The ecology of small mammals, in particular *Apodemus sylvaticus* L. in a silvoarable agroforestry system

by

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The candidate confirms that the work submitted is his own and that appropriate credit has been given where reference has been made to the work of others.

In the name of god, most gracious, most merciful

Dedicated to
my loving mother for all her sacrifices,
my wife for her unflinching emotional support
and
Abla, my source of inspiration

ABSTRACT

1. This research project on small mammals was carried out between December 1994 and August 1997 at the Leeds University Farms in West Yorkshire.

2. Densities of captures were assessed using weekly live trapping and mark-release-recapture (MRR) methods. One hundred and thirty two Longworth traps were set out in a complex farming landscape consisting of four replicate blocks of silvoarable agroforestry designed as a series of tree rows planted at low density (178 trees/ha) and separated by arable alleys cropped with cereals (wheat or barley). Adjacent to each of these agroforestry systems is an area of trees planted at forestry density (2500 trees/ha), an arable field and a mature hedgerow.

3. Overall 1680 captures were obtained, 70% of which were of *Apodemus sylvaticus*, 20 % of *Sorex araneus* and only 10% of *Clethrionomys glareolus.*

4. *A. sylvaticus* and *S. araneus* showed preferences for the agroforestry system, whereas *C. glareolus* prefered the mature hedgerows. Overall, the highest density of capture was found in the tree rows (13.4 animals per 100 trap nights) and the least in the arable field (4.2 animals per 100 trap nights)

5. Densities of captures of *A. sylvaticus* were greater in Autumn than the other seasons, notably in the tree rows when the arable areas provide little cover.

6. Population densities were calculated and showed the same seasonal pattern as densities of captures. The highest population density was in October 1996 (36 mice/ha).

7. Male *A. sylvaticus* bred extensively from mid-Winter until early Summer. The female had a longer and more sporadic breeding period. Overall, the animals showed little or no breeding condition during the phase of population increase in the Autumn-Winter period.

8. Radiotracking of *A. sylvaticus* was carried out from May 1996 until June 1997. Home ranges were estimated using cluster analysis.

9. Home range sizes of *A. sylvaticus*, estimated using 95% of the density distribution, were between 0.04 and 0.30 ha. Home ranges of males were larger than those of females and showed seasonal patterns, with larger ranges during the Spring-Summer period which corresponds to the breeding season.

10. All the individuals tracked had overlapping home ranges spreading over the different habitats, particularly in the agroforestry system (tree rows and arable alleys) where most of the activity of the animals was recorded throughout the year.

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1. INTRODUCTION

Within the extensive literature related to ecological topics there have been many studies on the population ecology of small mammals in Britain (Delany, 1974; Flowerdew, 1987; Gurnell, 1982; Harris *et al.*, 1990; Corbet and Harris, 1991; Mallorie and Flowerdew, 1994).

It is known that, before modern practices in agriculture, mammals such as *Apodemus sylvaticus,* and to a lesser extent *Clethrionomys glareolus* and *Sorex araneus,* used to live primarily in woodlands (Pollard and Relton, 1970, Alibhai and Gipps, 1985). However, with increase in the area of land under cultivation these species have tended to exploit these new habitats with respect to their needs, notably food. In woodland, seeds are the main food of microtines, particularly in the Autumn and Winter, but arthropods are also taken. On arable land the diet is influenced by the crops, and it is likely to vary according to the weeds and arthropods available as well. In fields of winter wheat, for instance, sown grain is taken in quantity in the Autumn and early Winter. In Summer the bulk of the diet is made of weed seed and grass flowers. Insectivorous small mammals, notably shrews, take a wide variety of prey from tiny springtails to large earthworms but occasionally, small quantities of plant material may be eaten.

In recent years some agricultural land has been used for ‘set-aside’ and for agroforestry systems. The former is a European community scheme introduced in October 1988 to reduce surplus arable crops in an attempt to reduce over-production whilst at the same time providing a way of enhancing and conserving the environment. Small mammals have certainly made use of ‘set aside’ and Rogers and Gorman (1995) suggested that set-aside is a sub optimal habitat for both *Apodemus* and *Clethrionomys.* However, there seems to have been no earlier intensive studies devoted to these vertebrates in the agroforestry systems, but there have been some long term monitoring of small mammal populations by the Yorkshire mammal group as well as two short student projects at the University of Leeds (Wright, 1994).

One of the systems commonly used in modern agriculture is the agroforestry. It is a land use system combining agricultural and tree crops of varying longevity, arranged either temporally (crop rotation) or spatially (intercropping), to maximise and sustain aggregate yields (Vergara, 1987). Silvoarable agroforestry (one of the systems in use) has been found to affect the abundance of both aphids and their enemies on the crop. Indeed, greater pest population densities have been found in the arable control plot than in the arable strip flanking the tree rows (Callow, 1995; Naeem, 1996).

The obvious shortage of studies related to wildlife in agroforestry systems was the prime reason for carrying out the present study. Moreover, the agroforestry system offers useful opportunities for understanding the mechanisms that control changes in animal populations. As far as mammal populations are concerned, changes related to environment (notably habitat), even though well known, are an interesting area to investigate, particularly with regard to population dynamics, including demographic changes, and the use of space.

1.1 Population changes in mammals

A population is usually defined as a group of animals belonging to the same species. In nature populations are in a varying environment; from year to year factors regulating these populations may shift under the influence of changing weather, predation pressure or even strength of competition.

Internal problems such as diseases or stress, or the need for emigration, may play a major role in reducing peak population by increasing mortality or decreasing reproduction (Pearson, 1966). Changes in populations have always been found to be influenced by the environment. However, the interactions between populations in a community may give rise to irregularities not necessarily related to varying external conditions (Nicholson, 1954). It has been assumed that there is a finite rate of population change as the population grows (Davis and Golley, 1963).

At the University of Leeds farm, live trapping in agroforestry plots has been practised for some time by the Yorkshire mammal group for survey purposes and to monitor demographic changes in small mammal populations (Wright, 1984). They have recorded numbers, sex and age of the animals caught twice a year in an attempt to determine any relationship between these and environmental variables. Such assessment may take years before any conclusive statements can be made to explain population fluctuation phenomena. Some of the current records will contribute to this survey plan.

1.1.1 Seasonal changes

Variation in numbers of small mammals during the year have been reported by many authors. For example, *A. sylvaticus* are normally caught in small numbers during the Summer, and it has been suggested that this may be due to a negative response to traps (Berry *et al.*, 1967; Tanton, 1965). This is probably a consequence of increased food availability during the Summer but there may also be some aspect of social behaviour limiting numbers at higher density despite a surplus of food (Flowerdew, 1972). The possibility of seasonal variations is generally accepted but is subject to further variations under specific conditions. Thus Pollard and Relton (1970) expressed the possibility that the variations in trappability during the Summer could differ from one habitat to another, stressing the interrelationship of density-dependency and habitat.

1.1.2 Competition

It seems likely that competition is density-dependent among small mammals. Rivalry between two species arises when they are using the same resource at the same time. Food availability, the requirements of the animal and time are amongst the factors which generate competition.

Interspecific competition is still a subject of controversy, since it has not been clearly shown that antagonism can have an important effect on fluctuations of population numbers. When *A. sylvaticus* and *C. glareolus* share the same habitat there is a well marked alternation of activity, the former being nocturnal and the latter diurnal. Also, the division of breeding habitat permits coexistence of the two potential competitors (Montgomery, 1978). Competition for space use and home range delimitation cannot be a threat, and the trophic relationship is more complex in situations were a variety of plant species are consumed by both animals in variable proportions (Delany, 1974). Competition occurs when both antagonists are using a common resource. Hence, the more diverse the habitat, the less competition should occur. However, the extent to which shrew communities that are also present can influence the activities of mice and voles has yet to be determined (Brown, 1954). With regard to shrews, *Sorex araneus* and *Sorex minutus* often share the same habitat but, even though these species are present in unequal numbers, this does not mean that competition occurs between them. If it was occurring, one could expect to see *S. minutus* more numerous when its congener was absent, but this does not happen (Ellenbroek, 1980).

Intraspecific regulation is more likely to operate by increasing antagonistic behaviour, in particular between the males. This causes a deterioration in adult and juvenile survival during the Spring (Watts, 1969) and the adult males can affect the growth, survival and recruitment of juveniles (Flowerdew, 1974).

1.1.3 Predation

Small mammal populations are not self-regulated which means that their fluctuating numbers depend on the effect of external factors. The number of animals is determined by the interactions in the three component system: food - small mammals - predators (Hansson, 1979b). Predation is considered by certain authors (Brown 1955; Pearson, 1966, 1971) as the most important factor affecting the probability of survival in small mammals.

The major predators are birds of prey, foxes and mustelids. Indeed, weasels: *Mustela nivalis* (particularly females, because of their small size in comparison with larger males) have been known to enter small mammal traps, presumably in pursuit of a prey (Stoddart, 1982; this study). Predator - prey interactions are reported by Pearson (1966) as an important if not essential part of the microtine cycle. In nature, however, fluctuations of mammals do not meet all the requirements of the predator-prey cycle. In some cases, predator numbers increase after those of the prey decline (Davis and Golley, 1963). Pearson (1966) believes that predators play an important role during the low phase of the population cycle by retarding premature recovery of the population. This may cause recovery to take some time. Such an hypothesis could explain the length of the cycle.

1.2 Breeding patterns

It has been suggested that the breeding season of *A. sylvaticus* starts early in the Spring and ends by late Summer or early Autumn (Rood, 1965). The most reliable indicators of reproductive activity are the transformation of the genitalia and the birth of young, the latter coinciding most often with an environmentally favourable time of the year (Delany, 1974). However, the breeding timing is not restricted and it may extend well into the Winter (Green, 1979); it depends both on an unusually abundant good quality food supply, which may stimulate breeding in female microtines, and on the availability of adequate shelter (Negus and Berger, 1977). However, there are other factors just as important as food abundance which may influence Winter breeding. Thus, high population density, or changes in population quality associated with it, could inhibit breeding even when food is sufficiently abundant (Smyth, 1966). Breeding may also be affected by climate characteristics. In the coastal zone of Algeria (and probably in all North West Africa) reproduction of *A. sylvaticus* seems to be restricted to Autumn and Winter (Kowalski, 1985), probably because of the mildness of climate during this period and the heat of the Summer which might be inhibitory. A knowledge of Winter breeding is essential to understand the fluctuations in mammal populations.

1.3 Habitat use and home range

Small mammal species present different patterns of distribution. *A. sylvaticus*, which is a habitat generalist, is widely distributed in Europe, temperate Asia and Northern Africa (Bernard, 1969). It requires less stringent conditions than, for example, *C. glareolus* and *S. araneus*.

Animal conservation studies often look at the relationship between the animal and its environment, notably the habitat it uses particularly for shelter, source of food, and as a corridor for its movements. Thus, animal conservation depends enormously on habitat protection, and hence on its rational management.

Habitat type seems to be important in the population dynamics of small mammals. It affects successful reproduction and survival (Rogers and Gorman, 1995). In accordance with the animals' needs, the habitat is used to fulfil these requirements. *A. sylvaticus*, for instance, is able to recognise and take advantage of local conditions of high food abundance (Tew, 1992). In the agricultural landscape, *A. sylvaticus* and *C. glareoluss* differ in their use of the available habitats. In a study in Berkshire, England, Kikkawa (1964) reported that *C. glareolus* occurs mainly in woodland and adjacent hedgerows, although it can certainly make use of dense cover hedgerows running alongside arable land (Pollard and Relton, 1970). *A. sylvaticus,* however, tends to reside in woodland during the Winter but moves into the surrounding fields during the Summer (Kikkawa, 1964), where it exploits both cultivated fields and adjacent hedgerows (Pollard and Relton, 1970).

Mammals move around an area which may include a selection of different habitats. These movements may occur in relation to exploration of food resources, to reproductive behaviour or to some other activity pattern. The area visited by the animal is called its home range. It is the area in which an animal normally lives, exclusive of migration, emigration or any erratic wanderings (Brown and Orians, 1970).

Determination of the home range size, shape and pattern of utilisation is of importance for studies in animal ecology and behaviour. It helps to shed light on population parameters, it provides information on the activity of individuals and measures the interactions and most important overlaps between individuals, it shows the spatial distribution of the animals during the period of study, and is probably also useful for information on space selection.

1.4 The aim of this research

The aim of the study reported here is to investigate some of the ecological aspects of small mammal populations present in an agroforestry system. This could be valuable for the conservation of biodiversity as it brings three habitats: cultivated, woodland and hedgerows into close proximity. Habitat fragments are considered as refuge for small mammals, especially during Winter (Ylönen *et al.*, 1991) and thus this study focuses on the distribution of species between the different habitats present in the agroforestry system.

The population sizes of *A. sylvaticus, C. glareolus* and *S. araneus* have been investigated in relation to this fragmented habitat. In addition, the probability of survival and the added population are investigated to monitor the rate of changes in the most abundant species (*A. sylvaticus*) throughout the period of study.

The investigation of space use, using *A. sylvaticus* as a model to determine home ranges in relation to habitat, is assessed through self made topographic and vegetation maps. Data processing, analyses and results are displayed using Geographic Information System support. The information concerning spatial distribution and movements of this rodent will help us to assess habitat functions and dynamics in one of the agroforestry systems, silvoarable (described in the next chapter).

2. AGROFORESTRY SYSTEMS

2.1 Introduction

The International Council for Research in Agroforestry (ICRAF) based in Nairobi (Kenya) defined agroforestry as a collective name for all land use systems and practices in which perennials are deliberately grown on the same land management unit as crops and/or animals. This involves the integration of agriculture and forestry in the same piece of land exclusive of naturally or casually occurring mixes of trees, crops and animals.

This definition is general and probably reflects the only principle on which agroforestry is based. In fact, there is a multitude of agroforestry systems world-wide set up for particular purposes in relation to patterns in space and time involved in land use, with different systems and practices existing in different parts of the world (Nair, 1987). Gholz (1987), lists the most important and widely used ones, which are mainly in developing countries:

- The agrosilvicultural system, also called silvoarable system. This involves mixed trees and crops and is mainly used as improved fallow, multipurpose trees and shrubs on farmlands, notably for fuel production.
- The silvopastoral system, involving trees or shrubs on pasture.
- The agrosilvopastoral system which is a combination of the above two systems involving trees, crops, and pasture with the possible presence of animals.

