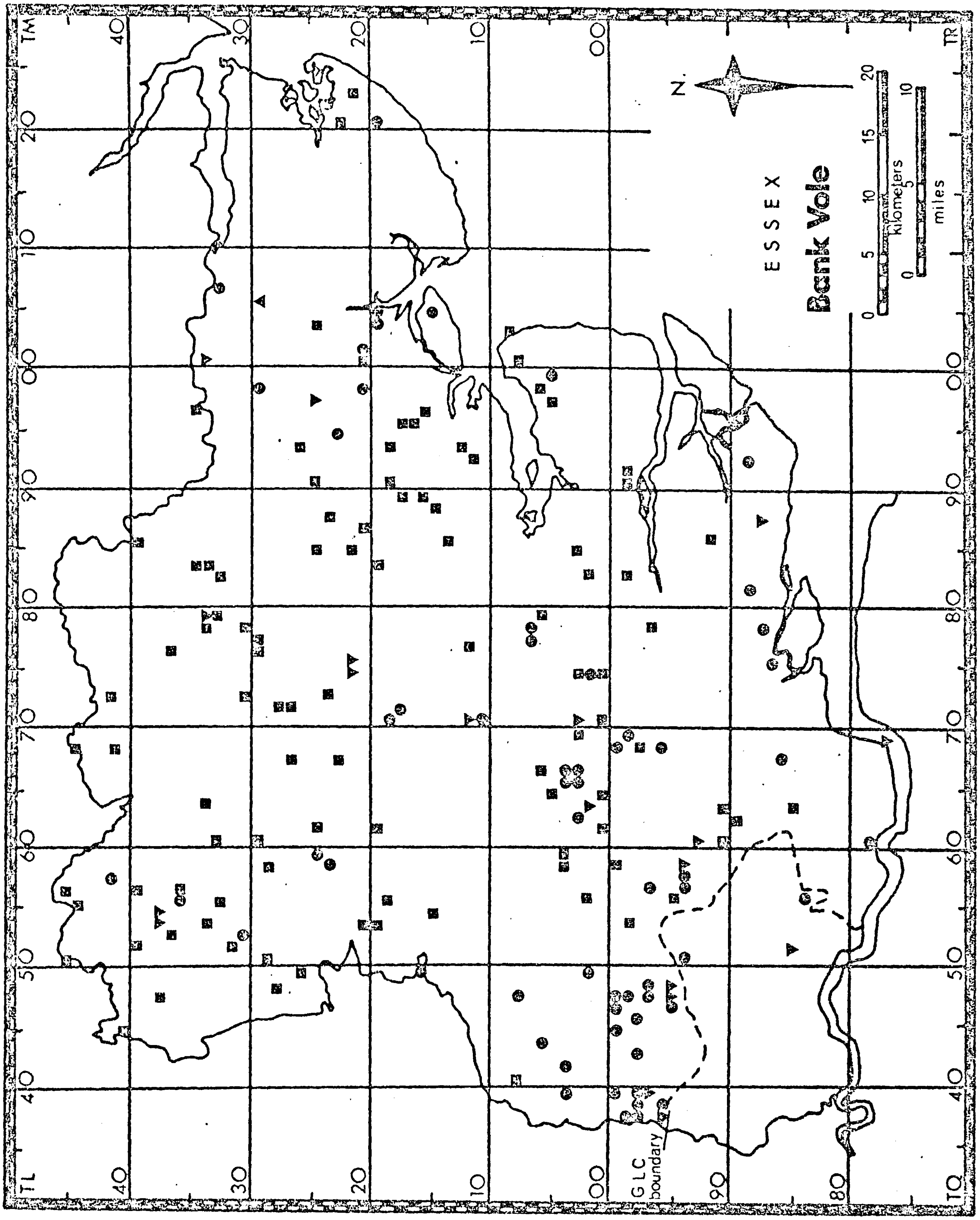


Figure 34 The distribution of *C.glareolus* in Essex

Key on page 264

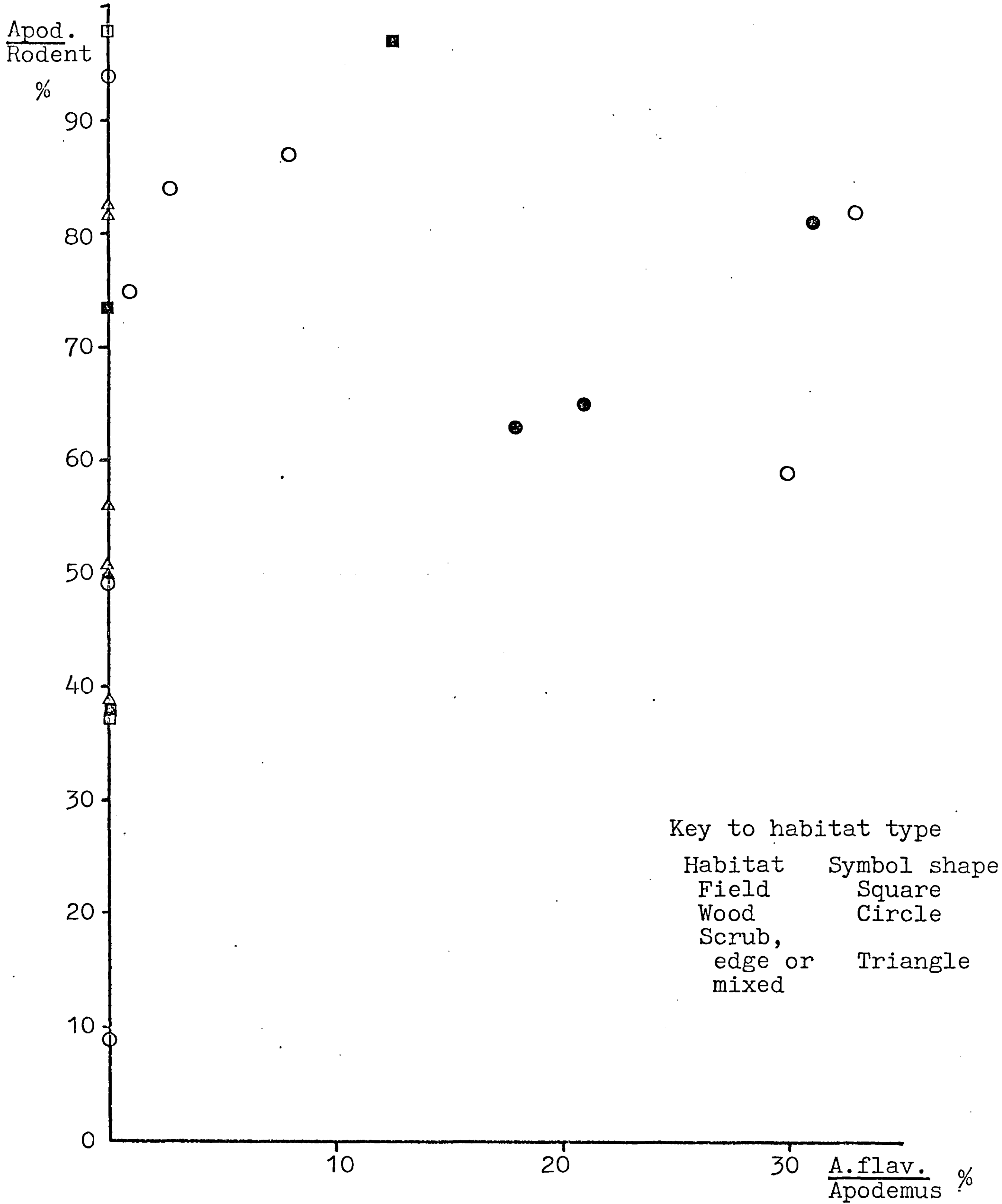


Key to Figures 32 - 34 The distribution of three rodent species in Essex

Each dot represents a 1 Km National Grid square for which at least one record exists in the period 1960 - 1972.
The types of record are indicated as follows:-

● Live trapping
■ Found dead in a discarded milk bottle
▲ Found in an Owl pellet
▼ Casual record - sighting, dead on road etc.

Figure 35 The relationship between the percentage of *Apodemus* in the catch of rodents and the percentage of *A.flavicollis* in the *Apodemus* catch



Solid symbols indicate results from intensive surveys (at least 80 rodent captures) and open symbols indicate results from the extensive survey with between 10 and 40 rodent captures per area.