Looking at the elements that agroforestry involves, it appears that this is not a new concept. However, although the art of agroforestry is old, the science is new

(Nair, 1984). In fact, old practices applied the agroforestry variance in a variety of ways for specific purposes.

We witness today a resurgence of agroforestry systems supported by the international scientific community, launching vigorous campaigns to convince sponsors about the importance of this technique both commercially and in terms of biodiversity. In Europe, for instance, the traditional silvopastoral system has been in decline during the latter half of this century, but recently the economic biodiversity and heritage potential of this system has been realized (Newman and Gordon, 1997).

About 20 years ago there was an emergence of interest in the tropical and subtropical regions. The practice of these techniques was seen to be particularly important in these regions because of the absence of fossil fuels and, within about the last decade, their possible importance in temperate zones has been realised (Buck, 1995). Indeed, this resurgence of interest in the agroforestry concept is a response to worldwide concern about the failure of large agriculture and forestry monocultures in the less well developed world, particularly in the tropics. These regions of the world witness a high rate of forest destruction and loss of the multitude of natural products they yield. Ironically, in the temperate zones, it has been suggested that the expected impact of agroforestry systems (in the short term at least) may lead to a situation where food surpluses disappear (Corry, 1990).

In the United Kingdom neither the Agroforestry Research Trust nor the other groups of research such as the Silvopastoral National Network Experiment or the Silvoarable Research Group show much concern about the ecological impact of such systems. The main concerns so far have been crop and animal production.

2.2 Does agroforestry lead to modern and successful agriculture?

Increasing deforestation (to provide land for agriculture and livestock) and the subsequent environmental degradation, notably in Central America, encouraged development projects and programs for tree growing to be put into effect (Current and Scherr, 1995). Moreover, there have been recent moves to make greater use of agroforestry practices in temperate agriculture, to produce diversification, to rehabilitate land, to convert land (mixed crop control), to enhance habitat and to control food production to avoid food surplus production (Buck, 1995).

In the current practice of using large fields which are cropped annually, the major problem faced is encountered during the period post-harvesting. At this time the soil moisture and the nutrient content decrease due to the lack of vegetation above ground and nitrogen fixing systems below ground. The rationalisation of cropping methods is one of the key reasons behind the success of agroforestry systems. To perform a continuous productivity of food crops with optimal yield, intercropping agroforestry systems have been set up (Figure 2.1). Intercropping silvoarable agroforestry is one of the most commonly used systems, notably in the temperate zones, and its technical potential allocates it a key role in rural development and environment protection. This system infers the continuous presence of woody perennials (trees and shrubs) and an annual crop.

The biological efficiency of intercropping agroforestry is assessed by the concept of land equivalent ratio (LER). It expresses the advantage of intercropping over sole cropping (Ong *et al.*, 1991):

$$\mathrm{LER} = \Sigma i/s$$

where i = yield per unit area of intercrop and s = yield per unit area of sole crop.

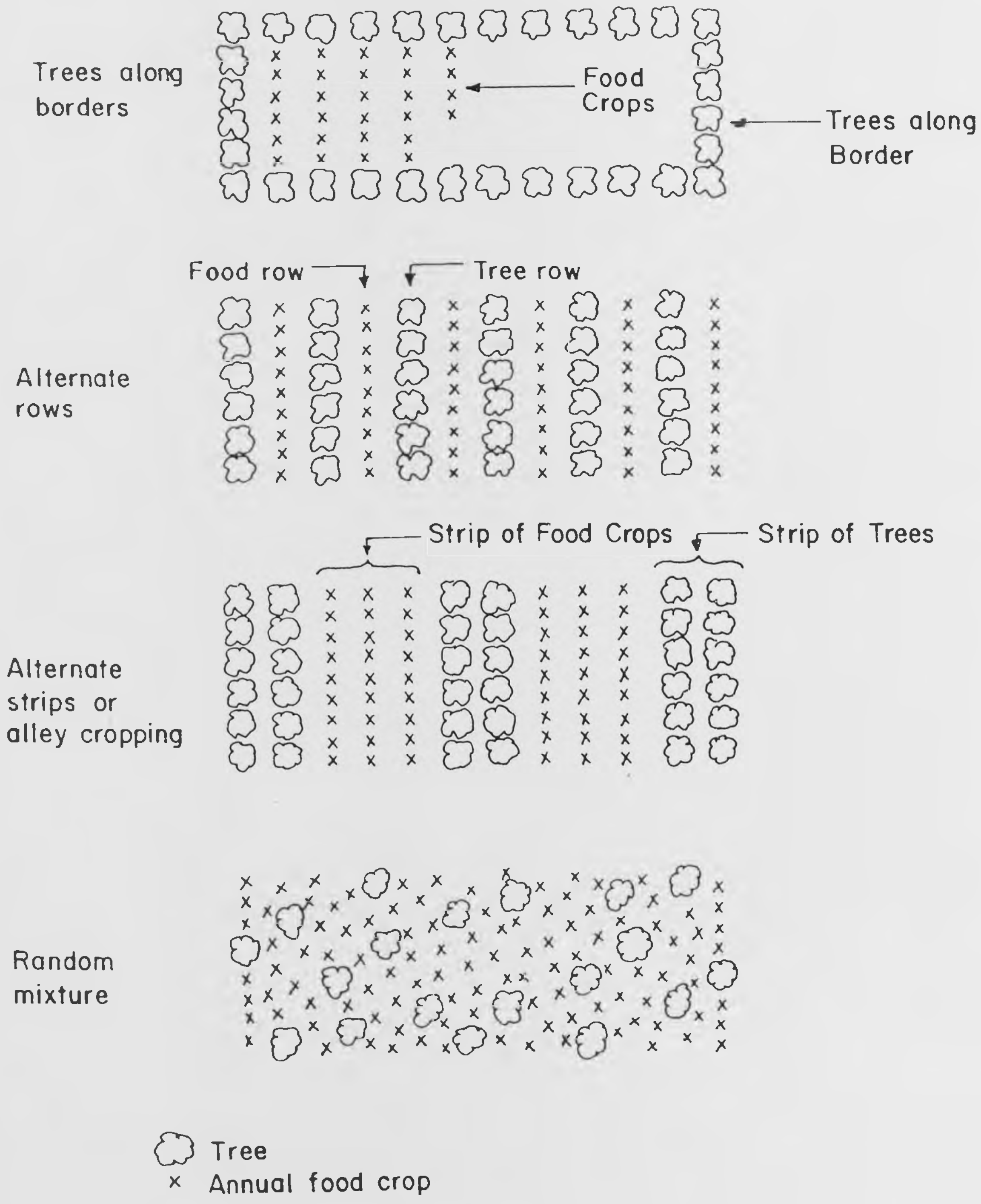


Figure 2.1 Integral agroforestry systems under various spatial arrangements (After Vergara, 1987).

The long term nature of the interplanted trees is to reduce nutrient losses and maximise nutrient inputs (Vergara, 1987). Thus, leguminous trees have a great effect on soil fertility through nitrogen fixation. They play major roles in alley farming systems by providing green manure to intercropped food plants (Brewbaker, 1987). Even though competition will occur, the nearby trees are not a threat for annual crops; the alley ploughing avoids competition for soil nutrients within the top 25 centimetres of the soil, notably during the early stage of seed growing, as the woody perennial roots are pruned by the plough (Corry, 1990). The organic input from trees is yet another advantage for improving crop yield as many of the woody perennials produce sufficient pruning biomass and contain enough nutrients to meet crop demand (Palm, 1995). However, tall trees, notably eucalyptus, may cause damage to neighbouring crops by reducing the incident light to the crop, which is of great importance for cereals in particular, and by reducing the available water in the soil (Brewbaker, 1987).

Research is making progress to emphasise the effectiveness of such mixed land use. However, studies have been highly descriptive and empirical (Gholz, 1987). Improvement or development of prototype systems for broad regional application is an important emphasis of international research centres such as the ICRAF (Rocheleau, 1987).

Since 1977, in which year agroforestry systems were recognised and defined, governments have shown more and more interest in this system as a useful approach to land use, and have provided funds for running scientific projects (Jarvis, 1991). In Great Britain, Moore (1987), studying the impact of agriculture on nature conservation, suggested that formal consultation on change of land use in sites of special scientific interest (SSSIs) should be extended to cover agricultural and forestry operations. One of the reasons for such interest in agroforestry is that it is now widely recognised as more conservation effective (e.g. preventing soil erosion) than current methods used in agriculture. It has been suggested that such systems should be included amongst conservation technologies (Grewal *et al.*, 1994).

The man and biosphere programme has revived a concept in land use planning, involving multiple land use, with attempts to preserve biodiversity (Eisenberg and Harris, 1987). Agroforestry could make this approach effective with successful implementation on a large scale.

From the economic point of view, there are particular environmental, social and financial benefits to be gained from managing a woody plantation with an annual intercrop system. There will be intensification of land use and hence increase in productivity, the diversity will improve the wild life habitat, and the farmers will raise their income and share costs of plantation maintenance with enterprises in charge either of agriculture or forestry (Sargent and Bass, 1992). However, a systematic and quantitative investigation of the claimed benefits is required as a precursor to fuller economic evaluation (Price, 1995).

2.3 Agroforestry and wildlife relationships

Botany and zoology are based on a framework of evolutionary relationships (Moore, 1987). Broad-leaved angiosperm forests underwent their evolution at the time that mammals and birds were also rapidly evolving. As a consequence, interesting co-evolutionary symbioses were established (Eisenberg and Harris, 1987). In term of nature conservation, the rich potential of agroforestry systems for increasing wildlife productivity and biodiversity is very important. Although maximising production, it minimises adverse environment impact (Watson *et al.*, 1991). There is, however, still much to be learnt about what is making this system ‘environment friendly’.

Agroforestry provides an opportunity to examine the influence of the diversity in plant-soil relationships and its effect on the wildlife that it supports. This is achieved by providing extra habitats over and above those found in the countryside. Tree rows in a field may be used as corridors which link scattered populations and hence help to ensure their survival (Moore, 1987). It has been shown for instance that habitat diversity in agroforestry has an important effect on population levels of insect pests and their natural enemies sharing the same habitat (Altieri *et al.*, 1987; Callow, 1995;

Naeem, 1996; Peng *et al.*, 1993). Moore (1987) asserted that, on the better land, the croplands will become less and less suitable for most species of wildlife which will depend increasingly on forest and on areas deliberately set-aside for them. Very often animals such as small mammals prefer set-aside areas surrounded by habitat of high productivity (Rogers and Gorman, 1995).

2.4 Perspectives

Among the reasons for the slow achievement of world-wide use of such a beneficial system are the actual institutions and policies ruling environment management. These are usually set up to support conventional models of agriculture, forestry and rural development, but may be counter effective for modern mixed systems. Laws and regulations are generally absent to designate responsibility for such matters. In Great Britain for instance, the real difficulties of co-ordinating conservation, agriculture and forestry on the ground are worsened by the way that the administration functions, which has allowed dissension between the departments most concerned with land use (Moore, 1987). In some wealthy parts of the world, the huge oil and gas deposits make decision makers safe from food production shortage (at least temporarily) and hence such planning is not a priority. Finally, agriculturists tend to be conservative. They need to be convinced that agroforestry systems are an improvement on current practices. Their long term success has not yet been demonstrated and it is important that this should outweigh the initial loss in cropping. The establishment of agroforestry based on indigenous tree species may take 50 to 70 years to become mature and show results (Grewal *et al.*, 1994). However, fast growing trees such as poplars may alleviate this problem.

In the temperate zones research is increasing. A great number of studies are being carried out in these zones and results presented at forums and seminars. In North America, a biannual conference series on temperate agroforestry was initiated in Guelph, Canada, in 1989 (Gordon *et al.*, 1997), while in the UK a similar event has taken place annually since 1990 and the proceedings are published in Agroforestry in the UK, the Newsletter of the UK Agroforestry Research Discussion Forum. This has been published fairly regularly, three times a year, since February 1990. Moreover, a European Research Program on agroforestry was launched in 1992, supported by the European Union, to boost research in agroforestry. However, there is still considerably less research being carried out in temperate regions compared to that in the tropics. Only six publications in the first 30 volumes of Agroforestry Systems are related to European research on agroforestry (Dupraz and Newman, 1997). This is partly due to the fact that the greatest concentration of life is in the tropics. The tropical rain forests hold by far the greatest number of species of all the habitats which mankind inherited from the past (Moore, 1987).

3. EXPERIMENTAL SITE, MATERIAL AND METHODS

3.1 Experimental site

The field experiments were carried out at the University of Leeds experimental farm in North Yorkshire, about 21 kilometres north-east of Leeds, England (1° 19' 30" W, 53° 52'N) (British National Grid Reference SE/445415). This site is characterised by a mosaic of landscapes: cropped fields, hedges, grassland, small woodlands and in addition, a set of four silvoarable agroforestry replicates recently set out as an experimental site (Figure 3.1).