Figure 36

see page 276

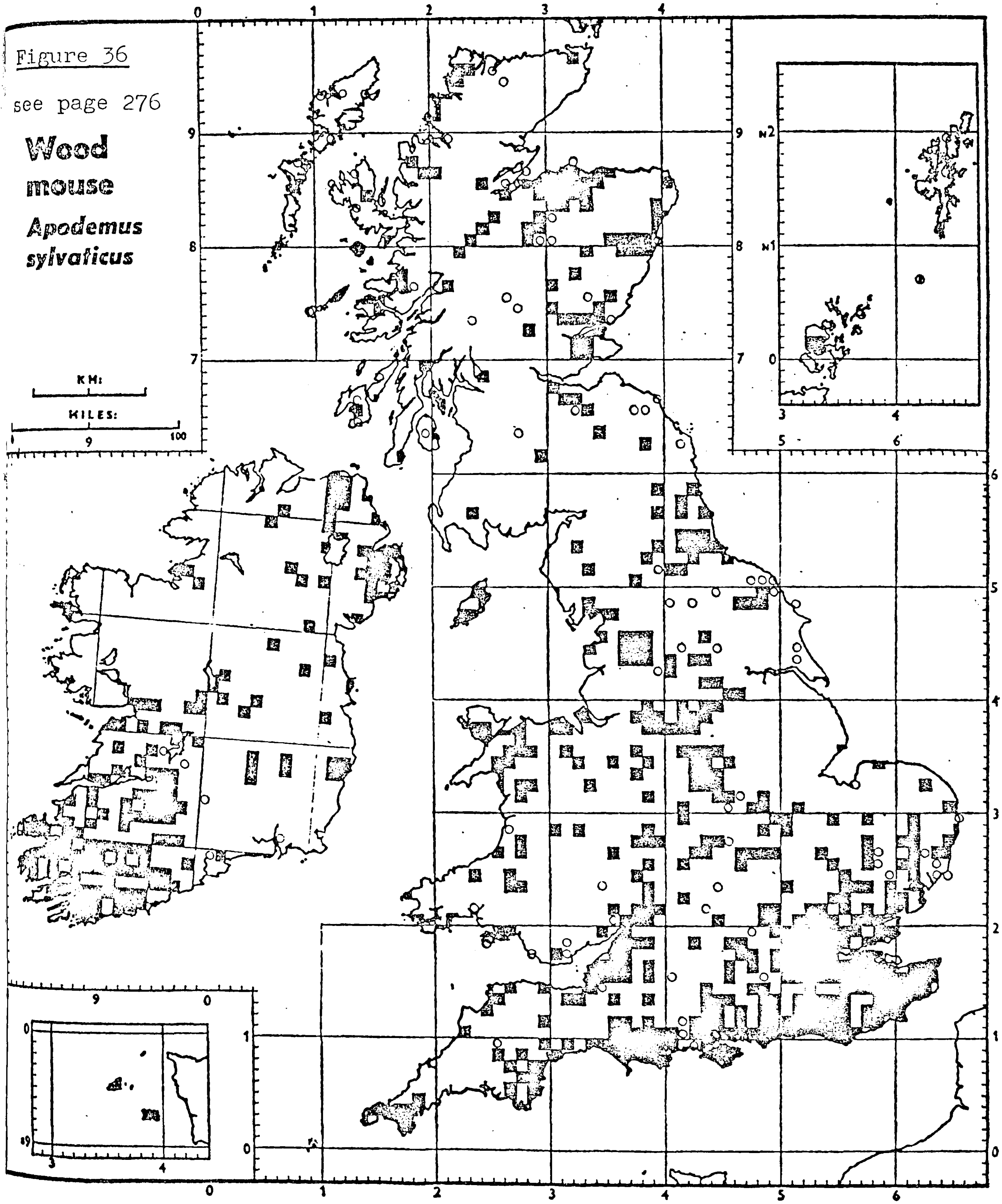
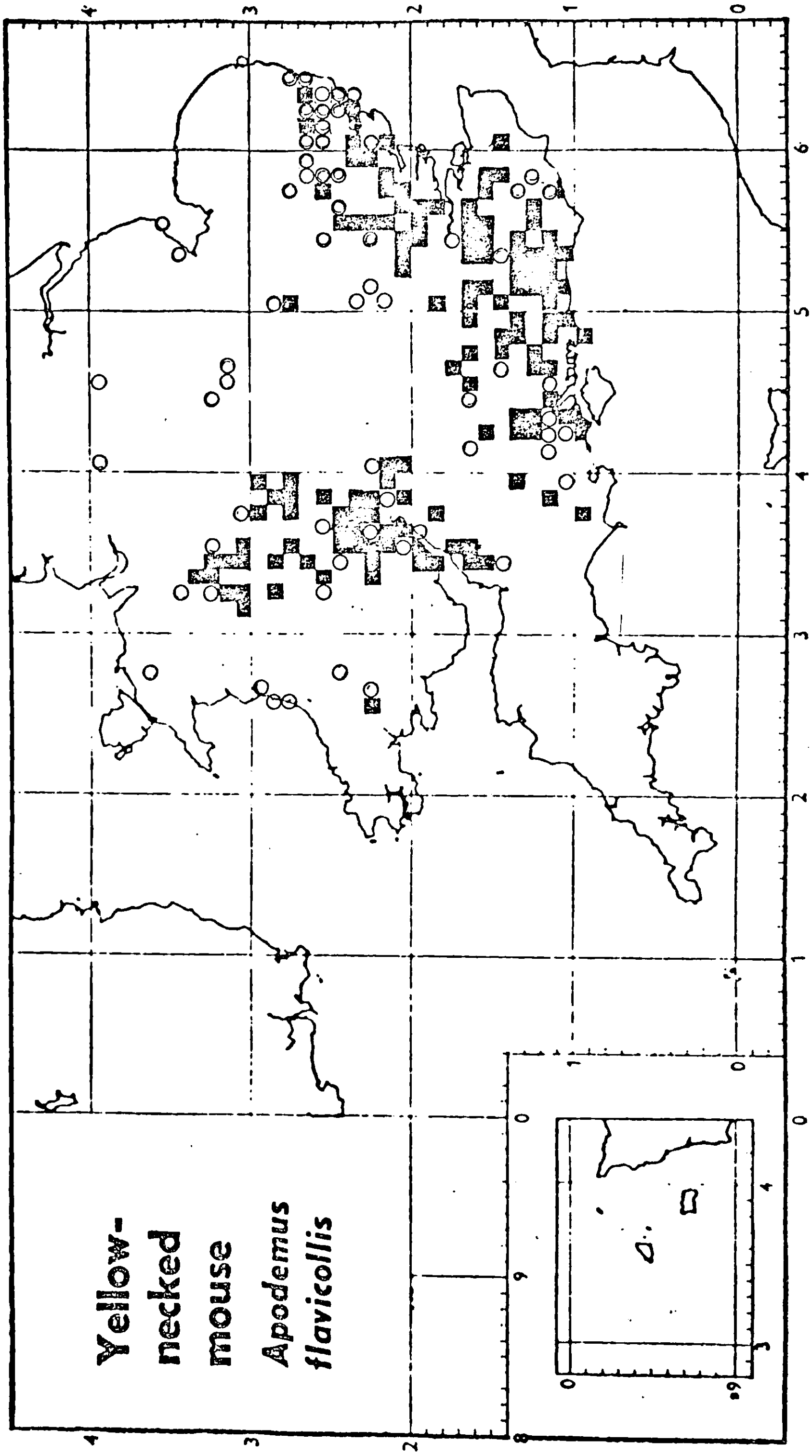


Figure 37 The distribution of A.flavicollis in the British Isles

(see page 276)



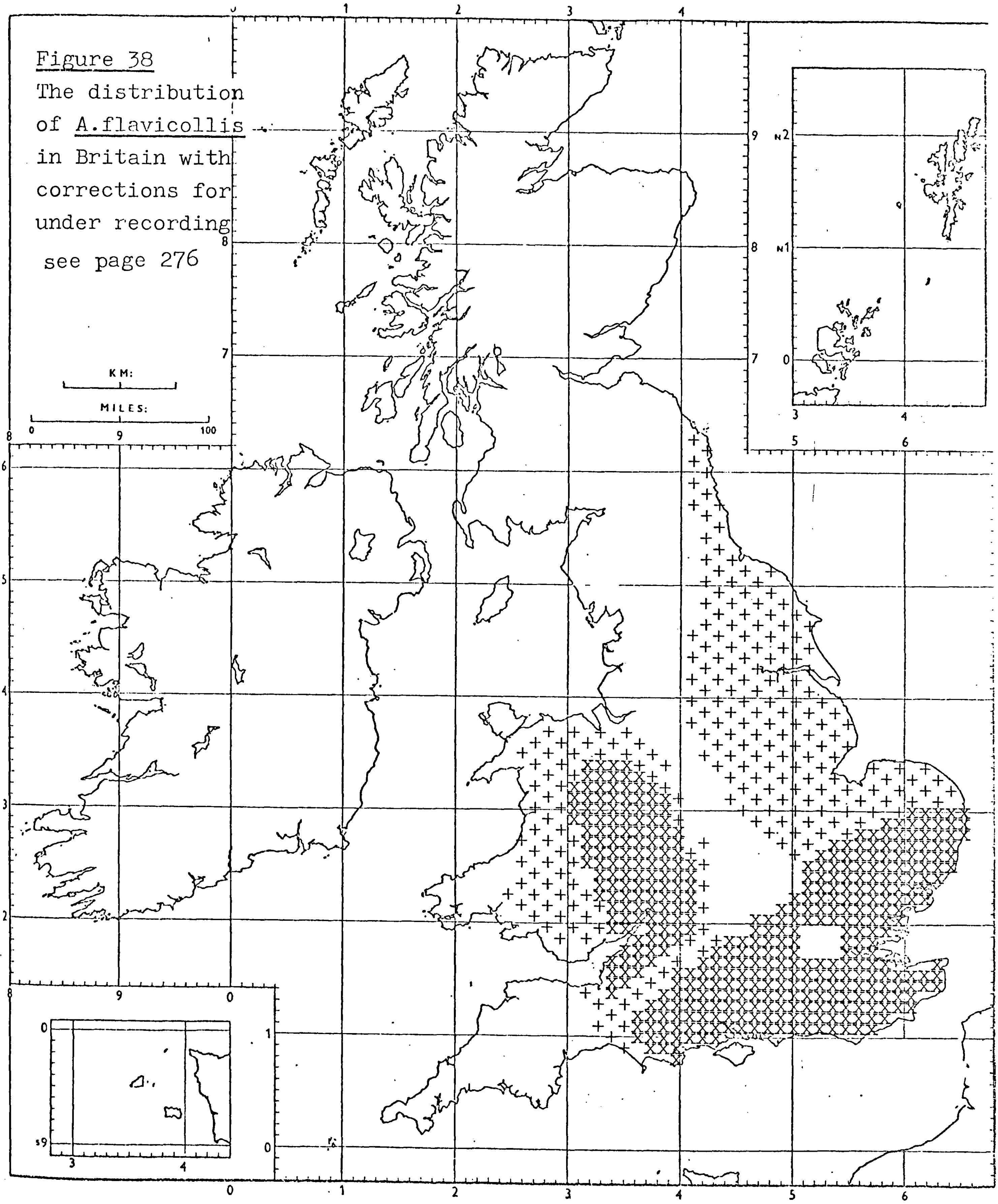
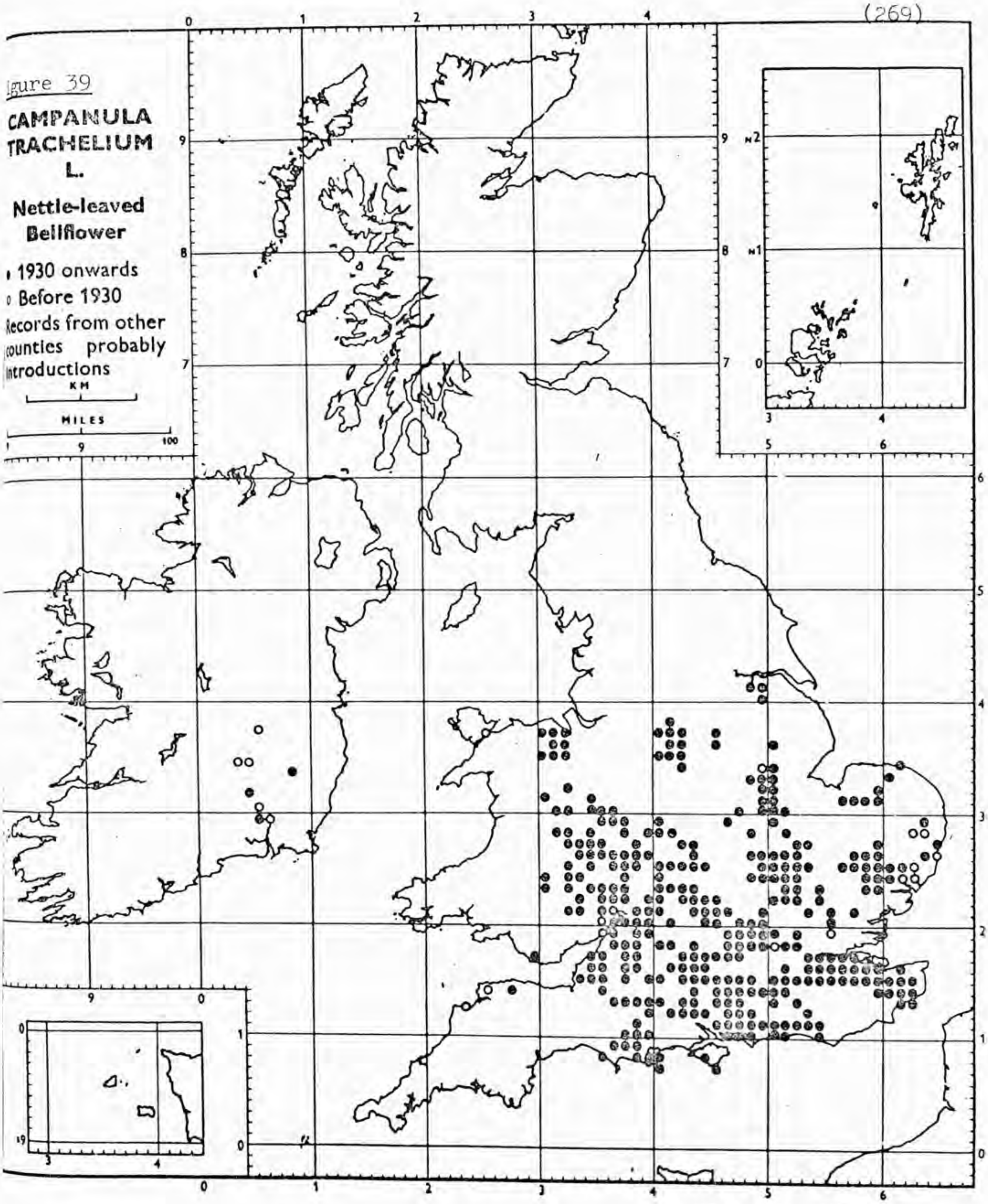