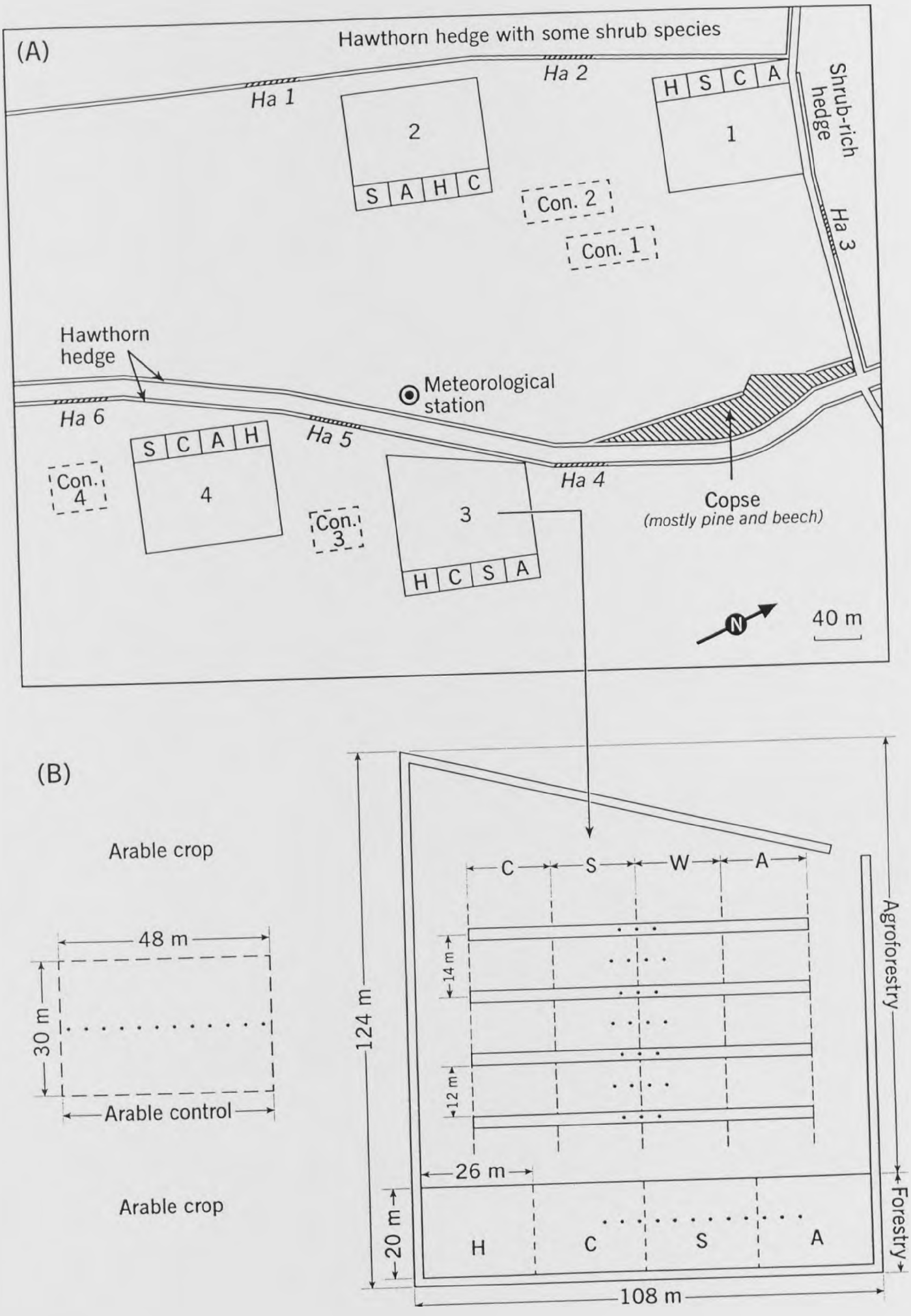


Figure 3.1 The experimental site at the University of Leeds farm at Bramham in North Yorkshire (England). A) Layout of the four agroforestry replicate blocks (numbered 1 to 4), the arable controls (Con. 1 to 4) and the hawthorn hedges (Ha 1 to 6) where traps were laid out. B) Plan of replicate 'Block 3', showing the trap locations (dots) within the agroforestry system, the forestry control and the arable control. Tree species in the tree rows and the forestry control are: A, ash; C, cherry; H, hazel; S, sycamore and W, walnut.

3.1.1 The replicates

Four replicates have been established. Each is designed as a series of three cropped alleys, 12 metres wide, separated by four rows of high quality timber trees (*Acer pseudoplanatus* L., *Fraxinus excelsior* L., *Prunus avium* L. and *Juglans regia* L.) planted regularly at 4 metre intervals. Each row contains four sets of five trees; and each set of one species is separated by *Corylis maxima* Mill. Adjoining the agroforestry treatment, a forestry control has been set up. It consists of a hazel orchard plot planted at 4m x 4m spacing and one plot of each species of tree cited above (except for *Juglans regia*), planted at conventional forestry densities (2m x 2m spacing). The height of the trees was measured in 1995/96 and 1996/97. In the former period they were 5.14 m and 3.92 m high in the forestry control and the agroforestry respectively. In 1996/97 the corresponding heights were 5.55 m and 4.49 m.

Each replicate is surrounded by a windbreak of eleven cultivars of poplars and four of willow (Peng *et al.*, 1993). Figure 3.1B shows one of the four replicates blocks set up in 1987 as a silvoarable agroforestry experiment. There is an adjacent arable control area consisting of a large field sown with the same crop as in the arable alleys, following a cropping rotation system. In 1994 - 1995 and 1995 - 1996 the fields and arable alleys were sown with Winter wheat *Triticum sativum* L. and in 1996 - 1997 with Winter barley *Hordeum vulgare* L. Both crops were sown each year late in September. Winter wheat was harvested by the end of July and Winter barley early in June.

3.1.2 The old hedges

Along the west side of each replicate there is a mature old hedge of hawthorn (*Crataegus oxyacantha*) containing a variety of shrub species. The thorn, trained as a low hedge and hence used as fence, is standing very hard cutting. As Beddall (1957) says, it has all the virtues but no vices. One of these virtues is that it presents shelter and food for the fauna. Small mammal species use the hawthorn hedges either as living habitat or at least as a corridors for their movements. The most common inhabitant of the hawthorn hedges at the farm are *Clethrionomys glareolus, Sorex araneus* and *Apodemus sylvaticus* which accounts for the most.

3.2 Material and methods

3.2.1 Small mammal sampling

The use of sampling methods for the enumeration of a population has become widely known and accepted only within the past generation (Chapman, 1954).

Small mammals were trapped in Longworth live traps (as designed by Chitty and Kempson (1949) and manufactured by Penlon, Abingdon, UK) which are suitable for catching *Apodemus sylvaticus, Clethrionomys spp.* and the lighter *Sorex spp.* They were baited with pea seeds and/or, more often, with wheat, together with dipteran pupae as food for any shrew that may be trapped. These traps incorporate a nest box, and bedding (mostly hay) is provided, to keep animals warm. The traps were methodically laid out within each particular area (Section **3.2.1.1**). Reasonably accurate census information at closely spaced intervals is a prerequisite for determination of population dynamics (Krebs *et al.*, 1969).

Single night live trapping sessions started on 20 December 1994, twice a week. However, modifications were made a few weeks later in order to minimise the effects of trap addiction and disturbance of the animals. The number of sessions per week was reduced to one and the number of traps set out each session was increased, so that a set of two blocks was sampled every two weeks, as recommended by Gurnell and Flowerdew (1982). The single night trapping allowed for each session was motivated by the fact that results from long trapping periods may be affected by animals moving into or out of the trapping area during this period which can give rise to misleading estimates of population size. The traps were set out on a Thursday evening and checked the following morning. Once emptied, they were collected and stored in a compound after each session.

3.2.1.1 Trapping pattern

As the field work was conducted in a relatively small experimental site, the guide to trap spacing of Gurnell and Flowerdew (1982) could not be followed. The number of traps used would have been too few because of the size and the shape of the areas (e.g.: the alternate tree rows arable alleys in the agroforestry) to be sampled.

Within the blocks, an octagonal and relatively compact grid was designed for the trap setting. 24 traps were laid out within the agroforestry system (Figure 3.1B). With twenty or more traps, it is possible to carry out systematic sampling and obtain quantitative data. The grid lines were 7 m apart (equal to half the tree row spacing) and the traps were 4 m apart in the line (equal to the tree spacing in a row).

In each of the forestry control and arable control areas 12 traps were set, 4 m apart in one north-south row (Figure 3.1B). This gave 48 traps in total for each block. The four replicate blocks were sampled in pairs, using either blocks 1 and 2 together or blocks 3 and 4 together.

In addition, 36 traps were laid out in the mature hedge adjacent to the pair of blocks being trapped. These were in three sets of 12, one set in the section of hedge between the blocks and the other two sets in sections of the hedge at each side of the blocks (Figure 3.1A). Sets Ha 1, Ha 2 and Ha 3 are in the mature hedge adjacent to blocks 1 and 2; they constitute a single habitat called ‘Mature Hedge I’ (MH I) and sets Ha 4, Ha 5 and Ha 6 are in the mature hedge adjacent to blocks 3 and 4; they constitute another single habitat called ‘Mature Hedge II’ (MH II). Thus 132 traps were used each week with 96 to sample the agroforestry plots and control areas in two blocks and 36 to sample the adjacent mature hedge. MH I and MH II were sampled along with Block (1 + 2) and Block (3 + 4) respectively, on the same day.

3.2.1.2 Catch handling

The method of analysis of Mark, Release, Recapture (MRR) is used for estimating population numbers. This method involves marking individual animals and relies on recapturing marked individuals in subsequent samples. Each trapped animal was weighed to the nearest half gram, sexed, its breeding condition checked (looking for signs of sexual activity, or pregnancy in fertile females), and marked with a unique mark.

The techniques of marking were different from one species to another and needed to be efficient while causing as little harm as possible. As the study progressed it was found that fur clipping was not very efficient for long lasting marks. The fur was clipped in different parts of the body (e.g. right shoulder, middle back, etc.) and combinations of clips was used as series of individual numbers. The use of metal numbered ear clips was investigated; these were supplied by Brookwick Ward (Fife, UK). These clips were used on *A. sylvaticus* only, as *C. glareolus* has a small hidden pinna and *S. araneus* are too small to carry such a heavy load. Fur clipping was used on the latter two species, using a clipping diagram. The animals were then released at the same capture point.

Individuals of *A. sylvaticus* were placed in one of two groups according to their age:

- Juveniles: under 17 g mass and with remains of juvenile coat,
- Adults: Over 17 g or in breeding condition (scrotal condition for males and perforate vagina plus prominent nipples for females).

Information concerning sex, age, weight, possible previous capture and breeding condition were immediately recorded. A Microsoft Excel spreadsheet was used for storing and sorting weekly trapping data.

3.2.2 Radiotracking

3.2.2.1 Radiotracking equipment

- The transmitter

The transmitter used in this study was a radio-tag with a cable-tie whip supplied by Biotrack company (UK), specialists in animal radio monitoring. The Ag 361 cell used lasted up to 8 weeks and was connected to a tiny antenna made of 4.5 kg fishing trace (a light conductor for lower frequencies). Once the wires were soldered to activate the transmitter they were covered with a deep layer of a material called plastidip. The whole set weighing 2.4 g was then coated to prevent it from weather conditions (Figure 3.2).

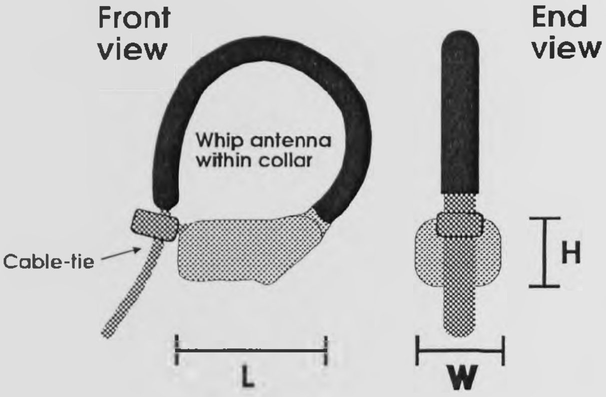


Figure 3.2 Cable-tie collar for small mammals. The antenna is concealed within part of the collar. L, W and H are successively the length, the width and the high of the cell, a Maxell Ag 361. (Drawing: Biotrack).

The pulse parameters and power output were set up to optimise the battery life versus range specification. The pulse length was 14 milliseconds and was emitted at a rate of 33 pulses per minute.

- The receiving equipment

The receiver used to monitor the movements of the animals was a Mariner Radar M-57 (150 KHz) from Biotrack. It has integral dial illumination for nocturnal radiotracking and panel meters to indicate signal strength and to check the voltage of the batteries. Its separated volume and gain controls make it useful for close contacts with a transmitter. The M-57 used had a working frequency band of 173.20 to 173.35 MHz (The United Kingdom protected frequency allocation for radio-tracking). Note that the difference between the highest and lowest frequencies is 150 Khz. The three-element Yagi aerial was used to pick up the signal from the transmitter and relay it to the receiver.

3.2.2.2 Radiotracking sessions

The radiotracking sessions were held three nights each week, from dusk to dawn. Each consisted of taking bearings of the transmitter at as regular times as possible. The time defined for recording a fixe (location of an animal at a time ‘t’) was 30 minutes, but the reality in the field sometimes differed from this because of the long time spent looking for the animals. However, the time between two readings never exceeded one hour. The method of taking bearings is described by Kenward (1987).

When bearings were taken, the strongest signal position had first to be found. The gain was then turned down so that only the tag is heard, to be sure that this was the real signal and not a reflection or a back-bearing. The antenna was immediately swung to the right side until the signal disappeared and swung back to recover the signal again. When the signal was just becoming detectable, a landmark (e.g. a tree trunk or a bush) was noted along the line of the aerial boom. This procedure was then repeated to the left side. The transmitter direction is the line that bisects the angle between the two side directions. The bearing of an observed point is the angle between a reference direction and the line from the observer’s position to a distant point (Kenward, 1987).

Sometimes the weakness of the signal made it hard to obtain the transmitter direction, so triangulation was used to locate the animal with as much accuracy as possible. To avoid excessive disturbance, no attempt was made to approach the animal closer than what was necessary to determine its position to within

2 m (Wolton, 1985). From time to time continuous movements of certain animals were recorded in order to assess movement patterns and distances.

Fixes were plotted on a hand drawn grid covering the research area (experimental 'Block 3'), where each pixel represented 2m x 2m. Each fix was recorded as a spot in the square representing the area where the signal was located and later represented at the centre of the grid cell; thus the fix resolution is set at 2m. The time of registration of the fix was reported on the same sheet.

3.2.2.3 Local grid survey

The studied site had never been surveyed before and there was no information which could have been used to tie it to the British National Grid, so an arbitrary co-ordinate system was used as a basic framework to carry out a local grid survey. Only Block 3 was surveyed (with the help of the students of Leeds College of Building) as most of the radiotracking sessions were carried out in this Block.

3.2.2.3.1 The surveying equipment

The equipment used for surveying the enclosure in block 3 was an integrated survey system called, Total Station, (the brand name is SOKKISHA DT4/RED2A/L). It is a combination of an electronic digital theodolite (5 seconds accuracy), electromagnetic distance measuring (EDM) equipment and a data processor which gives x, y and z co-ordinates directly (Clancy, 1991). This compact device, when in use, was mounted on a tripod. Its main function was to analyse field data to determine angles of slopes and horizontal distances, as well as differences in elevation (Herubin, 1991).

3.2.2.3.2 Field work

A closed traverse was defined as a means of horizontal control. The traverse consisted of a set of four stations each marked by a peg into which a nail was driven. Each station was located by direction and distance from the adjacent stations. All stations were connected by fictive lines called courses. The trapezoid shape of the enclosure made it impossible to have a squared traverse, so only two of the angles were squared.

Once the traverse was set up, the positions of few chosen trees and hedges were determined by the direction and distance from each of the four stations. These results were recorded and subsequently treated. The objects chosen were:

- The corners of the wind break hedge of the enclosure;
- The first and the last tree in each tree row;
- The corner trees located in the forestry control;

The total station (theodolite + EDM), using a ‘Radiation Detail Survey System’, works out distances and angles of all the elements determined such as horizontal angles, vertical angles and horizontal distances. EDM is based on measuring the transit time of an electromagnetic beam emitted from a transmitter/receiver to a reflecting target prism and back again. The direct slope distance is measured and displayed digitally.

The dense vegetation in the tree rows and the high crop made it impossible to do the elevation survey of the whole site from one station. The observations were therefore made from two stations, while the others were used as reference objects. A selective strategy of sampling was adopted. It should have required more than 3000 samples if the 2m x 2m grid was fully surveyed, which was too time consuming. The observations recorded were the horizontal angles (degrees, minutes and seconds), the horizontal distances and the height differences.

Data input was processed by the combined data processor which immediately gave x, y, and z co-ordinates straight away. A map was drawn, using the information collected in the field and computed in the laboratory, showing the natural features defined above (See Figure 6.1).

4. DISTRIBUTION OF SMALL MAMMALS

4.1 Introduction

Although woodlands are typical fragmented habitat for most small mammals of the agricultural landscape (Zhang and Usher, 1991), some authors have found that *A. sylvaticus*, for instance, prefers arable farmland (Pollard and Relton, 1970). However, they are unanimous in describing hedgerows, narrow strips of woody vegetation, as barriers between fields, which also connect isolated woodlands (Zhang and Usher, 1991). The cropped fields may also connect wooded areas but only when the crop is high enough to provide cover against predators (pers. observation). In agricultural regions, scattered woods may provide, in addition, useful and vital refuges for woodland animal communities (Wegner and Merriam, 1979; Ylönen *et al.*, 1991).

The agroforestry system represents a ‘coalition’ between arable land and isolated woody areas, thereby generating a more diverse environment. It provides an arable crop, timber, fodder and fruit, thus diversifying and even increasing crop yield (Atta-Krah and Francis, 1987). The experimental agroforestry site at the University of Leeds farm is described in Chapter **2**. Although the distribution of small mammals is unknown in such a system, the isolation of the tree rows would imply that the replicate blocks are fragmented habitats. The distribution of small mammals on the site was investigated with regard to the following hypotheses:

1. The blocks are replicates and thus the probability of captures remains the same for all of them;
2. Small mammals are distributed within blocks as well as along mature hawthorn hedges;

3. The animals are equally distributed between treatments within the agroforestry system, including the forestry and arable control treatments;
4. There is no difference in the number of captures within treatments between blocks;
5. Season and weather do not affect the distribution of small mammals.

4.2 Methods

For the purpose of analysis, capture data was pooled by block, 'mature hedge' and treatment. The number of traps set in the treatment areas were different from those laid out along the mature hedges, so capture numbers were standardised in relation to the number of trap-nights set by habitat during the whole period of trapping (Wegner and Merriam, 1979). Zhang and Usher (1991) defined the average density as the number of animals caught per 100 trap-nights.

It is necessary to describe here the main steps of the analysis of these preliminary data. Species caught only a few times have been ignored to avoid any undue bias. The average density of each species that was caught in reasonable numbers was calculated for each habitat in each block and for each of the mature hedges. The data needed to be normalised as we are dealing here with samples of counts (number of captures) which have, most probably, been drawn from a freely distributed population, therefore presenting substantial differences between the variances of mean captures. The homogeneity of variance was tested using the F_{max} test. The number of captures was normally distributed when the year was divided into quarters corresponding to the seasons, i.e. Winter (mid - December to mid - March), Spring (mid - March to mid - June), Summer (mid - June to mid - September) and Autumn (mid - September to mid - December). This division was also convenient for a comprehensive analysis of the effects of season on animal distribution.

The density of captures was calculated for each habitat as follows:

$$100\frac{N_A}{S_A \times T_A}$$

where N_A is the number of captures in an area A, S_A the number of trapping sessions carried out in this area and T_A the number of traps set out in each of these sessions.

To overcome the problem of zero observations the next step was to apply logarithmic transformation to the data set and add 1 to each observation so that; $y = \log(x + 1)$, were x is the mean captures over 100 trap nights.

A single factor Analysis of Variance F-test, backed with t tests, was carried out to test for differences in density of captures between replicate blocks and mature hedges. Variation and interaction between treatments were investigated using a two factor ANOVA, where either replicate blocks or season of capture were used as a second independent variable. A more sensitive test for distinguishing differences between mean density of captures by habitat was used afterwards. The Tukey test was applied here as it is especially designed for pairwise comparisons. This method makes several mean comparisons without increasing the risk of rejecting the null hypothesis when it is true or accepting it when it is false (at the 5% level of significance). The construction of a trellis for the comparison of all sample means was made using a FORTRAN 77 program. Mean differences were tested against the critical value.

$$T = Q_{(a,v)}\sqrt{\frac{MS}{N}}$$

Where Q is given by the distribution of Q in a Tukey table for a number of samples and v degrees of freedom. MS is the within samples variance obtained from the ANOVA output. N is the number of observations per sample.

Correlation between weather variables and number of captures was investigated using the Spearman rank correlation coefficient test.

4.3 Results

4.3.1 Species caught

The main species caught during the three years of study were *Apodemus sylvaticus* (Rodentia, Muridae), *Clethrionomys glareolus* (Rodentia, Cricetidae) and *Sorex araneus* (Insectivora, Soricidae). *Mus musculus* (Rodentia, Muridae) and *Sorex minutus* (Insectivora, Soricidae) were also caught, but very occasionally.

A total of 1680 captures were recorded between 20 December 1994 and 8 August 1997. Of these *A. sylvaticus* comprised 69% of the catch, *S. araneus* 20%, *C. glareolus* 10%, and *M. musculus* and *S. minutus* together 1% (Figure 4.1). In the analysis, the number of captures was related to the number of trap nights used over the three years. It is important to note that *A. sylvaticus* is more attracted by food within traps than the other species and thus the ‘trap shy’ animal that avoids traps and the ‘trap addict’ which will enter them at every possible opportunity tend to bias the results (Delany, 1974).

Neomys fodiens (‘the water shrew’: a large shrew with a dark coat, white fur in the ventral side, and white tufts of fur around the eyes and the ears) was caught on two occasions within the forestry control in Block 1. This is an important observation as the habitat at the farm does not correspond to its aquatic way of life and also this species has not hitherto been recorded as present in the area. It occurs throughout the British mainland and most of the islands but it tends to have a localised and sporadic distribution (Churchfield, 1986).

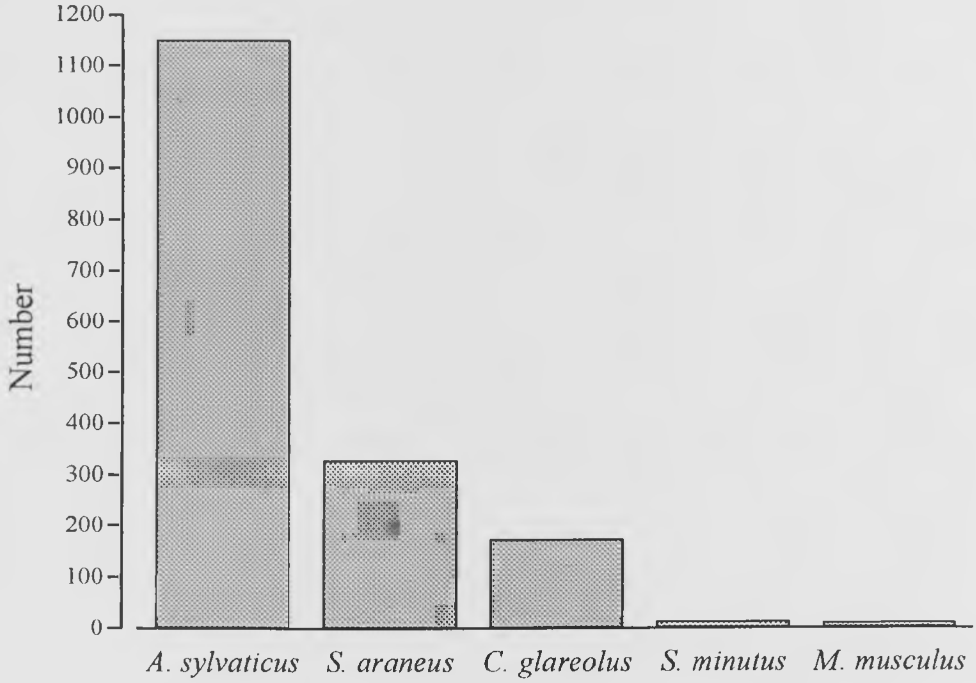


Figure 4.1 The total number of captures of small mammals between December 1994 and August 1997 at the University of Leeds farm.

4.3.1 Density of trapping within blocks and mature hedges

4.3.1.1 Overall distribution

The number of captures of small mammals recorded within replicate blocks and mature hedge units during the whole study period are presented in table 4.1. In examining the trapping results for all species together, it appears that their average density in the replicate blocks and along the mature hedges show no significant variation in number (F = 0.28, P = 0.92). Despite the differences in density of captures between blocks and mature hedges (Figure 4.2), none of the comparisons carried out show any statistical difference at the critical level of P = 0.05.

The density of captures recorded in each of the three years of study was compared to look for any annual variations. This shows a highly significant difference between the means (F=11.85, P = 0.0008), with the number of captures recorded during 1996 being greater than the year before (t = 5.42, P = 0.0002) or the year after (t = 3.60, P = 0.0029). However, trapping was stopped in August 1997 and hence the Autumn 1997 data were missing, which could have affected the last comparison.

Table 4.1 Number of captures within replicate blocks and along mature hedges.

	Location					
	Block 1	Block 2	Block 3	Block 4	MH I	MH II
Species						
A. sylvaticus	189	199	287	188	124	166
C. glareolus	17	12	6	1	95	43
S. araneus	64	66	44	40	43	71
S. minutus	0	0	2	3	3	5
M. musculus	1	3	1	1	1	5
Total caught	271	280	340	233	266	290
Number of TN*	3072	3360	3120	3360	1764	2232

(*) TN = Trap nights

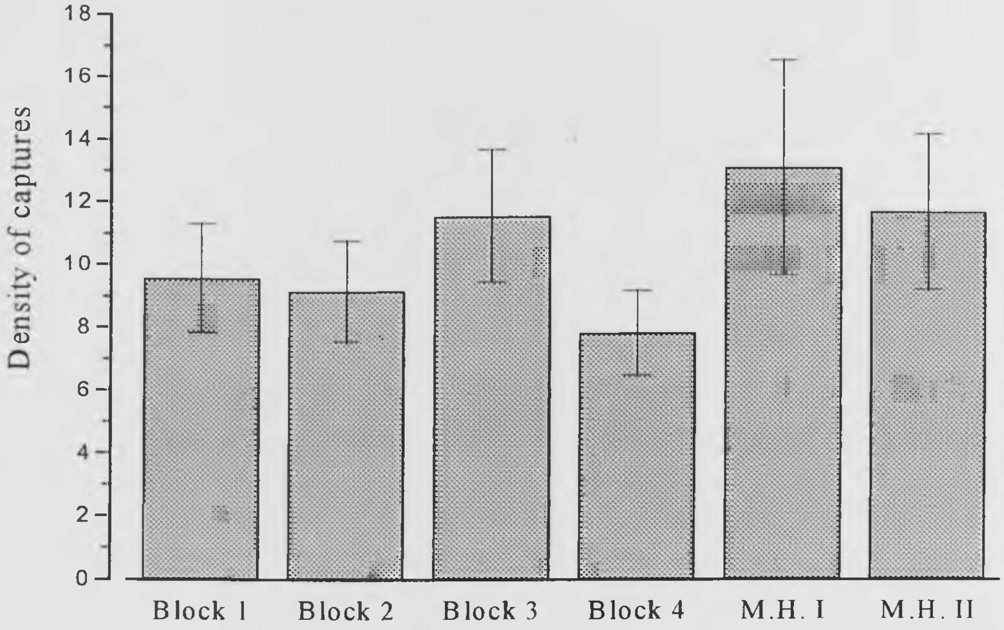


Figure 4.2 Density of captures of small mammals in blocks and mature hedges (mean of captures/100 trap nights ± 1 standard error) between December 1994 and August 1997.

4.3.2.2 Distribution of species

In an ANOVA the average density of *A. sylvaticus* showed no significant differences between blocks and hedges throughout the period of study ($P = 0.33$). This species was caught wherever trapping was carried out (Figure 4.3). In contrast, *C. glareolus* was mainly distributed in the wooded vicinity of the replicate blocks rather than in them. 80 % of the catch was made along the mature hedges and thus a highly significant difference in the average density of captures was registered between blocks and mature hedges ($P < 0.001$). The paired comparison of the distribution along mature hedges and replicate blocks is presented in Table 4.2. Moreover, the density of captures of *C. glareolus* in mature hedge I (4.89 ± 1.47 SE) was more than twice that in mature hedge II (1.73 ± 0.52 SE); thus $t = 1.90$ for $P = 0.04$ (Figure 4.3).

Table 4.2 Comparison of the densities of captures of *C. glareolus* between replicate blocks and mature hedges.

	Significance (P)	
	Hedge I	Hedge II
Block 1	0.003	0.006
Block 2	0.001	0.001
Block 3	0.001	0.0004
Block 4	0.0005	0.0001

C. glareolus had almost vanished from the catch in block 4 after a few animals were caught in the first year of trapping, and hence significant differences were observed when block 4 data was compared with block 1 (t = 2.16, P = 0.02), block 2 (t = 2.10, P = 0.03) and block 3 (t = 1.88, P = 0.04).

Although the overall distribution of *S. araneus* showed no significant variation between the different blocks (F = 1.07, P = 0.39), this species presented low densities of captures in blocks 3 and 4 (east) combined and compared with blocks 1 and 2 (west), t = 1.82, P = 0.03. Densities were also different between mature hedges I (west) and II (east); t = 1.94, P = 0.02 (Figure 4.3).