Figure 38
The distribution of *A.flavicollis* in Britain with corrections for under recording see page 276



igure 39

see page 276

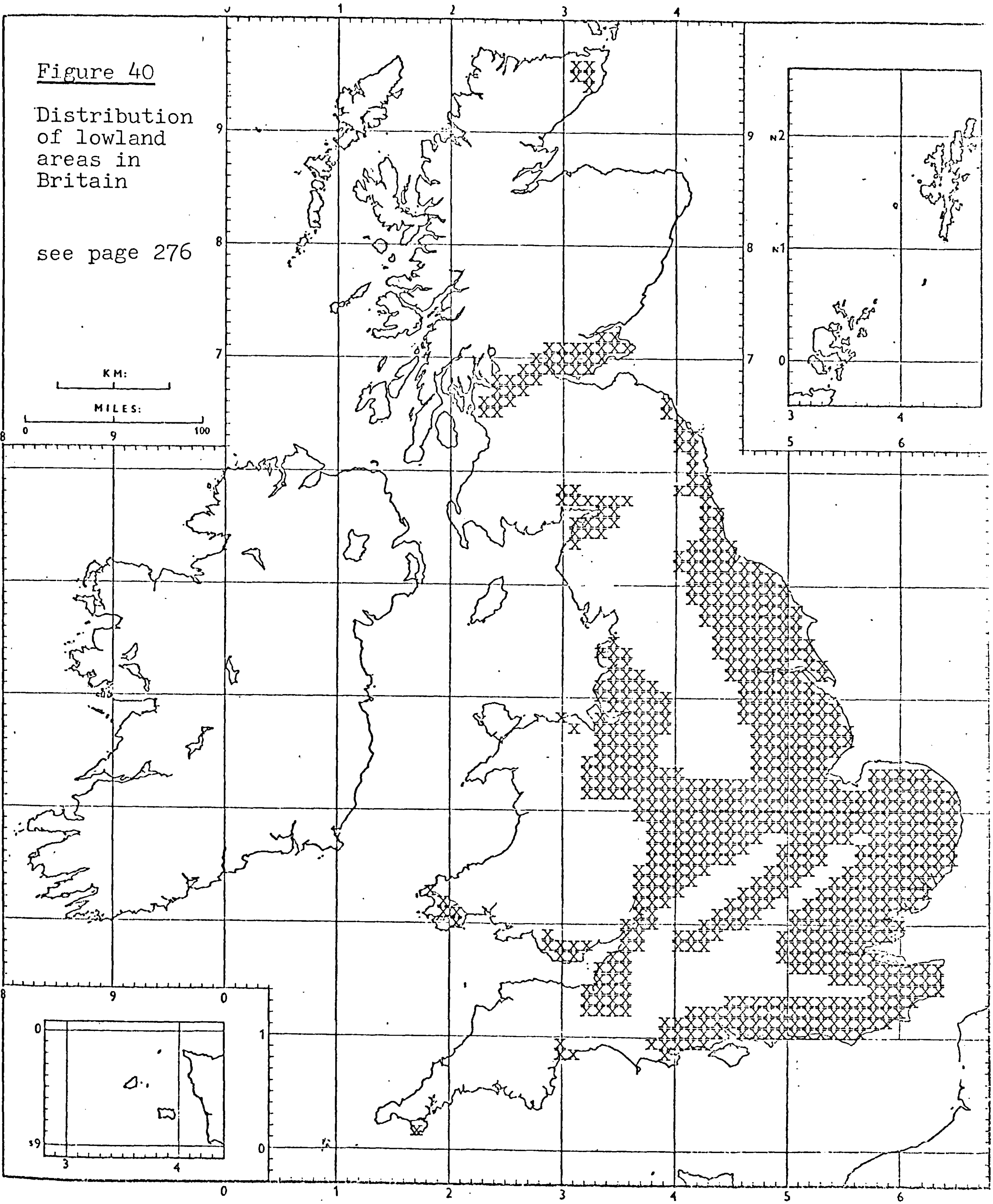


Figure 40

Distribution of lowland areas in Britain

see page 276

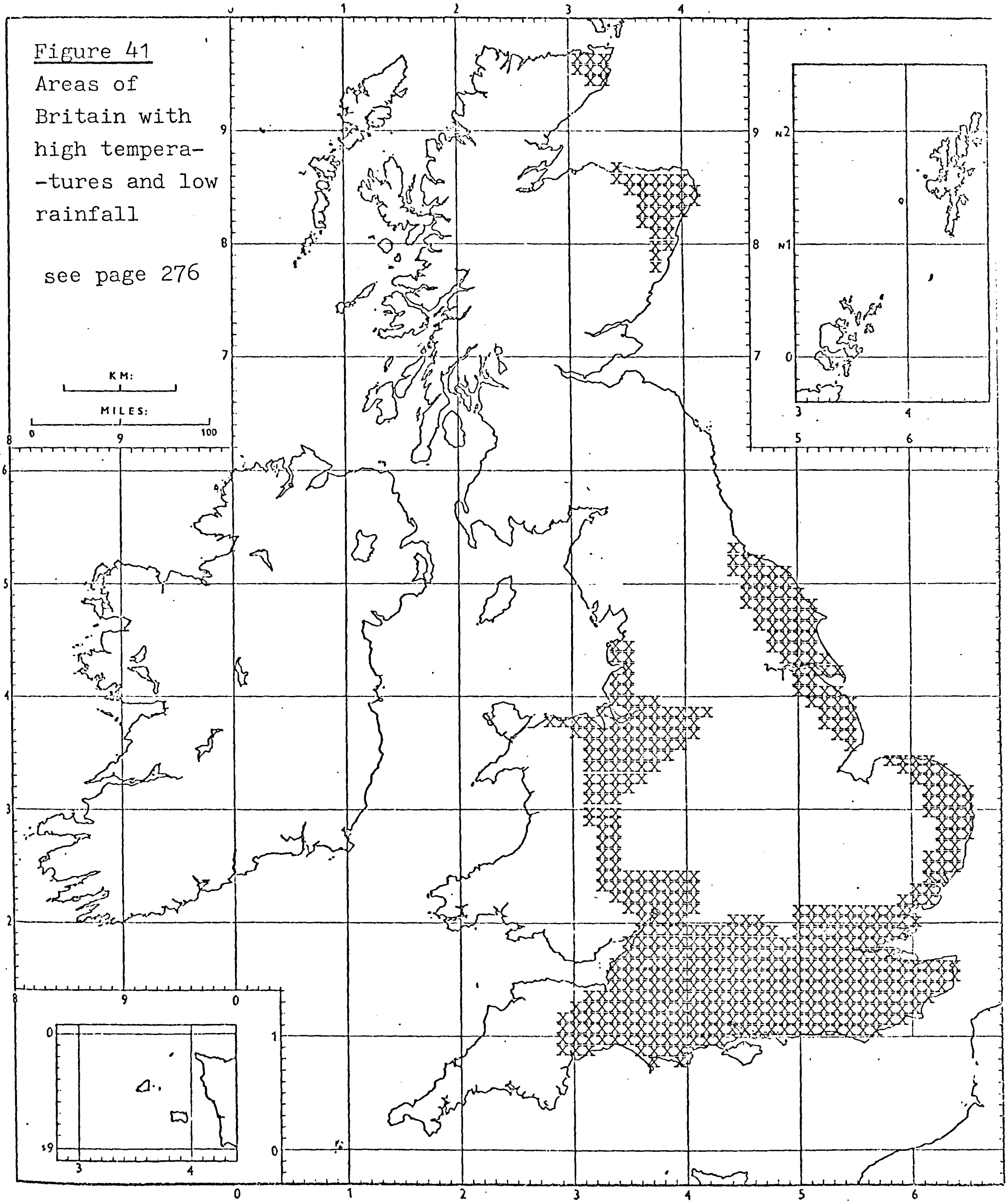


Figure 41
Areas of
Britain with
high tempera-
-tures and low
rainfall

see page 276

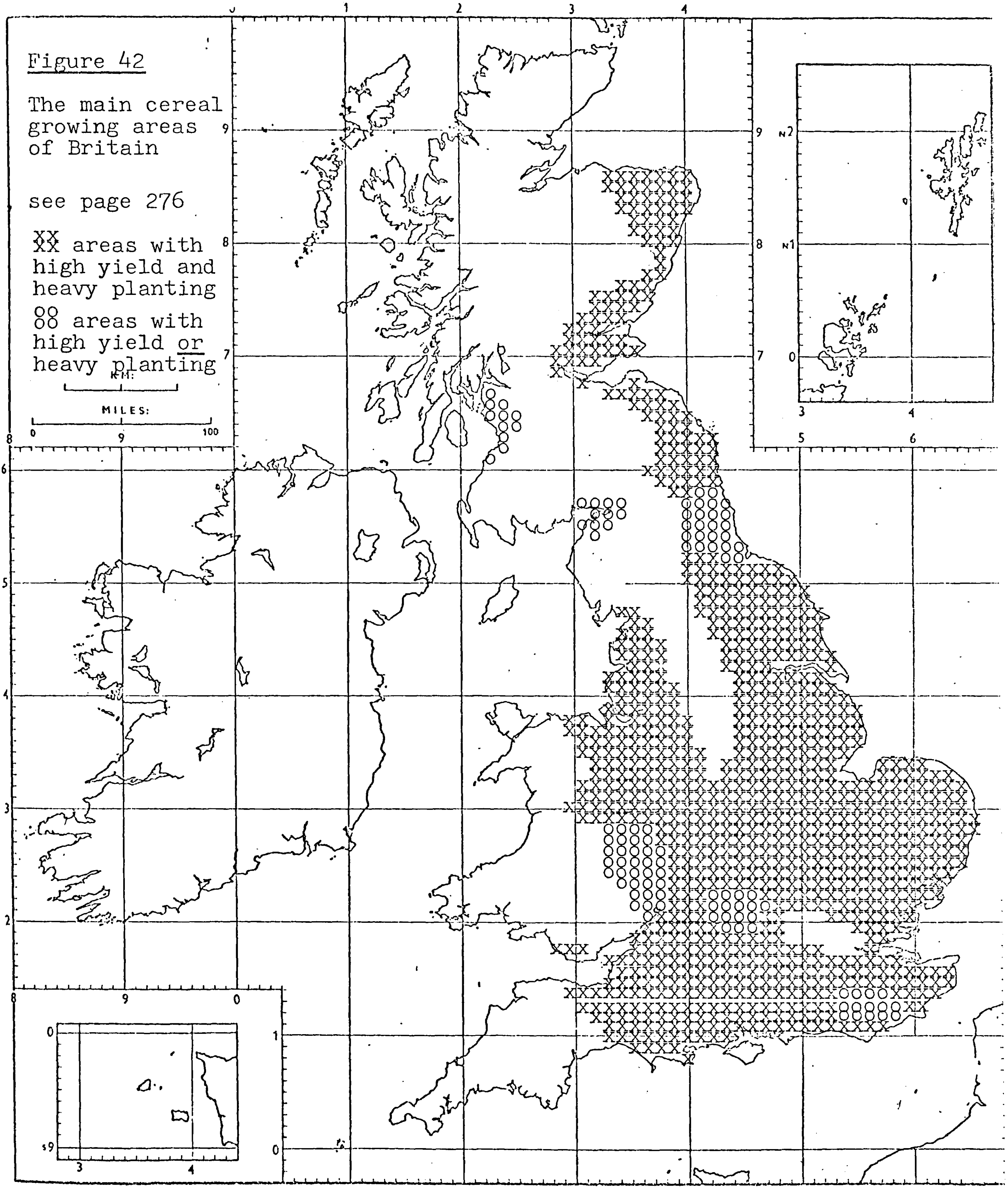


Figure 42

The main cereal growing areas of Britain

see page 276

XX areas with high yield and heavy planting

OO areas with high yield <u>or</u> heavy planting

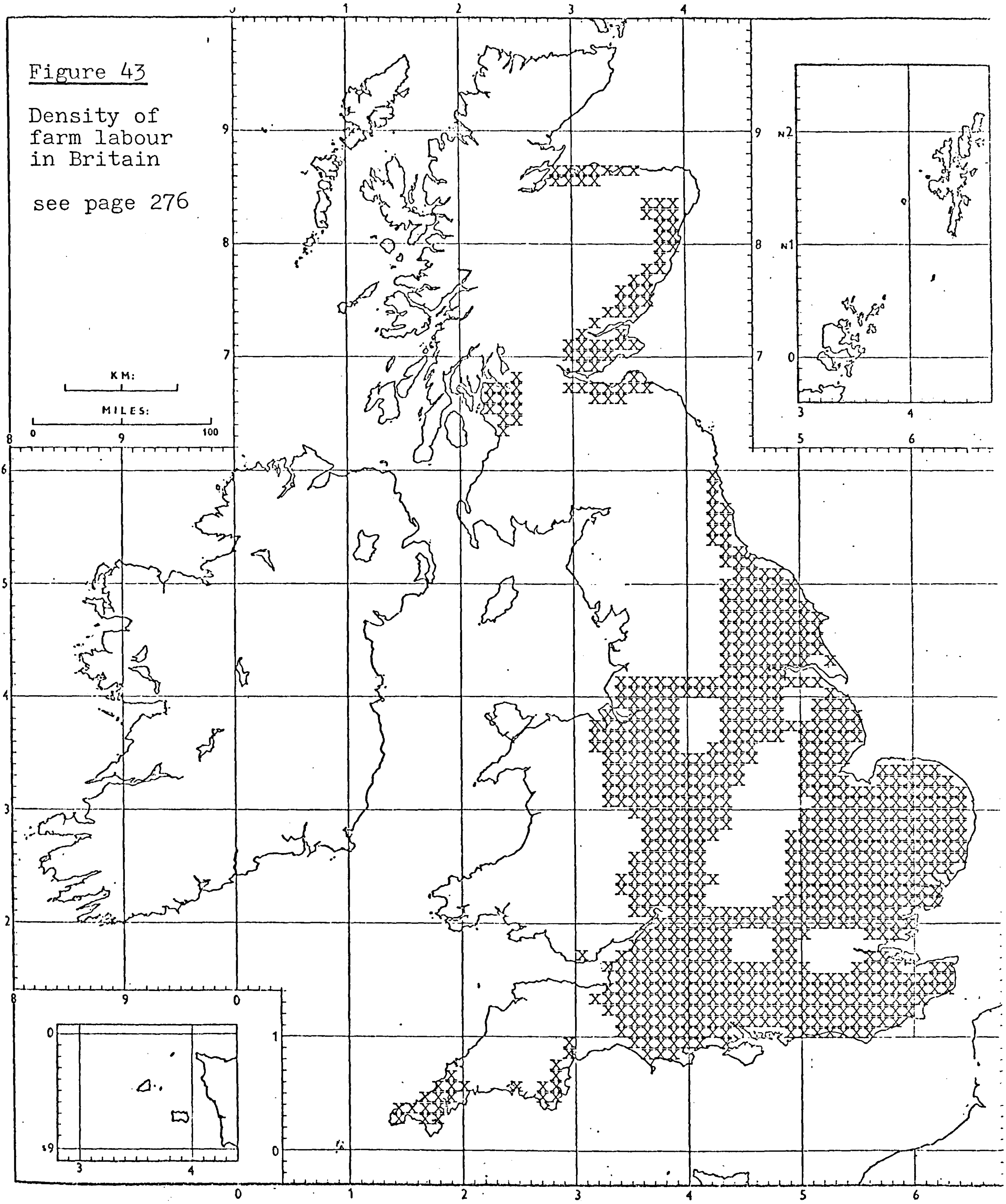


Figure 43

Density of farm labour in Britain

see page 276

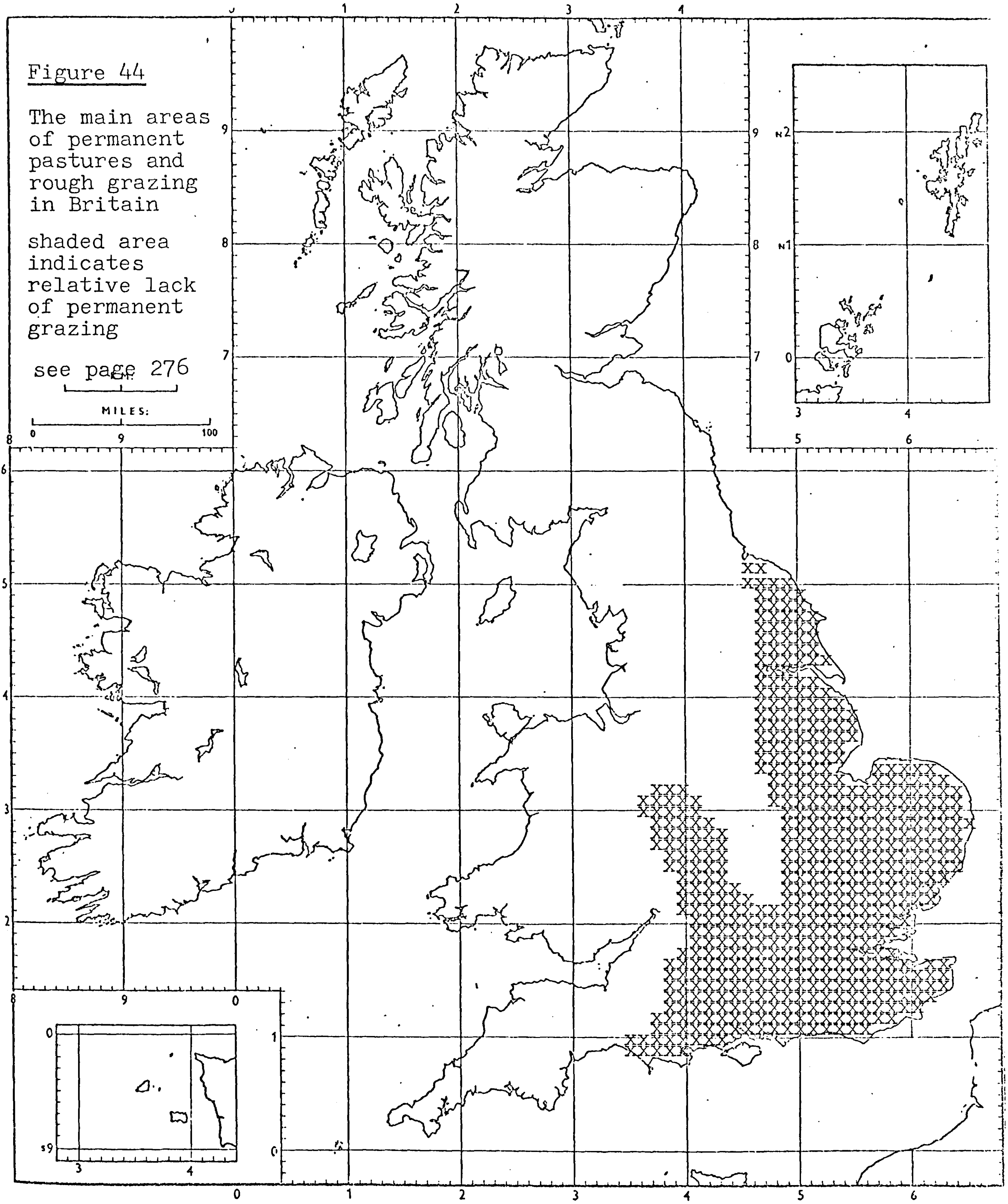


Figure 44

The main areas of permanent pastures and rough grazing in Britain

shaded area indicates relative lack of permanent grazing

see page 276

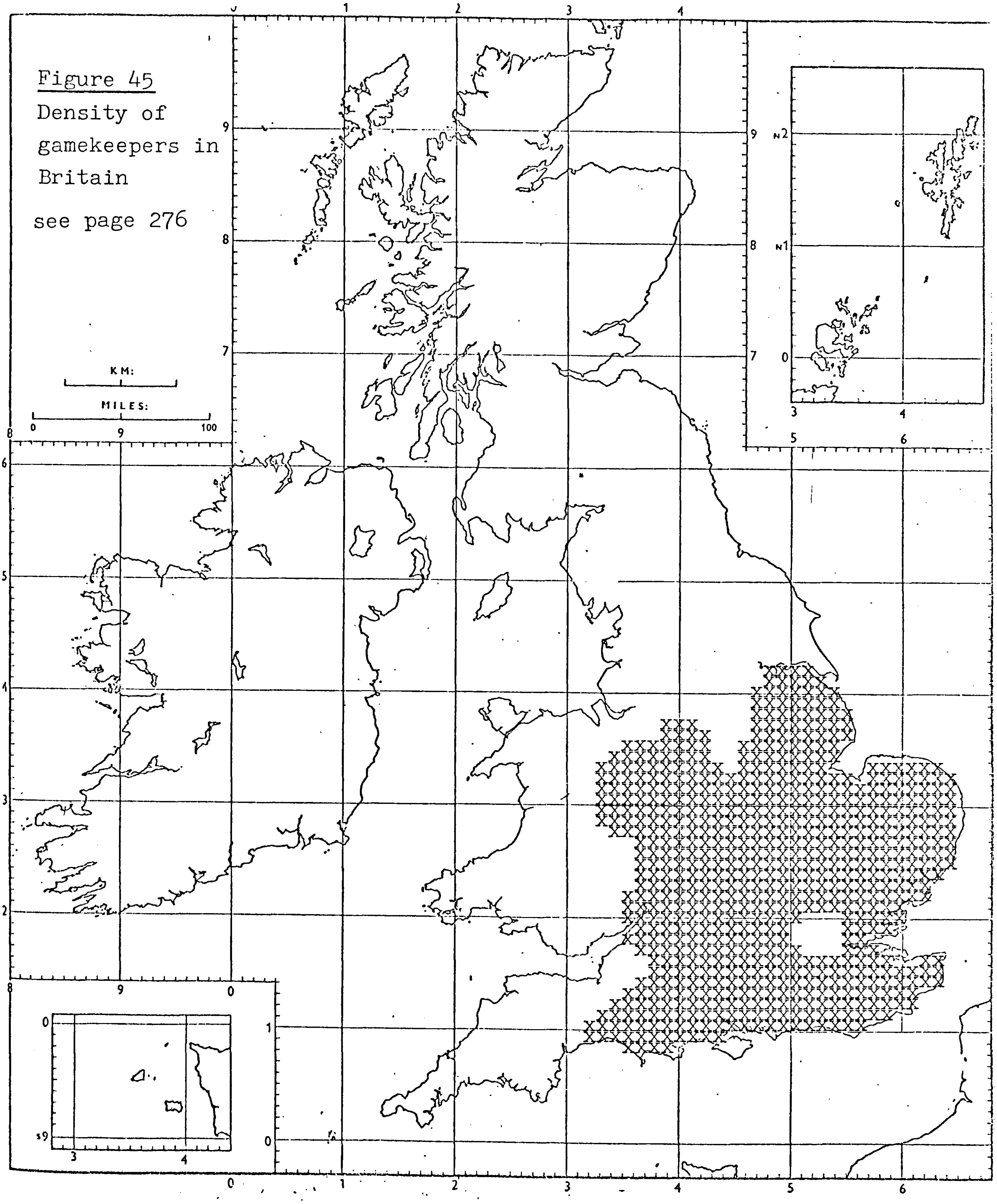


Figure 45

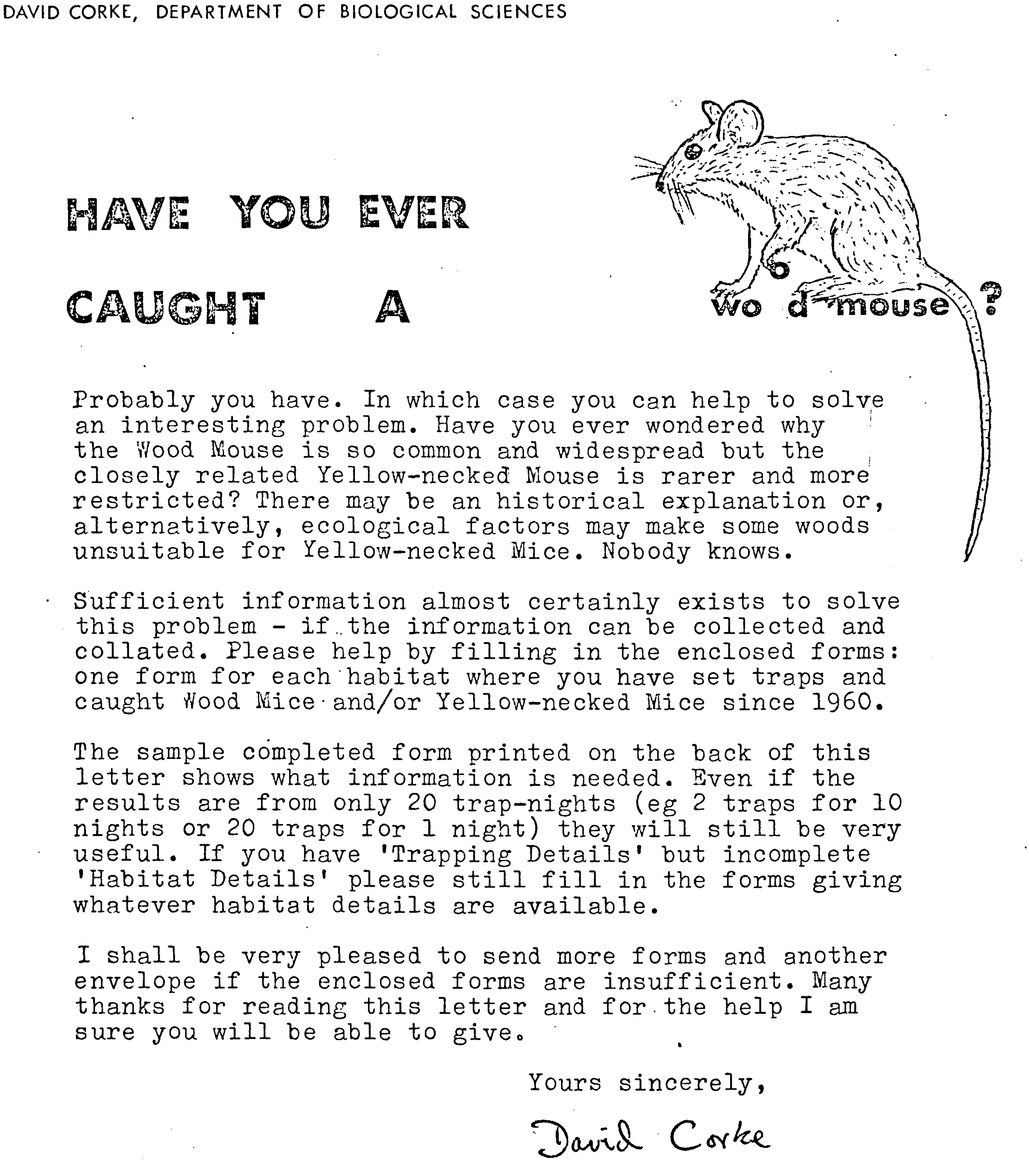
Density of gamekeepers in Britain

see page 276

Notes on figures 36 - 45

36. From Corbet (1971)
37. From Corbet (1971) with later corrections (Corbet personal communication).
38. Based on figure 37 but with allowances for under-recording. Dense hatching indicates areas where *A.flavicollis* is probably common, light shading where scattered colonies may occur.
39. From Perring and Walters (1962).
40. Simplified from the gradient map in Bickmore and Shaw (1963). Shaded area is fairly flat with much land below 100 feet above sea level.
41. Shaded area has a February mean temperature of 34.5°F or above *and* a mean annual rainfall below 40 inches. From the overlays in Perring and Walters (1962).
42. Shaded areas are important cereal growing areas. A combination and simplification of the Wheat, Barley and Oats maps in Bickmore and Shaw (1963).
43. Shaded area has 1.5 or more farm labourers per 100 acres. Simplified from Bickmore and Shaw (1963).
44. Simplified from Bickmore and Shaw (1963).
45. Shaded area has one or more gamekeepers per 100 sq. miles. Simplified from Mellanby (1967).

Figure 46 Copy of letter sent to prospective participants in the national distribution survey of *Apodemus*.



DAVID CORKE, DEPARTMENT OF BIOLOGICAL SCIENCES

HAVE YOU EVER CAUGHT A wood mouse?

Probably you have. In which case you can help to solve an interesting problem. Have you ever wondered why the Wood Mouse is so common and widespread but the closely related Yellow-necked Mouse is rarer and more restricted? There may be an historical explanation or, alternatively, ecological factors may make some woods unsuitable for Yellow-necked Mice. Nobody knows.

Sufficient information almost certainly exists to solve this problem - if the information can be collected and collated. Please help by filling in the enclosed forms: one form for each habitat where you have set traps and caught Wood Mice and/or Yellow-necked Mice since 1960.

The sample completed form printed on the back of this letter shows what information is needed. Even if the results are from only 20 trap-nights (eg 2 traps for 10 nights or 20 traps for 1 night) they will still be very useful. If you have 'Trapping Details' but incomplete 'Habitat Details' please still fill in the forms giving whatever habitat details are available.