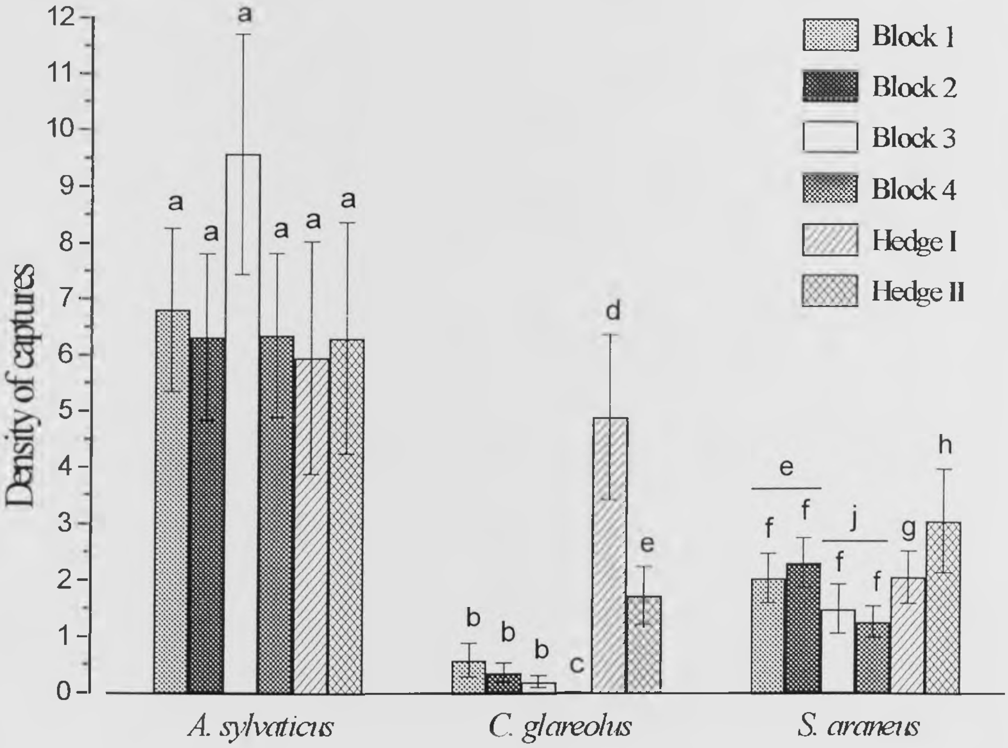


Figure 4.3 Density of captures of *A. sylvaticus*, *C. glareolus* and *S. araneus* in blocks and mature hedges (mean of captures/100 trap nights ± 1 standard error) between December 1994 and August 1997. Values with the same letters are not significantly different at $P = 0.05$.

4.3.3 Distribution within treatments

4.3.3.1 Overall distribution

The number of animals caught in each treatment is shown in Table 4.3. A significant variation in the mean density of captures was found between these treatments ($F = 4.30$, $P = 0.01$). Overall, there were higher capture in the agroforestry areas compared with the controls ($z = 4.41$, $P < 0.001$). Moreover, the tree rows show higher density of captures than the arable alleys ($z = 1.90$, $P = 0.02$).

Table 4.3 Number of captures registered between December 1994 and August 1997 within Agroforestry and Control treatments (AA = arable alleys, TR = tree rows, FC = forestry controls and AC = arable controls). Based on 3228 trap nights.

	Habitat			
	Agroforestry		Controls	
Species	TR	AA	FC	AC
A. sylvaticus	330	233	177	123
C. glareolus	10	3	23	0
S. araneus	90	38	75	11
S. minutus	2	3	1	0
M. musculus	0	2	2	1
Total caught/habitat	432	279	278	135

4.3.3.2 Distribution within-treatments between-blocks

A two way ANOVA was carried out to estimate the effect of blocks on density of captures within the same treatments. A considerable difference in density was revealed when all the habitats were compared at the same time ($F = 10.43$, $P < 0.001$). In the same treatment, there were no differences between the blocks except for arable control captures (Table 4.4).

Table 4.4 Comparisons between density of captures ± 1 standard error between blocks within the same treatment (AA = arable alleys, TR = tree rows, FC = forestry controls and AC = arable controls). Values with the same letters are not significantly different from each other at $P = 0.05$ (ANOVA).

Treatments	Block 1	Block 2	Block3	Block 4	F	P
AA	0.86 ± 0.12	0.90 ± 0.006	1.11 ± 0.07	0.81 ± 0.09	2.46	0.08
TR	1.04 ± 0.13	1.11 ± 0.11	1.04 ± 0.15	0.92 ± 0.16	0.31	0.82
FC	0.89± 0.16	0.94 ± 0.12	0.79 ± 0.12	0.78 ± 0.09	0.33	0.80
AC	0.42 ± 0.11^a	0.40 ± 0.10^a	0.87 ± 0.09^b	0.69 ± 0.06^b	6.14	0.002

4.3.3.3 Distribution of the species caught

The habitat effect on density of captures for *A. sylvaticus* and *S. araneus* was examined by comparing the mean density of captures of each species in the four habitats constituting the experimental replicate blocks (Figure 4.4). The small number of captures of *C. glareolus* recorded during the whole study period within the agroforestry and the control habitats meant that a corresponding analysis could not be carried out for this species.

A. sylvaticus was widespread over the whole area but preferences are indicated by the analysis ($F = 5.74$, $P = 0.0009$). Thus the agroforestry habitats seem to be more attractive to this animal when compared with the controls. In fact the tree rows shelter more *A. sylvaticus* than the forestry control ($Z = 2.13$, $P = 0.008$), as do the arable alleys when compared with the arable controls ($Z = 3.64$, $P < 0.001$). Despite the greater number of captures recorded along the tree rows in comparison with the arable alleys, no significant trend was registered in the distribution of this species between the different agroforestry habitats (AA and TR); $Z = 0.58$, $P = 0.14$. Densities of captures within arable alleys (AA) when compared with those of forestry control (FC) showed a significant trend ($Z = 1.89$, $P = 0.01$) just as for the controls (AC and FC) compared together ($Z = 1.31$, $P = 0.04$).

S. araneus seemed to prefer the agroforestry habitats to the controls. Their densities were greater along the tree rows than within the forestry controls (Z = 1.85, P = 0.01) and even more within the arable alleys compared to the arable controls (Z = 2.30, P = 0.005). However, in contrast to *A. sylvaticus*, *S. araneus* showed higher densities along the tree rows compared to the arable alleys (Z = 3.92, P < 0.001). Between controls comparisons of density of captures showed a significant trend towards the wooded area both for *A. sylvaticus* (Z = 1.31, P = 0.04) and particularly for *S. araneus* (Z = 4.22, P < 0.001).

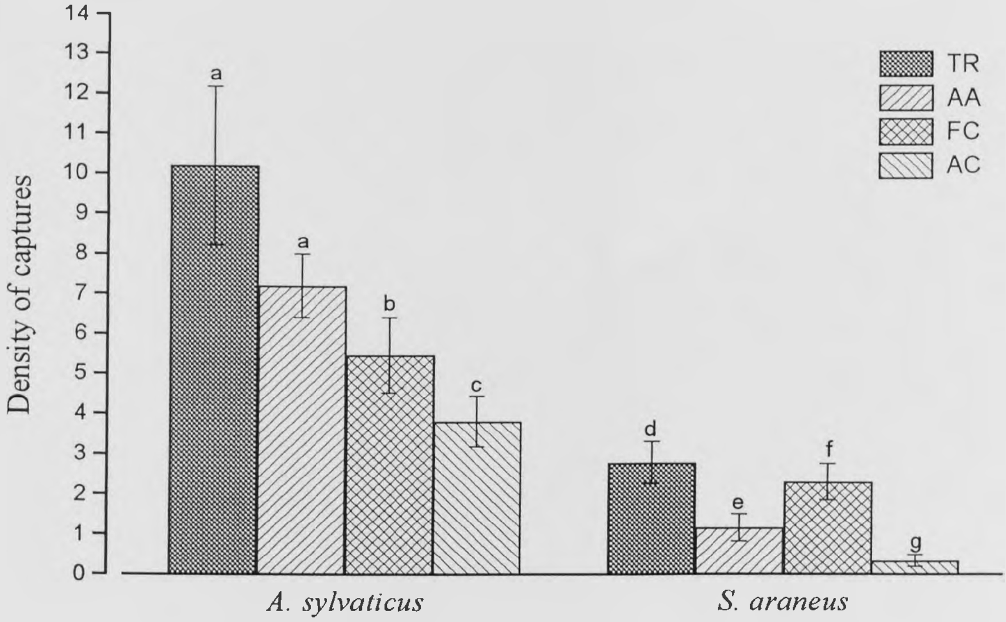


Figure 4.4 Density of captures of *A. sylvaticus* and *S. araneus* (Mean of captures/100 trap nights ± 1 standard error) within the different habitats (AA = Arable alley, AC = Arable control, FC = Forestry control and TR = Tree row) between December 1994 and August 1997. Values with the same letter are not significantly different from each other at P = 0.05.

4.3.4 Effects of season on captures

4.3.4.1 Overall captures

Density of capture varies according to the time of the year ($F = 9.47$, $P < 0.001$). Autumn was the season with the highest density of captures as compared with Spring ($t = 11.88$, $P < 0.001$) or Summer ($t = 5.79$, $P = 0.0003$) in 1995. The following year the same pattern of distribution of density of captures was observed.

Density of captures in the Autumn were highly significantly different from those of Spring ($t = 8.57$, $P < 0.001$) and Summer ($t = 5$, $P = 0.0008$). No significant differences between mean density of captures were registered between the other seasons within each year (Figure 4.5).

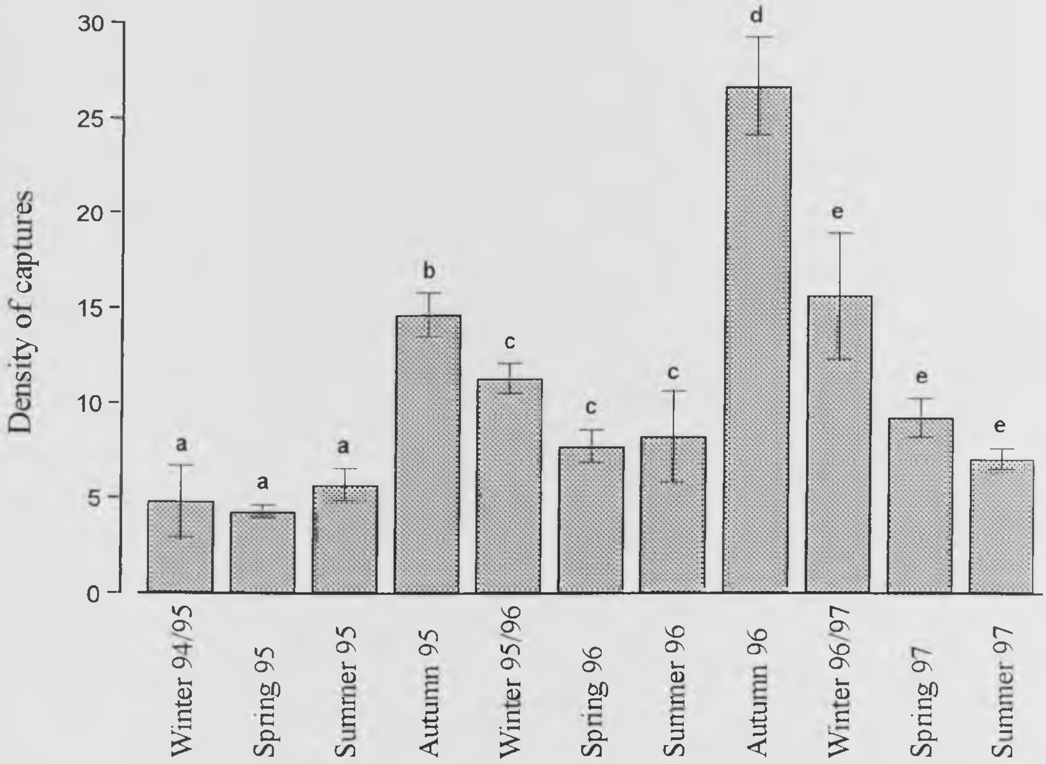


Figure 4.5 Density of captures (mean captures/100 trap night ± 1 standard error) recorded by season. Values with the same letters are not significantly different from each other at $P = 0.05$.

4.3.4.2 Within block captures

Each block contains a cereal crop, an understorey beneath the tree rows and a forestry area, all of which show seasonal changes. This variety of changing habitat causes the animals to have a seasonal, periodic pattern in their distribution ($F = 6.04$, $P < 0.001$), except for *C. glareolus* which is constantly found in the undergrowth of the mature hawthorn hedges whatever the trapping period ($F = 1.11$, $P = 0.35$).

A. sylvaticus numbers declined by late Winter and were very low during Spring. Indeed, only 1 to 5 animals were caught during some sessions in April. The poorest records were, nevertheless, generally registered during July. Following this, numbers rose sharply and remained high throughout the Autumn and a large part of the Winter. Thus, there was a clear seasonal pattern of distribution ($F = 11.65$, $P < 0.001$). *S. araneus* showed a similar seasonal pattern ($F = 4.20$, $P < 0.001$) but with a difference in timing with regard to the periods of increase and decrease in density of captures.

Even though variations in density of captures were influenced by changes over the seasons, weather conditions do not seem to have played a major role in these differences. The only significant correlation found between climate variables (grass temperature, rainfall, wind speed and maximum temperature) and number of captures was a weak negative correlation with maximum temperature ($r_s = -0.21$, $P = 0.013$).

4.3.4.3 Interactions

The effect of density of captures and type of habitat in different periods of the year are not additive. Thus the transition from one season to the next did not add or subtract an equal number of captures from each habitat. Catch numbers were not following the same pattern in these habitats. Therefore, there was a significant interaction in the distribution of the animals between habitat and season. Overall, there were a negative interaction ($F = 3.20$, $P < 0.001$). The interactions of both *A. sylvaticus* (Figure 4.6) with $F = 3.67$ at $P < 0.001$ and *S. araneus* ($F = 1.63$, $P = 0.03$) showed this significant trend.

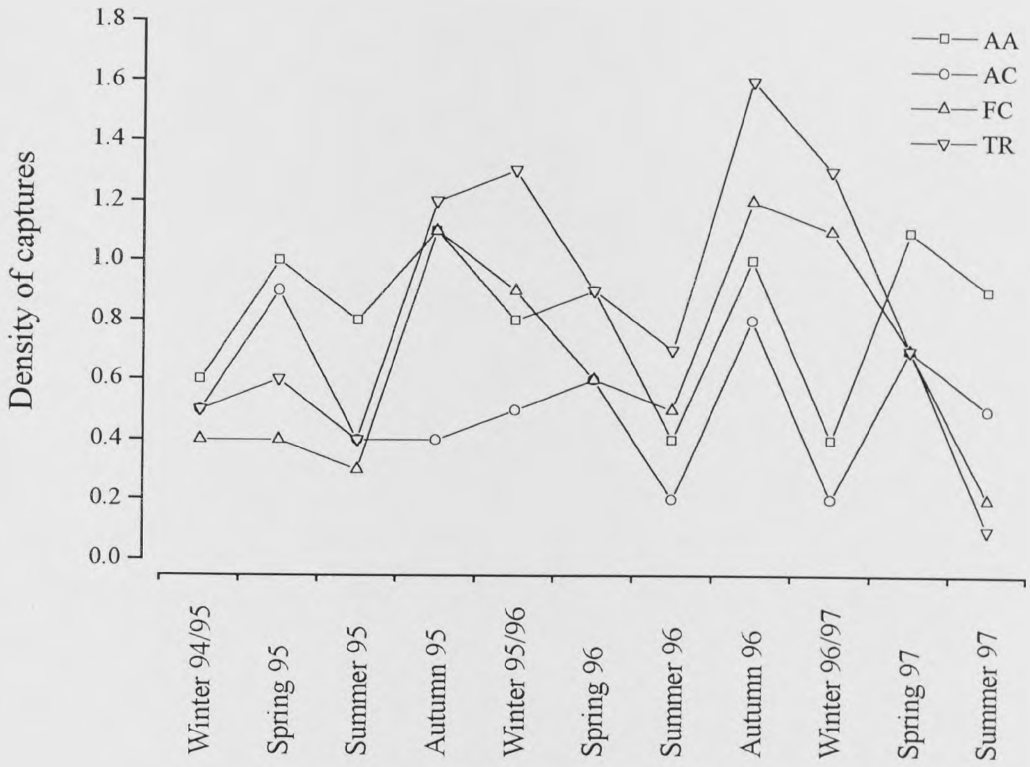


Figure 4.6 Density of captures of *A. sylvaticus* within each habitat in each season.

4.3.4.4 Seasonal changes in relation to habitat

More than 10% of the comparisons made between density of captures of *A. sylvaticus* during the different seasons over the period of study revealed significant differences compared to the critical Tukey value T = 0.811, P = 0.05. Three quarters of these, that is 71 out of 96, involved density of captures within tree rows compared with densities in other habitats at different periods of the year. Forestry control habitats were involved in 44 comparisons, arable controls 32 times and the arable alleys 26 times. Most of the comparisons concerned density of captures during the Autumn and Winter. In fact 61 out of the 96 significant trends involved captures during the Autumn. This is clearly shown by the large discontinuous band on the seasonal distribution diagram (Figure 4.7). These significant differences were often revealed by the comparisons made between capture densities recorded in different habitats but it happened that sometimes the same habitat showed significant trends at different seasons. This was particularly the case in the wooded areas (tree rows and forestry controls).

Overall, wooded areas showed significant differences compared to cropped areas, notably during the Autumn. This pattern was particularly noted during 1995 and 1996. The most significant trend was shown by the comparison of density of captures involving tree rows. In 1996, differences in density of captures between tree rows and arable alleys during the Summer and the Autumn/Winter period were highly significant. The same tendency was found in the comparison of capture densities in the tree rows and the controls (AC and FC) for the same year. No significant differences were registered between density of captures in the arable alleys and the tree rows in relation to seasonal variations.

Few significant results concerning the distribution of *S. araneus* in relation to season were revealed by the Tukey method (11 significant pairs out of 946 possible pairs). The density of captures of this species did not reveal any differences either between wooded areas (TR and FC) or between arable areas (AA and AC). However, as for *A. sylvaticus*, capture densities registered during the Autumn of 1996 in the tree rows were highly significant compared to the arable alleys or to the arable control at different periods of the year (Figure 4.6).

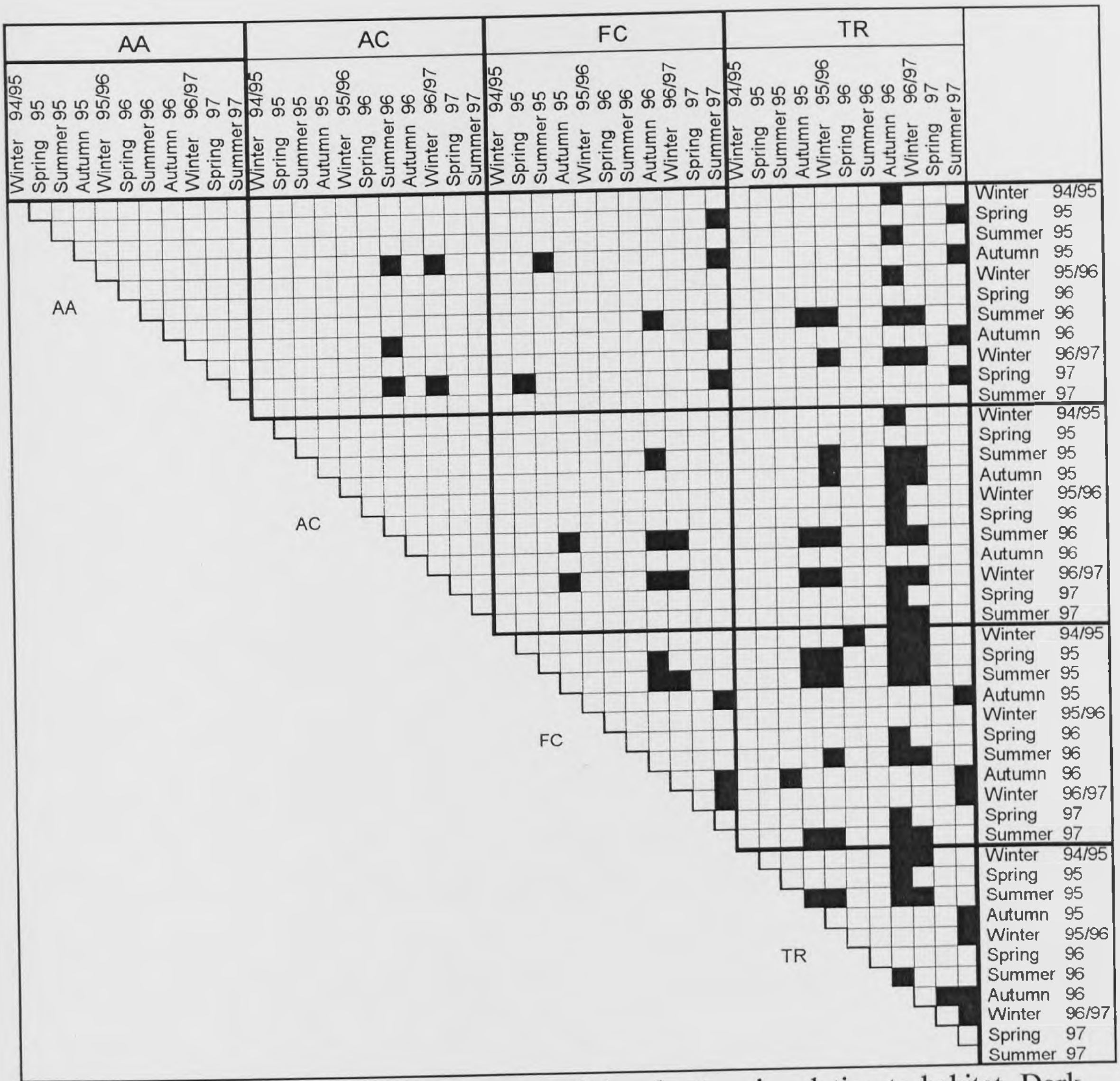


Figure 4.7 Influence of season on captures of *A. sylvaticus* in relation to habitat. Dark squares represent significant comparisons (Tukey test).

4.4 Discussion

None of the studies so far carried out in the agroforestry environment at the University of Leeds farms has examined the distribution of small mammals. The benefits to fauna of agroforestry have nevertheless been highlighted in insect distributions (Naeem, 1996; Callow, 1995; Peng *et al.*, 1992; Peng *et al.*, 1993), with overall results that have implications for agroforestry.

The first statement to make is that in no way should small mammals be considered as a threat to the system in general or to the crops in particular. No damage has been reported, so far, due to the presence of the rodents. Thus the overall density of captures reflects an acceptable level of presence.

We have seen that, from year to year, the density of captures changed. Although it is true that the size of any animal population tends to change with the amount of food available (Nicholson, 1954; Smith, 1971), it must not be assumed that food abundance is the only factor which explains changes in density of captures. Overall, increases were observed in 1996 as compared with 1995 and in particular for *A. sylvaticus* capture density, despite the same abundance and type of natural food. Flowerdew (1972) experimented variation in abundance in relation to food supplies and reached the same conclusion, i.e., no regular pattern is shown from one year to the next. When natural food is abundant, its availability is not a proximate factor regulating the density of animals, particularly mice (Flowerdew, 1987). The most plausible explanation is that the offspring in 1995 overwintered in great numbers. Helped by a good Summer and a mild Autumn, they may successfully overwinter, even in arable land (Tew, 1994).

Weather may affect microtine populations (Davis and Golley, 1963; Krebs and Myers, 1974), and it is known that low temperatures stimulate the activity of small mammals (Davis and Golley, 1963). Nevertheless, the activity of the species studied here did not seem to be affected by climatic conditions. In fact only a slight correlation was detected between density of captures and maximum temperatures making it difficult to draw any meaningful conclusion.

4.4.1 Influence of the habitat on distribution

4.4.1.1 Block and hedge effect

The proportion of *A. sylvaticus* caught and their distribution led to the conclusion that this animal is a habitat generalist using the agroforestry in harmony with its needs. The switch from the arable field to this multi-habitat system is probably due to the diversification of plants found in the latter, these providing further diversification in the habitat available to this animal. In contrast, *C. glareolus* is considered as a habitat specialist (Rogers and Gorman, 1995) and is known to be a woodland species (Hansson and Zejda, 1977; Alibhai and Gipps, 1985). It was caught mainly along the mature hawthorn hedges in relatively small numbers. Appearance in such 'marginal' habitats is probably the result of the presence of *A. sylvaticus* in large numbers within the forestry controls and the tree rows. The risk of competition between these two rodents is high, making habitat selection weak for *C. glareolus* (Hansson, 1979a). The disappearance of the latter from block 4 in 1996 is a good example of competition, as at the same time the density of captures increased along mature hedge II, particularly at the far end alongside block 4. *C. glareolus* could have moved into the hawthorn hedge because of the pressure of the competition and the dominance of *A. sylvaticus* (Kikkawa, 1964). Moreover, the *C. glareolus* population failed to reach high numbers and the density of captures was low. In many northern habitats, the population of small microtine rodents show enormous changes over the years, alternately exploding and crashing.

The 'delicate' *S. araneus* is known to be more susceptible to noise or shock than any other small mammal (Crowcroft, 1957). They are often found dead in the traps, not only because of their sensitive reaction to shock but also because of their continuous need of food. They have to eat a large amount of food frequently to survive, and therefore have to find a sufficient quantity of prey. Despite their opportunist feeding habits, they penetrated deeply into fields, probably looking for invertebrates, which may explain the substantial number of animals caught in the arable controls. In terms of density of captures, they were higher in areas far away from disturbed areas such as the road (e.g. Block 3, Block 4 and MH II).

4.4.1.2 Distribution within treatments

In the habitats studied, the animals, except for *C. glareolus*, were unevenly distributed in the agroforestry system. This is due to the uneven presence of favourable components in this habitat, such as cover and food availability.

The comparison made between density of captures in the agroforestry habitats and the controls indicates that cover is the more important factor. Thus it is clearly shown that the presence of trees influences the distribution of animals such as *A. sylvaticus* and *S. araneus* and that the former is present in greater numbers than the latter. Agroforestry seemed to be the appropriate habitat, notably for *A. sylvaticus*, in providing food and shelter found in both habitats (tree rows and arable alleys). Within the tree rows (as in woodland), seeds were among the sources of food, particularly in the Autumn and Winter, but sown grain and later seedlings of the nearby arable areas as well as arthropods were part of this rodent's diet, whereas grass and weed leaves provided a thick cover all over the year. On the arable alleys the diet was influenced by both crop of the year past crop. Before the harvest, Winter wheat and Winter barley provided not only food but also thick cover.

A. sylvaticus is present in significant numbers within tree rows and forestry control areas. This is of interest, since this presence may be important in promoting tree regeneration, as the consumption of a certain amount of vegetation is important when the bulk of primary production is shed each year, and grazing assists regrowth of the plant biomass (Golley *et al.*, 1975; Hayward and Phillipson, 1979).

Although *S. araneus* should be assessed through numbers in wooded habitats (tree rows and forestry controls) rather than in the arable habitats, large numbers of captures were made within the arable alleys and even deeper within the arable control. If the density of captures still remains low, notably during the Winter, this may not reflect their real population density, as the type of traps utilised may not be suitable for catching such a small species (Evans, 1942). Movements of animals between the agroforestry habitats are generated by particular needs, specific to each period of the year. Indeed, it is hard to explain the preference shown by animals for certain habitats without putting it into a seasonal context.

4.4.2 Seasonal distribution

The classical pattern of seasonal distribution is clearly shown for *A. sylvaticus* but not for *S. araneus* and *C. glareolus*. Capture data for the two last species were too low to draw any conclusions about effect of season. During Spring, *A. sylvaticus* showed no habitat preference within the agroforestry system, being found throughout the area. The field and the arable alleys provide much more food than the wooded areas (TR and FC), which provide shelter and nesting sites (Alibhai and Gipps, 1985; Pollard and Relton, 1970). However, by the Summer, significant preferences were being shown, with the density of captures tending to decrease rapidly in the cropped areas (AA and AC) and to increase in the wooded area, following the harvesting of the crop. Thus, the animals moved into wooded areas looking for safer shelters. Decrease in densities within the arable areas after harvest may also be due to the high level of predation because of the lack of vegetation cover (Tew and Macdonald, 1993). However, Autumn and Winter are definitely the most important seasons for population movements in *A. sylvaticus.*

Captures within tree rows were very important during this period making it a ‘sanctuary’ for this species. This is supported by the recent work of Fitzgibbon (1997), who observed that there was a marked increase during Autumn and Winter in the number of animals in isolated woodland surrounded by a wheat field.