I shall be very pleased to send more forms and another envelope if the enclosed forms are insufficient. Many thanks for reading this letter and for the help I am sure you will be able to give.

Yours sincerely,

David Corke

Figure 46 (ii)

WOOD MOUSE / YELLOW-NECKED MOUSE SURVEY

Your name D. Corke

TRAPPING DETAILS

Dates of trapping; between Jan 1967 and Dec 1969

Locality King Wood, Ingatestone Grid Reference TL 66 03

Number of trap-nights (approx.) 9000

Total catch (including recaptures if any)

of Wood Mice(Apodemus sylvaticus) 764

of Yellow-necked Mice (A.flavicollis) 222

HABITAT DETAILS OF TRAP SITE

Type of Habitat Mixed, partly coppiced woodland

Tree layer; list commonest trees
Oak, Sweet Chestnut, Larch and some other conifers

Shrub layer; list commonest shrubs and bushes
Coppice Chestnut and Hazel, Birch scrub and bramble

Field Layer (up to 3ft) list common plants which form a reasonably dense ground cover (if any). Classify grasses simply as 'grass'.
Patches of bramble and bracken but mainly open

Is there any arable land (i.e. crop fields) within 400yds of the trap-site? YES / ~~NO~~

If 'YES' please list the crop(s) most frequently grown:
Wheat, Barley, Sugar-beet

Please return to: David Corke, Dept Biological Sciences,
North-East London Polytechnic, Romford Rd, E.15.

Reprinted from THE ESSEX NATURALIST, *Vol. 31, Part 4, 1965.*

Notes on Essex Mammals, 1963-64

By D. CORKE

INTRODUCTION

The following is a summary of the mammal records received for 1963 and 1964. As will be seen the records are from comparatively few observers and tend to indicate the distribution of recorders rather than mammals. Records of deer, badgers and bats are being dealt with in separate surveys by A. Heathcote, D. Scott and D. I. Chapman respectively, and reports of these surveys will appear elsewhere.

The records of the smaller mammals, studied by use of the Field Club's live traps, are arranged under geographic, rather than specific, headings.

All members are requested to send in records of any mammals which they see in Essex. The Club's live traps for mouse or rat-sized mammals are available for use, by members, in Essex.

CLASSIFIED NOTES

HEDGEHOG *Erinaceus europaeus* Linn.

Ashdon, near Saffron Waldon, one dead on road, July '64 (D. Ch.); Flatford Mill, several occurrences '64 (G. A.); Beazely End, near Braintree, one dead on road, August '63 (D. Ch.); Dunmow, forty-three dead and five living specimens, on roads over large area centred on Dunmow. First record May '63, last December '63. Over same area, fifteen dead and one living, seen between May and November '64 (D. S.). Writtle, one young specimen found caught in tennis net, '64 (A. D.). Great Baddow, frequently seen dead on roads '64 (R. T.). Theydon Bois, pair in garden since 1952; Burnham-on-Crouch, one dead on road, '64 (A. W.). Chingford, one in garden, October '63, also one dead in pond, January '64 (D. Co.). Buckhurst Hill, one dead on road, May '63; Collier Row, one dead on road, June '63 (A. H.). Hornchurch, three seen separately, August '63 (M. W.). Ilford, family in garden between '59 and '64. In '63 three young born, in '64 four born and one killed, probably by a cat (E. M.). Rushgreen, one dead on road, April '64 (A. H.). Dagenham, one adult in garden, May '64 (K. B.). Plaistow, two families in grounds of St. Andrew's Church, were present 1953-63 (J. S.).