5. POPULATION DYNAMICS OF *Apodemus sylvaticus* IN AN AGROFORESTRY ENVIRONMENT

5.1 Introduction

One of the most common problems faced by the field ecologist working on animal communities is to estimate the size of the population studied. Consequently the use of sampling methods in the enumeration of populations has become widely accepted. This is particularly true for populations which are mobile in space (Chapman, 1954). However, trapping in a population of wild animals does not give a sample covering all the possible individuals alive at a given time (Leslie *et al*, 1953).

Live trapping collects data at the level of the individual. Once gathered and processed, the information reveals details about the population, notably its density and other parameters related to it. Many ways have been suggested in the literature concerning non-removal census methods, amongst them the Mark-Release-Recapture (MRR) (See reviews by Blower *et al.*, 1981 and Seber, 1986).

MRR methods use information from marked animals whether subsequently recaptured or not. The main ones often used are the Fisher-Ford method (Fisher and Ford, 1947), the Jolly-Seber method (Jolly, 1965; Seber, 1965) and the Manly-Parr method (Manly and Parr, 1968). These methods rely on assumptions that should not be violated but no one study ever satisfies all assumptions in detail (Begon, 1979). Furthermore bias might be attributed, among other things, to trapping frequency, trap spacing, individual trap response and heterogeneity of habitat (Kikkawa, 1964).

Data collected from December 1994 until July 1997 in the agroforestry plots contain information related to the structure and the dynamics of the population living within each block at various times of the year. The combination of habitat in the agroforestry system is yet another factor which is important in the study of population dynamics, notably in small mammals. Diversity of habitat is, in fact, an important factor affecting successful reproduction and survival (Rogers and Gorman, 1995). The response of populations to ecological changes can be related to behaviour (Sutherland, 1996) and it is now accepted that animal behaviour and population dynamics should be studied in conjunction.

The aim here is to investigate the population by estimating:

- The density of population (Number of mice/ha).
- The probability that an animal alive at a sampling session i survives and remains in the population at the following session ($i + 1$), hereafter called the probability of survival. Individuals which emigrate are considered as losses in the same way as individuals which die (Krebs, 1989).
- The dilution rate to the population between two successive sampling sessions, including both addition by births and by immigration (in recapture data there is no established way of distinguishing immigration into an area from births which occur there (Kikkawa, 1964)). This can also be expressed as the number of new individuals joining the population, also called the added population.
- The rate of change of the population knowing that mammals display a number of patterns over both short and long time periods (Delany, 1982).

The inferences that may be drawn from mark-recapture data are strongly affected by trappability (Krebs and Boonstra, 1984) and thus a measure of this parameter is required for this study. Continuous breeding of *A. Sylvaticus* was recorded as mentioned by Smyth, (1966) but do males and females show the same onset and duration of breeding?

5.2 Analytical methods

It is often difficult or impossible to count the individuals in a given place. This research aims to obtain a reliable estimate of the density of a population of *A. sylvaticus* living within an agroforestry system. The sampling design had to be appropriate to represent, with as much accuracy as possible, the potential of this small mammal population to occupy such a fragmentary habitat. The trapping layout was designed for each of the four blocks as described in section **3.2.1.1**.

The individuals caught were marked and released (Section **3.2.1.2**) and given time to become distributed at random in the population. In the following sampling session another sample of individuals was collected, which might contain previously marked individuals. This marked part of the population contains the information needed to perform estimations of the properties of the population at this date. Amongst all species caught, only *A. sylvaticus* showed sufficient recaptures to allow detailed analysis.

5.2.1 Estimates of population density and related parameters

Fisher and Ford's method uses an arbitrary chosen rate from which the number of marks expected to survive is calculated (Blower *et al.*, 1981). Their results on the spread of a gene in natural conditions in a colony of the moth *Panaxia dominula* L. (Fisher and Ford, 1947) were consistent with a constant death-rate. This assumption hardly holds in small mammals populations. However, this is not an assumption of the Jolly-Seber and the Manly-Parr methods. Nevertheless, all three methods assume a random sampling of the population. The estimate of the marked fraction before and after a sampling session *i* using for instance, the Jolly-Seber method can be compared with the Manly-Parr method (Seber, 1973). However, the Manly-Parr method requires many multiple recaptures and it is thus rarely possible to use it in practice. The minimum number of animals known to be alive (MNA) method (Krebs, 1966) can also be used to estimate the population density, particularly in small rodent populations. It is a direct enumeration method, sometimes called the direct census (Blower *et al.*, 1981).

The Jolly-Seber method is one of the best known and most useful methods for the analysis of capture-recapture data (Manly, 1984). However, its apparent inability to handle more than one class of age limits its utility for small mammal studies (Nichols and Pollock, 1983). The full model is used for the estimation of the population sizes and also for estimating the probability of survival of the marked part of the population. The Jolly-Seber method relies on the random sampling assumptions that every individual has the same probability of surviving from the ith to the $(i + 1)$th sampling session, marks are permanent and not overlooked at capture, sampling is instantaneous, and marked and unmarked individuals have equal catchability. The last assumption is the most critical (Krebs, 1989). Equal catchability can be tested by Leslie's method (Leslie *et al.* 1953). However, Roff (1973) has shown that the formulae proposed by Seber (1965) for estimating the population density and the other variables are not reliable for the calculation of their confidence intervals and thus estimates of standard errors cannot be relied upon to measure sampling errors. Therefore, the method proposed by Manly (1984) is used to calculate the 95%

confidence limits and ascertain the estimation of the size of population and the probability of survival made by the Jolly-Seber method.

Preliminary analysis of the results (Sections **5.3.1**, **5.3.2** and **5.3.3.1** below) indicated that use of the Jolly-Seber method was inappropriate. Subsequent analyses thus utilised the MNA method, which generate similar estimates to that of the Jolly-Seber method (Hilborn *et al*., 1976); both appear to provide good estimates of field populations.

The MNA method uses the number of captures during a trapping session i (week i) that is n_i and the number of marked individuals caught after i (Z_i), but not during i. Marked animals caught before i and subsequent to i are known to be alive during i. Thus, the estimated total number of individuals in the population during the sampling session i is obtained by adding (n_i) and (Z_i).

$$N_i = n_i + Z_i$$

The rate of population changes is then defined from the series of population estimates as:

$$100 \frac{N_{i+1}}{N_i}$$

The number of animals known to be alive within the trapped area is then extended to the number known to be alive in one hectare area to get the estimated density of population.

Variables such as probability of survival (Φ_i), and dilution rate were also estimated. The probability of survival helped in estimating losses and gains in the number of individuals due to migration, birth and death. It is also a way of quantifying life expectancy (Begon, 1979); the higher an animal's chance of survival, the longer it can be expected to live. The probability of survival is the probability that an animal alive at the moment of its release in the ith sampling session will survive until the (i + 1)th session. It is given by the ratio of the number of marked animals before sampling session (i + 1) (r_i) over the number of marked animals present after release on sampling session i (R_i).

$$\Phi_i = \frac{r_i}{R_i}$$

The estimate of the number of animals lost because of death or emigration is thus related to the survival rate estimate. On the other hand, a certain number of individuals enter the population through birth and immigration. They are therefore, called added individuals or new animals joining the population between sampling session i and sampling session (i + 1). It is the number of animals supposedly present on sampling session (i + 1) less those expected to survive from sampling session i. However, capture-recapture methods are unable to distinguish between these two variables. They must be considered together as ‘gain’ or ‘addition’ (Begon, 1979).

The density of population, the survival rate, and the dilution rate are all interconnected so that when one of them is poorly estimated, it influences the validity of the others (Krebs, 1989).

5.2.2 Trappability

The accuracy of population parameters by mark-recapture techniques is determined by the fraction of the population trapped (Hilborn *et al.*, 1976).

Three definitions of trappability have been given: maximum trappability (Krebs *et al.* 1969), minimum trappability (Hilborn *et al.*, 1976), Jolly trappability (Jolly and Dickson, 1983). The three methods are summarised in Krebs and Boonstra (1984).

The minimum trappability uses the number of trapping periods in which an individual was captured at least once, divided by the number of trapping periods in which an individual was known to be alive. The first and the last time of captures are excluded from the calculation, so that the minimum trappability is expressed as (%):

$$100\,\frac{\sum_{i=1}^{N}\frac{n_a-2}{n_b-2}}{N}$$

Where n_a is the number of captures for an individual, n_b is the number of possible captures for that individual and N is the number of individuals caught more than twice.

Jolly and Dickson (1983) suggested a definition involving the number of individuals marked during a given sampling session (n_i) and the estimated number of marked individuals before starting this sampling session (M_i) over the total number of sampling sessions (S). The Jolly trappability is expressed as (%):

$$100\,\frac{\sum_{i=1}^{S}\frac{n_i}{M_i}}{S}$$

If neither of these above methods can be used, the maximum trappability is an alternative. It is the total number of captures recorded during a sampling session i over the estimated number of animals known to be alive at this time. The maximum trappability is expressed as (%):

$$100\sum_{i=1}^{n}\frac{c_i}{N_i}$$

Where n is the total number of trapping sessions.

Trappability was estimated on a weekly basis. Data were then grouped for quarters of the year, corresponding to the seasons defined in section **4.2**. Male and female data were analysed separately and then grouped.

In an attempt to detect any competition for traps by the animals, the influence of the density of population on the trappability was tested using the Spearman Rank Coefficient of Correlation (r_s).

5.2.3 Breeding activity

Reproductive condition was determined by the condition of the vagina, the size of the abdomen and the nipples in the female, and by the size of the testis in the male of *A. sylvaticus*. In a non-reproductive condition, the vagina is almost always closed and most of the females caught during anoestrus showed a closed vagina and were classified as non-breeding. In a breeding female *A. sylvaticus* the vagina is perforated (sign of copulation). The season during which females are sexually active can therefore be determined approximately from the condition of the vagina. Moreover, two extra classes were defined for female breeding activity, that is pregnancy and post-pregnancy (lactation).

The size and location of the testes helped in defining the male breeding period. If the testes are located in the abdomen and thus not visible, males are considered not to be breeding and classified as ‘abdominal’. However, when breeding, testes are bulky and located in the scrotum, which is a sign of sexual activity, and such males were categorised as ‘scrotal’.

The number and percentage of breeding animals caught was calculated separately for each sex and compared with the total sample size.

5.3 Results

5.3.1 Frequency of recaptures

Many animals were caught only once (Table 5.1) making it difficult to utilise the Jolly-Seber or Manly-Parr methods; indeed there were also far too few recaptures to consider the latter method further. The animals caught once which means not subsequently recaptured are considered to have zero frequency of recaptures. The latter concerns individuals captured and released in a first sample and caught again in some later sample.

Table 5.1 Frequency of recaptures of *A. sylvaticus* within the four replicate blocks.

Frequency of recaptures	Block 1	Block 2	Block 3	Block 4
0	123	143	165	117
1	50	39	84	52
2	14	9	22	11
3	2	4	9	4
4	0	0	2	3
5	0	1	2	0
6	0	2	0	0
7	0	0	3	1
8	0	0	0	0
9	0	1	0	0
10	0	0	0	0

5.3.2 Test for equal catchability

The test of equal catchability of *A. sylvaticus* within the marked population by Leslie's method (Leslie *et al.*, 1953) (Table 5.2) showed that the number of animals caught in all the 'Blocks' but one, 'Block 1', exceeded the number expected. The same trapping bias was observed both in male and females treated separately. Thus animals did not have equal chances of being caught ($P = 0.05$). Thus individuals (marked and unmarked) could not be captured at random (Leslie *et al.*, 1953), making the Jolly-Seber method inappropriate for estimating the population density.

Table 5.2 Results of Leslie's test (Leslie *et al.*, 1953) of equal catchability of *A. sylvaticus* within the four experimental blocks. N = the total number of captures, $\bar{x}$ = mean number of captures per mouse. The value in brackets is the χ^2 converted to the standard normal deviate (where d.f. > 100).

	N	$\bar{x}$	χ^2	d.f.	p
Block 1	61	0.92	28.62	65	> 0.05
Block 2	66	1.18	128.29	55	< 0.05
Block 3	122	0.92	258.14 (7.2)	121	< 0.05
Block 4	71	1.00	94.05	70	< 0.05

5.3.3 Estimates of density

5.3.3.1 Jolly-Seber method

Estimates of population density were obtained from a test run using the Jolly-Seber method. This showed that densities were sometimes excessively overestimated with, for instance, a change from 26 to 512 mice/ha over one week in November 1996. Moreover, Manly's method used for obtaining confidence limits for the Jolly-Seber method invalidated most of the Jolly estimates, notably those made during the Summer, where numbers of captures and recaptures were very low.

5.3.3.2 Direct enumeration (MNA) method

The data for each of the four blocks were analysed separately, thereby providing replication. The annual fluctuations of the estimated population density (Figures 5.1 and 5.2) follow the same pattern as that shown in Chapter 4 for the density of captures. Quarters of the year (appendix) are used for showing data in tables or as labels in data plots.

The highest estimates of population densities were registered during the Autumn/Winter periods when offspring joined the trappable population. In 1995, the overall number of captures was very low, suggesting a density of only about one mouse/ha. Only Block 3 showed high proportions of male *A. sylvaticus,* increasing during the first quarter (Figure 5.3). The proportion of males in the population increased in late February. Note that the density of males was high during the first three quarters of the year (Figure 5.1 and 5.2). The male:female ratio (Table 5.3) was high during the first quarter of 1995, although it did vary from block to block. The highest proportion of males was found in late February-early March in Block 3 (7:1). A 1:1 ratio was registered by the end of June in Block 2. The proportion of males started decreasing by the end of the third quarter of 1995. During this period the male:female ratio was very low, notably in Block 1 and Block 3.