MOLE *Talpa europaea* Linn.

Flatford Mill area, common (G. A.); Chalkney Wood, one dead August '64, also many mole hills (K. Br.). Dunmow, two seen on surface, May '64 (W. Y.); Easton Lodge, one seen, October '64 (D. S.); Great Baddow, plentiful '63 and '64 (R. T.); South Weald Park, mole hills seen February '63 (D. Ch.).

WATER SHREW *Neomys fodiens* (Pennant)

Flatford Mill area, two seen '64 (G. A.); Tilby, near Dunmow, one caught, in R. Chelmer, by D. Bradenham (via D. S.). Dunmow, one seen in brook December '64 (D. S.). (See also trapping section.)

FOX *Vulpes vulpes* (Linn.)

Flatford Mill area, occasionally seen (G. A.). Fingringhoe Wick nature reserve, seen regularly, '63 and '64 (D. Ch. and K. C.). Felstead, two seen at Leigh Priory, October '64 (D. S.). Galley Wood, Chelmsford, bred in part of badger sett, '63 and '64 (R. T.). Galleyhill Wood, Nazeing, one adult seen August '63 (E. S.). Epping Forest, breeds in badger setts in and near the forest (W. P. and D. Co.). One seen in suburban garden, Woodford Green, February '63 (D. Ch.). Hainault Forest, regularly seen at two badger setts in the forest. Cubs reared '63 and '64 at one of the setts (W. P.). Chigwell Row, one dead in snow, February '63 (D. Ch.). Brentwood, two seen playing in school grounds, in snow, January '63 (M. P.). Romford Sewage Farm, one seen, August '64 (K. B.). Thundersley, cubs seen at badger sett, April '64 (D. Co.).

STOAT *Mustela erminea* Linn.

Flatford Mill area, occasionally seen, '64 (G. A.). Colchester, has bred in area, '64 (C. O.).

WEASEL *Mustela nivalis* Linn.

Flatford Mill area, seen occasionally, '63 and '64 (G. A.). Fingringhoe Wick nature reserve, one caught in live trap, September '64 (D. Co.). Rickling, one dead on road, July '64 (D. Ch.). Maldon, one seen pursuing harvest mouse, October '64; Marden Ash, one seen in sand-pit (E. S.). Great Canfield, one seen on road, April '64; Little Canfield, one seen on road, April '64; Aythorpe Roding, one seen on road, April '64 (D. S.). Great Baddow, several killed by a cat, '64 (R. T.). Chigwell, one seen, October '64 (D. S.). Sewardstonebury, one seen on road, October '63 (D. Co.). Wanstead Park, one seen, December '63, (R. C.). Romford Sewage Farm, several seen, August '64 (K. B.).

OTTER *Lutra lutra* (Linn.)

Flatford Mill area, twice reported '64 (G. A.). Fingringhoe Wick nature reserve, two seen on several occasions (H. C.). Roding valley tracks found at Navestock, '62-'63 winter, Passingford Bridge, '63 (A. W.).

COMMON SEAL *Phoca vitulina* Linn.

Walton-on-Naze, one seen off coast, December '63 (G. A.). Fingringhoe Wick, one seen off coast, July '63 (C. O.).

BROWN HARE *Lepus capensis* Linn.

Flatford Mill area, seen occasionally '64 (G.A.). Fingringhoe Wick, two seen in nature reserve, May '63, and one in July '63 (D. Ch.). Great Baddow, seen frequently '63 and '64 (R. T.). Epping Forest, frequent reports from the more open wooded areas, particularly beech woods, and also from farmland around forest (A. W., D. Ch. and D. Co.).

RABBIT *Oryctolagus cuniculus* (Linn.)

Flatford Mill area, fairly common, often with myxamatosis, '63 and '64 (G. A.). Steeple Bumpstead, one dead on road, July '64; Wendons Ambo, one dead on road July '64; Fingringhoe Wick nature reserve, plentiful '63 and '64 (D. Ch.). Great Easton, one found dead (not myxamatosis) May '64 (A. H.). Chalkney Wood, once exterminated but now returning (K. Br.). Coptfold Hall, Margaretting, plentiful on farm land, '63 and '64, some with myxamatosis in '64 (D. Co.). Willingale, one with myxamatosis, April '63 (A. H.). Great Baddow, common (R. T.). Mill Green, several seen, April '64 (K. B.). Hainault Forest, common on edge of forest and golf course (W. P.). Chigwell, one seen, March '64 (A. H.). Epping Forest, quite common now, seen frequently in Chingford area, '64 (D. Ch. and D. Co.). Report in local press of rabbits at Leytonstone, Green Man road works, November '64 (via A. H.). South Weald Park, some present, April '64; Cold Norton, some present, July '63; Rainham, some present, July '63 (D. Ch.).

RED SQUIRREL *Sciurus vulgaris* Linn.

Colchester, still occurs in woods in area, '64 (C. O.). Chalkney Wood, some present '64 (K. Br.).

GREY SQUIRREL *Sciurus carolinensis* Gmelin

Colchester, becoming more frequent, '63 (C. O.). Chalkney Wood, common August '64 (K. Br.). Broxted, one found dead, October '64; Elsenham, one seen, October '64; Rayne, one found dead, October '64; Tilby, one found dead, October '64 (D. S.)

Coptfold Hall, common, many shot by gamekeepers, '63 and '64 (D. Co. and W. P.). Roydon, one found dead, October '64; Fyfield, one seen, October '64 (D. S.). Great Baddow, common, '63 and '64 (R. T.). Mill Green, one seen, April '63 (A. H.). Epping Forest, very common in all parts of forest north of Chingford (many reports). South Weald Park, about twelve seen, February '63 (D. Ch.).

DORMOUSE *Mascardinus avellenarius* (Linn.)

Coptfold Hall, one captured in woodland, '64 (P. U.). Great Baddow, one adult seen, Autumn '63 (R. T.).

HARVEST MOUSE *Micromys minntus* (Pallas)

Flatford Mill area, fairly common in one locality (G. A.). Witham, one caught which produced young in captivity, '64 (C. O.). Maldon, Beeleigh Abbey, one seen being pursued by a weasel, October '64 (E. S.).

BROWN RAT *Rattus norvegicus* (Berkenhout)

Flatford Mill area, quite common around buildings and in some stream banks, '63 and '64 (G. A.). Rickling, one dead on road, July '64; Great Canfield, one found dead, May '64 (D. Ch.). Chelmsford, one seen on bank of R. Can, July '63 (A. H.). Great Baddow, common on farm land, '64 (R. T.) Abridge, occurs in Roding valley, '63 and 64 (A. W.). Chingford, seen occasionally in Yardley Lane area of Epping Forest (T. L. and D. Co.). Romford, common on sewage farm, '64 (K. B.).

WATER VOLE *Arvicola terrestris* (Linn.)

Flatford Mill area, common on R. Stour, '63 and '64 (G. A.). Easton near Dunmow, one seen, November '64; Great Canfield, two seen, May '64 (D. S.). Ongar, several in stream near Greensted church, June '63 (D. Co.). (See also trapping section.)

COYPU *Myocastor coypus* (Molina)

Dengie, Tillingham marshes, one killed, January '63. Thorpe-le-Soken, one killed, January '63. Glemsford, one shot in gravel pits, February '63. Dedham, one killed, June '63. (All data from J. D. Norris of Ministry of Agriculture.)

PORPOISE *Phocoena phocoena* (Linn.)

Walton-on-Naze, two strandings, April '63 and May '63 (Zoology Department, British Museum (Natural History)).

KILLER WHALE *Orcinus orca* (Linn.)

Walton-on-Naze, one reported stranded, September '63 (B.M. (N.H.)).

RESULTS OF LIVE TRAPPING

1963

Fingringhoe Wick. April, Wood Mice, *Apodemus sylvaticus* (Linn.), and Bank Voles, *Clethrionomys glareolus* (Schreber), caught (D. Ch.); September, Wood Mice only (Field Club meeting).

Coptfold Hall, Margaretting. June, Wood Mice, Yellow-necked Mice, *Apodemus flavicollis* (Melchior), Bank Voles and Field Voles, *Microtus agrestris* (Linn.), caught (D. Co.).

Alderwood, Lambourne End. April, Wood Mice and Bank Voles. (Field Club meeting.)

Hawkswood, Chingford. Several trappings March to July, Common Shrews, *Sorex araneus* Linn., Wood Mice, Bank Voles and Field Voles (D. Co.).

1964 (N.B.—Numbers of specimens caught include recaptures of the same animal.)

Fingringhoe Wick. 5 and 6 September. Nights 2, Trap-nights 63 plus 6 (with larger traps). Common Shrews (6), Wood Mice (12), Bank Voles (6), Field Voles (2), Weasel, *Mustela nivalis* Linn. (1). (Field Club meeting.). 25 and 26 September. Nights 2, Trap-nights 74 plus 12. Common Shrews (9), Water Shrew, *Neomys fodiens* (Pennant) (1), Wood Mice (10), House Mice, *Mus musculus* Linn. (2), Bank Voles (8), Water Voles, *Arvicola terrestris* (Linn.) (3, in large traps), Field Voles (7) (D. Ch.).

Coptfold Hall. August. Nights 8, Trap-nights 262 plus 60. Common Shrews (14), Water Shrew (1), Wood Mice (9), Yellow-necked Mice (8), House Mice (2), Brown Rat, *Rattus norvegicus* (Berkenhout) (1, large trap), Bank Voles (10), Field Voles (1) (W. P. and D. Co.).

Hawkswood, Chingford. March to June. Nights 10, Trap-nights 185 plus 18. Common Shrews (4), Wood Mice (9), Bank Voles (4), Field Voles (3) (D. Co. and T. L.).

ACKNOWLEDGMENTS

I am indebted to the British Museum (Natural History) and the Ministry of Agriculture, Fisheries and Food for permission to quote their records. Thanks are also due to those members who sent in records; their names are set out below with the abbreviations used in the text.

Mr G. B. T. Abbot (G. A.), Miss K. M. Bridges (K. Br.), Mr K. P. Byrne (K. B.), Mr R. Chaplin (R. C.), Mr D. I. Chapman (D. Ch.), Mr D. Corke (D. Co.), Mr K. R. Crawshaw (K. C.), Dr A. M. Davidson (A. D.), Mr A. Heathcote (A. H.), Mr T. Lording (T. L.), Mr H. D. Lunt (H. L.), Mrs E. Mitchell (E. M.), Mr C. Owen (C. O.), Mr W. W. Page (W. P.), Mr M. T. Parker (M. P.), Mr E. Saunders (E. S.), Mr D. R. Scott (D. S.), Miss J. Shipman (J. S.), Miss R. Tiley (R. T.), Mrs P. V. Upton (P. U.), Mr A. C. Wheeler (A. W.), Mr M. Wyatt (M. W.), Mr W. M. Young (W. Y.).

APPENDIX 3

J. Zool., Lond. (1967) **153,** 552

The deaths of small mammals in live-traps

At the start of a survey of a small mammal population in Essex many of the animals died in the Longworth traps. Besides shrews (*Sorex* sp.) which seldom survive overnight in a trap, deaths occurred in the three rodent species caught, viz. *Apodemus sylvaticus* (Linn.) *Apodemus flavicollis* (Melchior) and *Clethrionomys glareolus* (Schreber).

Excess food (oats and barley) was always available in the traps. The bedding was hay. The traps were sometimes left out for a few days between trapping nights and the bedding then became damp. When the technique was changed, the traps being collected after every trapping night and the bedding dried or replaced, there was a marked drop in trap deaths (Table I). Frost and fairly heavy rain occurred on trapping nights in both "damp bedding" and "dry bedding" periods. In addition to animals which were dead when the traps were examined, some animals were moribund. These were cold to the touch and suffered a partial paralysis of their limbs, staggering about in circles when released. Attempts were made to revive some of them by keeping them warm and offering food but all died within a few hours. The only mouse which revived was forcibly fed with warm milk laced with alcohol. Animals released from traps in this moribund condition are very unlikely to survive and are counted as trap deaths in the table.

TABLE I

Trap deaths

Species	Damp bedding No. caught	Damp bedding Percentage dead	Dry bedding No. caught	Dry bedding Percentage dead
A. sylvaticus	37	81	80	1·25
A. flavicollis	6	16	11	—
C. glareolus	8	25	34	—
Totals	51	65	125	0·8

Only one of the six *A. flavicollis* caught in the "damp bedding" period died compared with 81 % of the *A. sylvaticus*. The higher viability of *A. flavicollis* is presumably associated with its larger size and consequent lower relative heat loss.

Since a low trap death rate is essential to obtain meaningful results in population studies of small mammals, attention must be given to keeping the bedding dry.

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Department of Zoology,
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Englefield Green,
Surrey

J. Zool., Lond. (1969) **158**, 216–221

APPENDIX 4

Notes on the distribution and abundance of small mammals in south-west Ireland

Between 2 and 16 September 1967 a group of five members of the Mammal Society (including the authors) visited south-west Ireland the main object being to collect distribution records of all mammals, especially the smaller species, for the Mammal Distribution

Maps scheme organized by the Society. As so few published records of Irish small mammals are available it seems desirable to publish these records in a little more detail than will be given when they eventually appear as points on the Mammal Society's maps.

Most of the records were obtained using 100 of the standard Longworth live-traps. At the beginning of the survey 50 traps were set at each site and trapping carried out for two days but, since it was desired to obtain records from as many 10 km squares as possible, later only about 25 traps were set per site and left down for one night only. Traps were set in pairs, five to ten paces apart, in the afternoon and collected the following morning. No pre-baiting was carried out.

In addition to the "Longworths" some Museum Special break-back traps were also used. These were laborious to set and were less efficient than the "Longworths" with the result that they were not used all the time. Four wire live-traps designed to catch stoats and rats were also used but caught nothing.

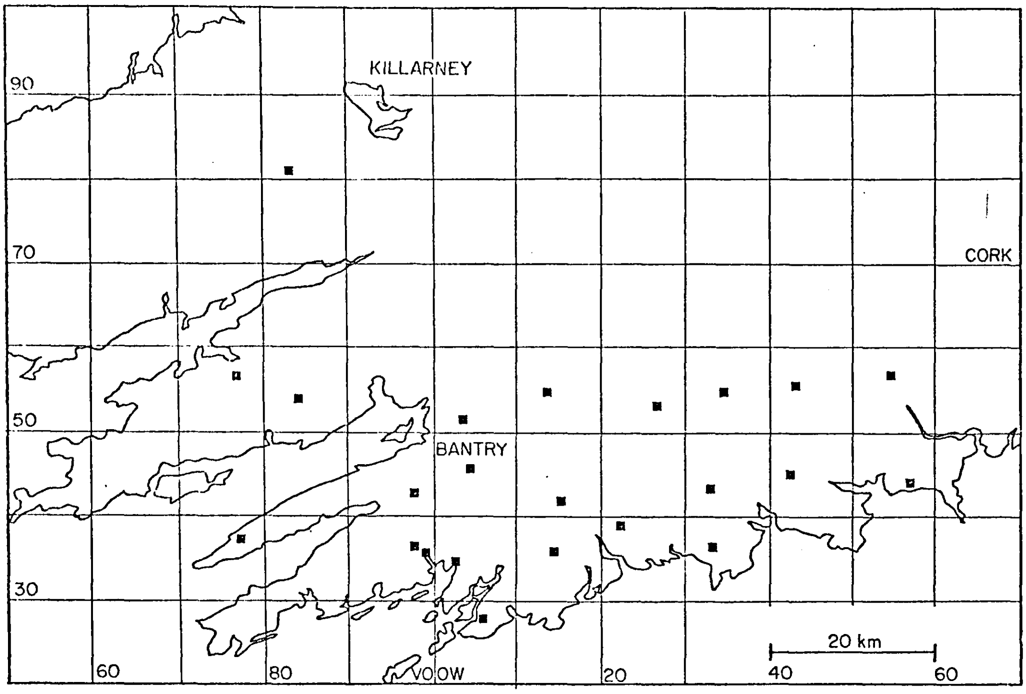

FIG. 1. Trapping sites in south-west Ireland.

The locations of the trapping sites are shown in Fig. 1 and the details of the captures and some habitat notes are given in Table I. 20 of the Pygmy shrews (*Sorex minutus* Linn.), 22 of the Wood mice (*Apodemus sylvaticus* [Linn.]) and seven of the House mice (*Mus musculus* Linn.) were preserved as dry skins and skulls or as whole animals in formalin. Before preservation they were weighed, measured and searched for ectoparasites. The preserved mammals and ectoparasites were deposited with the British Museum (Natural History). Details of the ectoparasites are given in Table III. Other mammals were released, after identification, at their point of capture.

TABLE I

Captures of small mammals in south-west Ireland

Grid reference of trap site	Habitat	Trapnights (Longworths)	Trapnights (Break-backs)	Catch (Longworths)			Catch (Break-backs)
				A. sylvaticus	*M. musculus*	*S. minutus*	*A. sylvaticus*
W0335	Hedge and stone wall	100		6	7	5	
W1436	Edge of track, hazel and Oak hedge	26	17	1			
W0352	Riverbank and hedge	25	12	5		2	1
W1355	Conifer plantation	25	12	2			
W5557	Mixed wood and plantation	25		3		1	
W4356	Hedgerow	25		3		1	
W4245	Hedge (old wall)	25		5		1	
V7757	Mixed wood	25		7		2	
V8454	Moorland	25		8		3	
W2239	Lake edge	25					
V9843	Young conifers	25		1		1	
W0446	Old railway cutting	25	18	1		2	
W2753	Dry ditch, hedge	26		1		2	
W3455	Hedge and wall	24		1		2	
W1542	Gorse, bramble hedge	26		3			
W0528	Gorse, thick grass	24		1		1	
V8381	Stream bank	46		3		1	
V7737	Marshy, Sallow hedge	50		5		3	
V9935	Gorse and bracken	100		2		2	
V9836	Gorse and bracken		26				1
W3336	Conifer plantation	24		3			
W3243	Hedge around Oat field	26		1	2		
W5744	Edge of Pine plantation	25		5		1	

TABLE II

Comparison of the catches of small mammals in Essex and south-west Ireland

Species	Catch in 460 trap-nights in Essex	Catch in 747 trap-nights in south-west Ireland	Catch per 460 trap-nights in south-west Ireland
Apodemus sylvaticus	21	67	41·27
A. flavicollis	6		
Mus musculus	1	9	5·54
Clethrionomys glareolus	23		
Microtus agrestis	2		
Sorex minutus	2	30	18·48
S. araneus	9		

Because of the small amount of data resulting from the use of the break-back traps, and the fact that these data would not be comparable with the Essex results quoted later, only the live-trapping data are considered in this discussion of the results.

A. sylvaticus and *S. minutus* were widely distributed and probably occur in all the areas trapped. In view of the fairly small number of traps used at each site it is likely that the failure to record *A. sylvaticus* from one site and *S. minutus* from seven was due to chance rather than to their genuine absence. There was no consistent pattern among the sites from which *S. minutus* was not recorded.

TABLE III

Ectoparasites collected from small mammals in south-west Ireland

Grid reference	Host species	Ectoparasite species
ACARINES		
W0335	*Mus musculus*	*Ixodes ricinus* (Linn.) 2 larvae
W0335	*M. musculus*	1 unidentified tick larva (mouthparts missing)
V8454	*Apodemus sylvaticus*	*Laelaps agilis* Koch (2 ♀♀ 1 protonymph)
		Eulaelaps stabularis (Koch) (1 ♀)
V7737	*A. sylvaticus*	*L. agilis* (2 ♀♀)
		I. ricinus (9 engorged larvae)
V7737	*A. sylvaticus*	*I. ricinus* (5 larvae)
W0446	*A. sylvaticus*	*L. agilis* (2 ♀♀ 1 protonymph)
W0446	*A. sylvaticus*	*I. ricinus* (2 larvae)
V2935	*A. sylvaticus*	*I. ricinus* (2 larvae)
V8454	*A. sylvaticus*	*I. ricinus* (3 larvae)
V8453	*A. sylvaticus*	*I. ricinus* (4 larvae)
FLEAS		
V7757	*Sorex minutus*	*Doratopsylla dasyonema* (Roths.) (1 ♂ 1 ♀)
V8454	*Apodemus sylvaticus*	*Nosopsyllus fasciatus* (Bosc.) (1 ♀)

M. musculus however, showed a more restricted distribution. It was captured at only two sites, at both of which more were caught than of *A. sylvaticus*. Both sites, although separated geographically, were similar in that they were borders of agricultural land and quite close to farm buildings.

It will be noted that no Bank voles (*Clethrionomys glareolus* Schreber) were found. This species was only discovered in Ireland in 1964 (Claasens & O'Gorman, 1965) near Listowell and in Counties Limerick & Cork. In most southern English *A. sylvaticus* habitats *C. glareolus* is also found, and is as abundant as *A. sylvaticus* when undergrowth is present in the habitat. Claasens & O'Gorman report that *C. glareolus* was common and easy to catch in their, Irish, localities. It seems likely, then, that our failure to catch this species indicates that it is absent, at least in south-west Cork where our trapping was most intensive. It is interesting to speculate on how and when *C. glareolus* arrived in Ireland. If, as seems possible, it is a recent, accidental introduction then it is likely to spread until its pattern of distribution is similar to that in England (or possibly even more widespread as *Microtus* is absent in Ireland). Since our main trapping area was not too far from the known Irish localities for *C. glareolus* repeat trappings in our area would be very valuable to discover if, and when, *C. glareolus* invades the area. On the other hand if *C. glareolus* is a native or an introduction of long standing its restricted distribution remains to be explained.

Very little is known about the relative abundance of Irish small mammals. Crowcroft (1957), when discussing the relative abundance of the two *Sorex* species in England and the numbers of *S. minutus* in Ireland, quoted only one set of data from Ireland. This was an analysis of Long-eared owl (*Asio otus*) pellets (Adams, 1898). We have been unable to find any reference to more recent work on this subject. Of the 387 small mammal remains examined by Adams only ten were *S. minutus*. This is very similar to the proportion of *S. minutus* in Tawny owl (*Strix aluco*) pellets (Southern, 1954) and live trapping results (Crowcroft, 1957) at Wytham. Crowcroft suggested that these data indicated that *S. minutus* was no more common in Ireland than in England; i.e. absence of a potential competitor, *S. araneus*, did not lead to an increase in *S. minutus* and hence presumably the two species are not in competition when they occur sympatrically.

Our results do not bear out this suggestion. The interpretation of live-trapping data is open to many criticisms—different catch rates at different times of the year as shown by Tanton (1965), differing trapping techniques of different workers and the varying sensitivity of the traps for example. In attempting a comparison of the numbers of mammals in Irish and English localities we have tried, therefore, to reduce the variable factors to a minimum. The Essex trapping results summarized in Table II were made in late July and August 1967 using the same traps and the same techniques. The traps were set in as great a variety of habitats as possible including stands of cereal and root crops, hedges, mixed woodland and coppice, but there was not quite such a variety of habitat as was trapped in Ireland.

In order to facilitate comparison between the catches in Ireland and Essex the Irish results in Table II are given as catch per 460 trap-nights. This figure can then be compared with the catch in 460 trap-nights in Essex.

In a detailed study of *S. araneus* and *S. minutus* in the Netherlands Michielsen (1966) has shown that these two species do compete and that at certain times of the year they occupy different niches. In the light of this work it is to be expected that *S. minutus* would be more common in the absence of *S. araneus*. Despite our small sample *S. minutus* can be shown to be significantly more common in Ireland ($\chi^2 = 14{\cdot}64, P < 0{\cdot}1\%$). Comparison of the total numbers of shrews caught (11 in Essex and 18·48 in Ireland per 460 trap-nights) suggests a greater abundance of shrews in Ireland but the difference is not significant (the probability is between the 10% and 5% levels). If *S. minutus* is occupying the niche which is occupied jointly by the two species of *Sorex* in England then it is to be expected that the Irish shrew-niche would support more shrews as *S. minutus* is a smaller species. It will be worthwhile therefore to compare the biomass of the captured shrews. Nineteen of the *S. minutus* captured in Ireland were weighed using a spring balance accurate to 0·5 g. The average weight was 3·29 g with a range of 2·5 g to 4·5 g. The Essex shrews were not weighed but Southern (1964) quotes average weights for *S. araneus* in June and July (7·2 g) and for *S. minutus* in the period July to February (2·8 g). These averages were used to estimate the biomass of the captured shrews.

Biomass of 18·48 Irish *S. minutus* = 60·8 g
Biomass of nine *S. araneus* and two *S. minutus* from Essex = 70·4 g

These two biomass estimates are quite close, in view of the small samples involved, and lend further support to the suggestion that in Ireland *S. minutus* is fully exploiting the "shrew-niche".

A. sylvaticus is also significantly more common in south-west Ireland than in Essex ($\chi^2 = 9{\cdot}94$, $P < 0{\cdot}5\%$). This suggests that in the absence of competing voles and *A. flavicollis*, *A. sylvaticus* can expand its niche. The total numbers of rodents caught are quite similar in the two areas. (Essex 53, Ireland 46·8 per 460 trap-nights.)

Thus it seems, from the admittedly small samples studied, that the paucity of the Irish small mammal fauna has not resulted in vacant ecological niches but in the expansion of niches of the fewer species present. Of course this does not preclude the possibility that introduction of a species would result in competition producing a pattern of abundance closer to that found in England. This may well be happening now in the case of *C. glareolus*.

We wish to thank the Mammal Society for a grant to cover part of the cost of this work. Royal Holloway College, the Essex Field Club and the Mammal Section of the British Museum (Natural History) kindly loaned us the traps. The ectoparasites were identified by Dr F. G. A. M. Smit (Fleas) and Dr W. M. Till (Acarines) to whom our thanks are due for permission to quote their work in this paper. Mr B. Eastcott and Mr P. Stothert, as members of the trapping expedition, assisted in all the work which forms the basis of this paper.

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APPENDIX 5

The local distribution of the Yellow-necked mouse *(Apodemus flavicollis)*

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INTRODUCTION

The Mammal Society's National Distribution Scheme has shown that the Yellow-necked mouse (*Apodemus flavicollis* Melchior) has a most peculiar pattern of distribution in England and Wales. Most of the records are from south and south-east England and the Welsh marches. (The distribution map is soon to be published in the *Mammal Review*, Corbet (in press) *q.v.*). Studies conducted at a more local and detailed level than the National Distribution Scheme may help to explain what factors determine the pattern of distribution.

Since 1967 I have been investigating the ecology of a mixed population of Wood mice (*A. sylvaticus* L.) and *A. flavicollis* on the Coptfold Estate in central Essex. In addition I have attempted to gather recent distribution records of these two species in Essex. Some of the results of this work, which may be relevant to the distribution problem, are the subject of this preliminary report.

DISTRIBUTION OF APODEMUS IN ESSEX

The maps (Figures 1 and 2) show the distribution records of the two *Apodemus* species in Essex between 1960 and 1969. Records which are not locatable to a 1 km square have been omitted.

In the Handbook of British Mammals (Southern 1964) it is stated that "In England, Yellow-necked mice tend to occur in small patches among the general Wood mouse population" although this statement appears to be based on the work of Thurlow (1958) involving the capture of only eight *A. flavicollis* and eleven *A. sylvaticus.* The Essex maps support the conclusion that *A. sylvaticus* occurs throughout Essex, as it does throughout the British Isles. However, before it is concluded that *A. flavicollis* has a restricted or patchy distribution in Essex some consideration of the way in which the records were obtained is necessary. The records were obtained in the following ways:

(a) By live-trapping with Longworth traps. These records are shown as solid circles.

(b) By analysis of the remains of small mammals collected from discarded bottles, the identity of the *Apodemus* skulls being decided using Fielding's (1966) method.

(c) Casual records of mice found dead or brought in by cats.

Records collected by methods (b) and (c) are shown as open circles.

If the distribution records of *A. sylvaticus* and *A. flavicollis* based on trapping records only (i.e. records from those localities where the rarer species is less likely to have escaped detection) there is a much greater similarity. The main difference is that *A. sylvaticus* extends further into urban London. Old or unconfirmed recent records of *A. flavicollis* exist for areas in the east

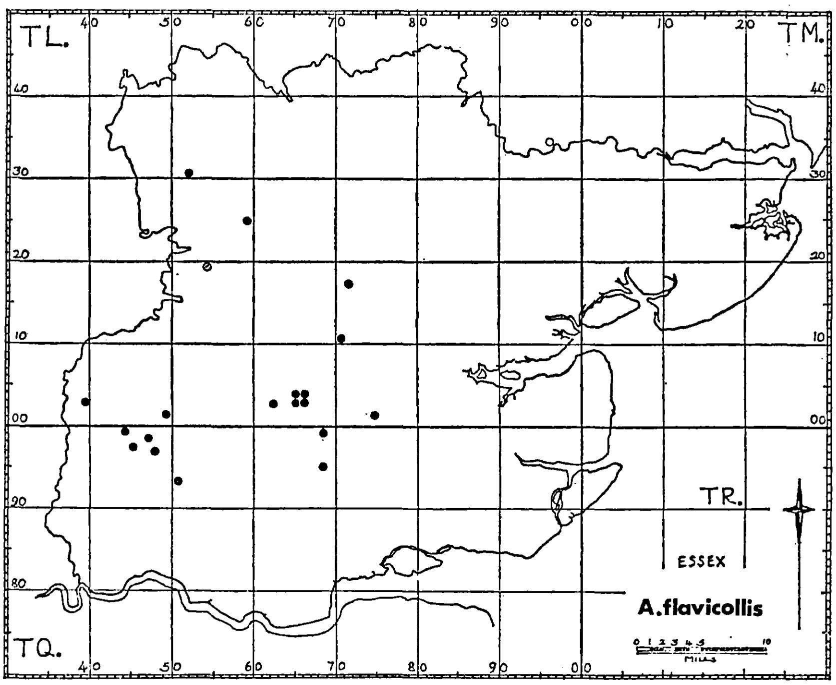

Fig. 1. Distribution map of *A. flavicollis* in Essex 1960–69

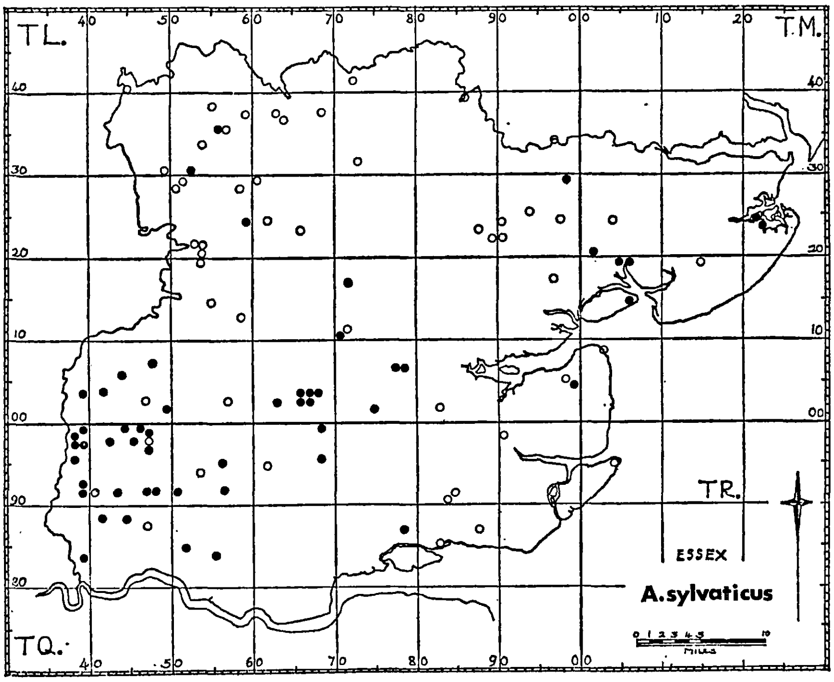

Fig. 2. Distribution map of *A. sylvaticus* in Essex 1960–69

and north of Essex and if more trapping is carried out in these areas it is probable that *A. flavicollis* will be detected.

HABITAT PREFERENCES

The results of my monthly trappings of *Apodemus* in a study woodland on the Coptfold estate will be reported in detail when the study has been completed. However, the results so far do enable some suggestions about the habitat preferences and seasonal distribution of the two species to be made.

Table 1 includes details of the three main habitat types covered by the study grid. It can be seen from this table that *A. sylvaticus* shows a clearly significant preference for habitats with undergrowth, either bramble or bracken. *A. flavicollis* does not show this preference, the distribution of captures being statistically random. Thus the idea that *A. flavicollis* is a mouse of more mature woodlands (Southern 1964, Corbet 1966) is supported in so far as this species does not show selection against the more open (i.e. usually the more mature) woodland habitats but *A. sylvaticus* does.

Table 1

Habitat preference of Apodemus

The study grid consisted of a 150 m square divided into 100 15 m squares with a trapping point at the centre of each (two traps per point). There were three habitat types covered by the grid: deciduous trees with a shrub layer of coppice chestnut; sparse standards with an undergrowth of bramble and conifers with an undergrowth of bracken. The table shows the total captures of *Apodemus* (including recaptures) in each habitat between 1967 and 1969 and the expected distribution of captures if the mice had shown no habitat preference.

Habitat type Grid squares	Coppice 52	Bramble 29	Bracken 19
A. sylvaticus			
captures	296	304	164
expected	397	222	145
		($P<0{\cdot}1\%$)	
A. flavicollis			
captures	121	63	38
expected	115	64	42
		($95\%>P>10\%$)	

The capture rate of *Apodemus* is much lower in the wood in spring and summer than in autumn and winter. This phenomenon has been reported many times although the explanations have varied (e.g. low breeding success in spring and summer followed by rapid breeding in autumn (Watts 1969); migration out of woods in spring and back into woodlands in autumn (Bergstedt 1965); reduced trappability of mice in the breeding season (Tanton 1965).) The fact that mice marked while they were living in the woodland have later been caught several times in the fields surrounding the wood after their final capture in the wood suggests that migration is at least part of the explanation. Movements in late summer in the reverse direction have also been noted. Figure 3 shows the fluctuation in capture rates through the first three years of the study of the woodland population. Although not as common as *A. sylvaticus*, *A. flavicollis* capture rates show a pattern similar to that of the commoner species. The autumn increase in captures coincides well with the harvesting of surrounding cereal crops.

Table 2 lists the *Apodemus* captures in the wood grouped into nine, four-monthly, periods. These periods were chosen to coincide with the three main phases in the yearly population cycle:—December–March population decline; April–July low summer population; August–November increasing population. During the first two years of the study the percentage captures of *A. flavicollis* increased between spring and late autumn and fell during the winter.

It is possible that the higher percentage catch of *A. flavicollis* in the autumn and the lower percentage in the spring reflects greater activity (i.e. trappability) of *A. flavicollis* in the autumn.

Or it may be that *A. flavicollis* survives the winter less well than *A. sylvaticus*. If this is so then the low spring population of *A. flavicollis* must breed more successfully than *A. sylvaticus* if the autumn increase in the proportion of *A. flavicollis* is to be explained. The start of the breeding season is marked by the movement of some mice of both species out into the surrounding crop fields. Perhaps the relative increases of the two species depends on the type of breeding habitats available. It is noticeable that in 1969, when sugarbeet and beans but no cereal crops were grown in the fields adjacent to the study wood, the *A. flavicollis* percentage in the autumn was less than in the preceeding late winter.

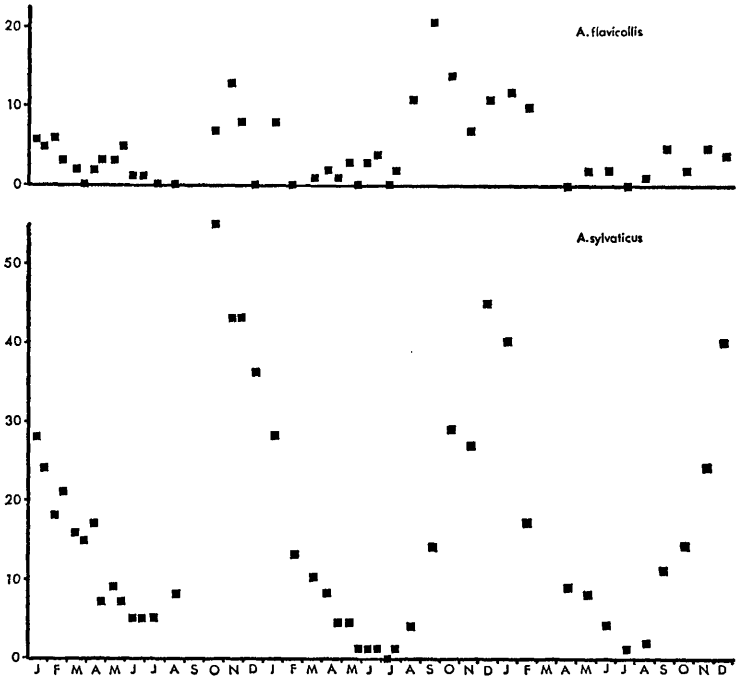

Fig. 3. Seasonal captures of *Apodemus* on the study grid. The number of individuals of each species caught, per trapping session of 200 trap-nights. 1967–69 inclusive.

Table 2

Seasonal captures of Apodemus

Results from the study detailed in table 1

Trap period	Trap-nights	*sylvaticus*	*flavicollis*	*% flavicollis*
1967				
Jan-Mar	1200	135	27	16·9
Apr-Jly	1400	71	16	18·4
Aug-Nov	800	159	36	18·5
1967-8				
Dec-Mar	800	75	11	12·8
Apr-Jly	1600	25	16	39·0
Aug-Nov	800	80	61	43·3
1968-9				
Dec-Mar	600	89	35	28·2
Apr-Jly	800	32	4	11·1
Aug-Nov	800	54	13	19·4

Investigations to test the hypothesis that one or both species of *Apodemus* breed most successfully in non-woodland habitats are being continued. It is too early to draw any firm conclusions but it is worth noting that an hypothesis like this could explain two points which have puzzled many mammalogists:

1. How can two such similar species as *A. sylvaticus* and *A. flavicollis* persist in the same environment? (See for example, Miller 1967). If a difference in breeding habitats and success were detected this question could be answered.
2. What factors determine the presence of *A. flavicollis* in some woods and its absence from other apparently similar ones? The answer to this may be that *A. flavicollis* has not had an opportunity to colonize all the ecologically suitable habitats. But before this is accepted the possibility that the habitat in the area adjacent to the woodland, over-wintering habitat is important should be tested. Live trapping results from Essex localities other than the Coptfold estate are grouped by land usage in Table 3. From these few results it seems that *A. flavicollis* may be associated mainly with woodlands in arable areas. An attempt is now being made to collect trapping details from other counties to see if the same pattern of habitat preference applies.

Table 3

Land usage and the presence of Apodemus

In this table the results of trappings in 50 Essex habitats are classified as follows:
"Arable" habitats within 200 m of arable fields
"Non-arable" habitats in rural areas not close to arable land
"Urban" habitats

Habitat	Habitats trapped	Habitats where *sylvaticus* caught	Habitats where *flavicollis* caught
Arable	28	25	12
Non-arable	12	12	2
Urban	10	4	0

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