In 1996, estimated population density peaks were reached in early Autumn (Figures 5.1 and 5.2) starting at the beginning of the fourth quarter (i.e. in October). The highest overall densities were 18 mice/ha in Block 1, 21 mice/ha in Blocks 2, 36 mice/ha in Block 3 and 23 mice/ha in Block 4. The average male:female ratio varied from block to block and also from quarter to quarter of the year (Table 5.3). The Spearman Rank Correlation Coefficient (r_s) used for looking for dependence between sex ratio and density of population in *A. sylvaticus* has shown no evidence of correlation between these two variables within the four agroforestry replicate blocks.

Table 5.3 The male:female ratio of *A. sylvaticus*. The average ratio was calculated quarterly from January 1995 until August 1997 for the four Blocks.

	Block 1	Block 2	Block 3	Block 4
1995				
Q1	0.8:1	0.9:1	4.9:1	2.3:1
Q2	0.6:1	1:1	0.5:1	0.3:1
Q3	0.6:1	0.5:1	*(1)	0:1
Q4	0:1	*(1)	0:1	*(1)
1996				
Q1	2.1:1	1.5:1	1:1	1.9:1
Q2	0.1:1	2.2:1	1:1	1.6:1
Q3	0:1	0:1	1:1	0.5:1
Q4	0.9:1	2.4:1	1.2:1	0.4:1
1997				
Q1	2.3:1	1.3:1	0.8:1	0.2:1
Q2	1.3:1	2.9:1	0.4:1	0.6:1
Q3	0.3:1	0:1	0.5:1	1.0:1

*(1) = The male:female ratio could not be calculated.

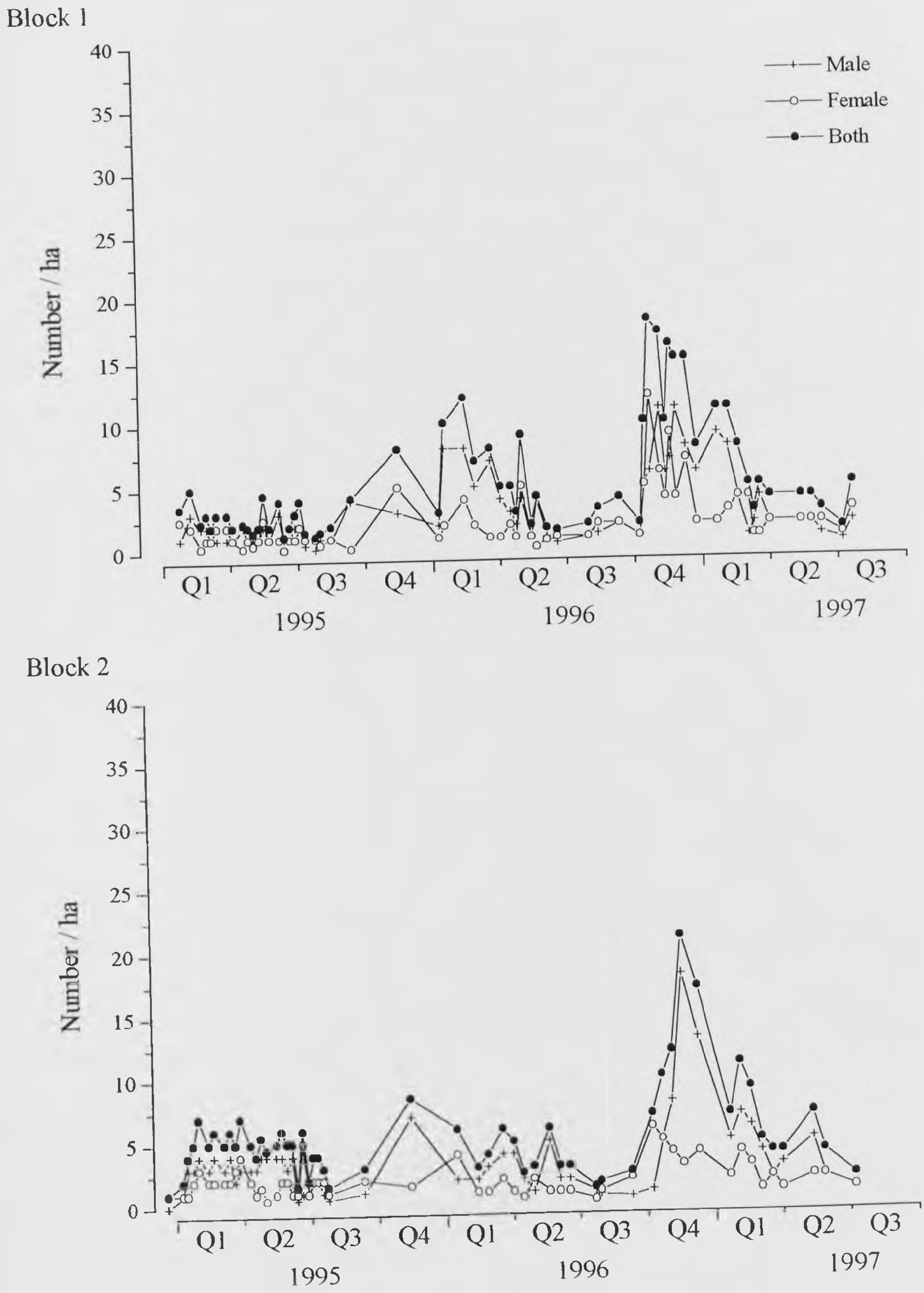


Figure 5.1 The estimated density of population obtained by direct enumeration (MNA) of *A. sylvaticus* in the trapping area (agroforestry Blocks 1 and 2). Q1 to Q4 represent the quarters of the year.

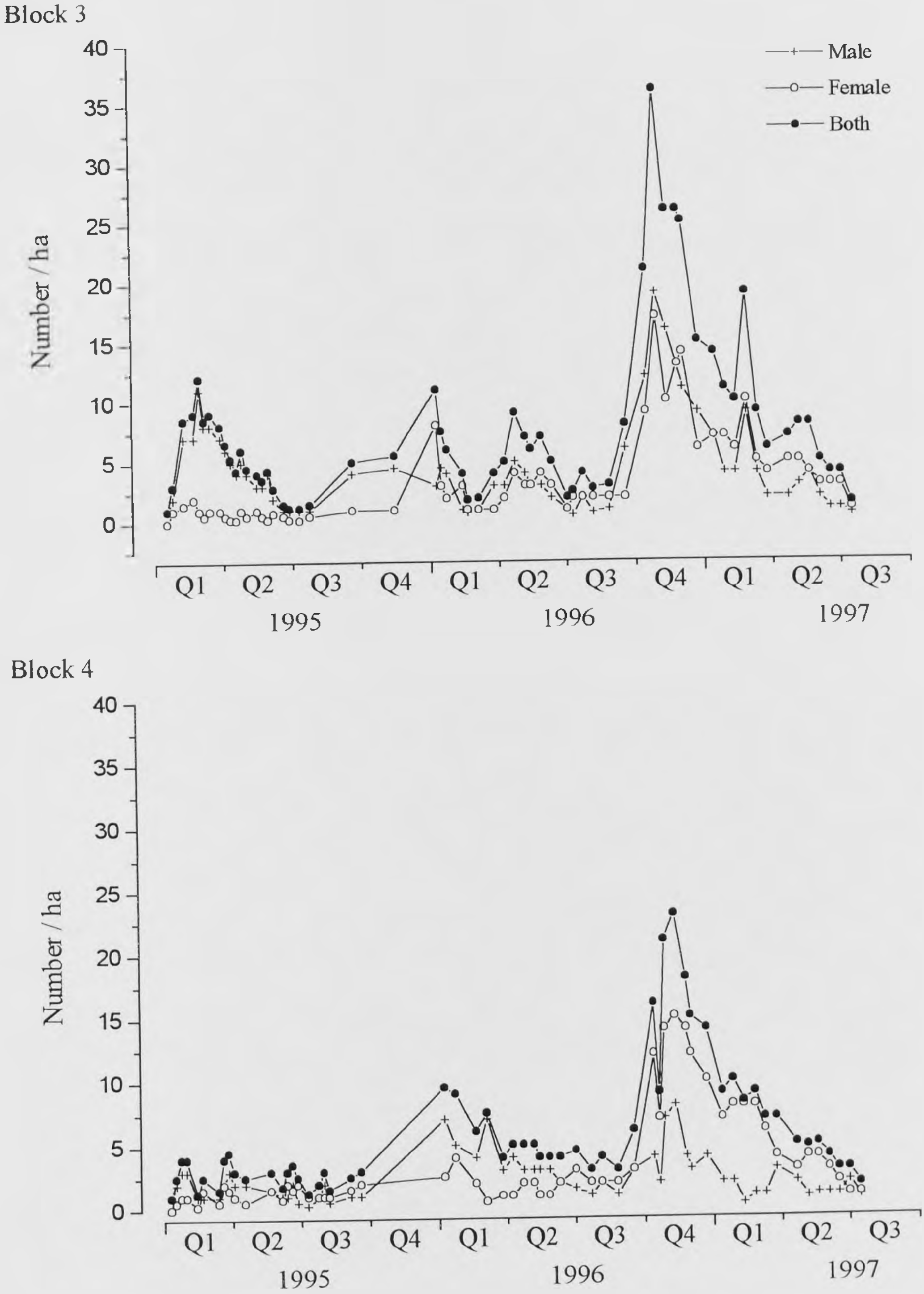


Figure 5.2 The estimated density of population obtained by direct enumeration (MNA) of *A. sylvaticus* in the trapping area (agroforestry Blocks 3 and 4). Q1 to Q4 represent the quarters of the year.

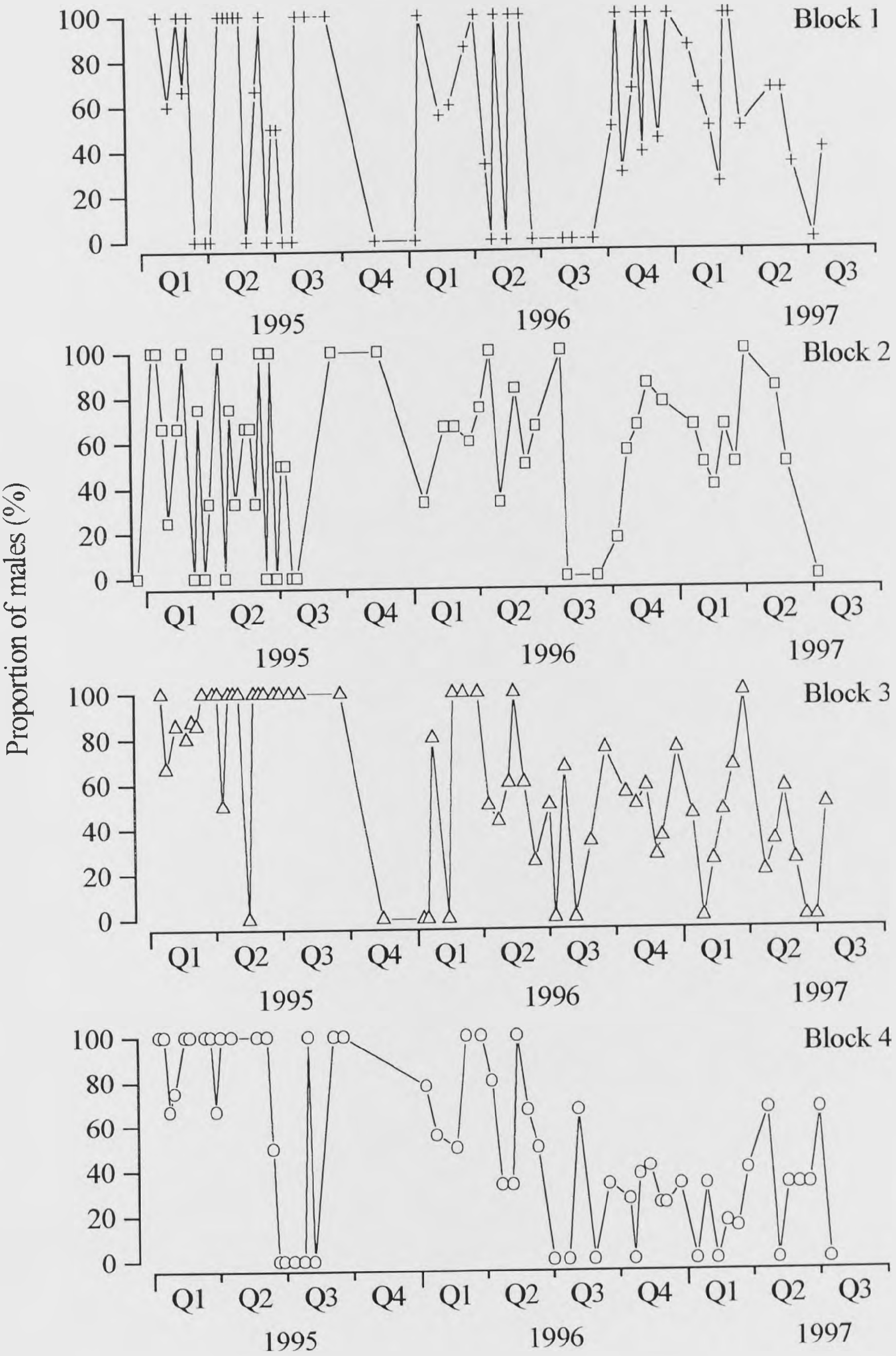


Figure 5.3 Proportion of males (%) trapped within the four agroforestry replicate blocks.

5.3.4 The rate of population change

The calculated rate of population change of *A. sylvaticus* varied from season to season. Overall, rates were greater during the Summer-Autumn period; thus the highest rate of population change was registered during Autumn 1995 (Figure 5.4) in the third week of November (8%) in Block 3. In Autumn 1996, the highest rate (4.5%) was registered in the third week of September also in block 3. Note that in early January in Block 1, the rate of population change was high (7.3%). The rates were low during most of the first and second quarters of the each year (during the Winter-Spring period). The lowest rate (0.3) was generally registered during May and June.

Female rates varied steadily between 1 and 2% during Spring and Summer, whereas changes were considerable during Autumn and Winter (up to 8%). The number of females grew at a variable rate of between 3 and 8 % a week, in Blocks 3 and 4. As a result, the numbers of females known to be alive were higher during this season in these two blocks, particularly in Block 4.

The rate of population changes in males rose steadily during the breeding period, with maximum values of 5% registered in Block 2 during the last week of April 1996. Overall, male rates of population change were between 0.5 and 5% during the Spring/Summer period and between 0.3 and 7 % during the Autumn/Winter period.

The changing numbers of individuals estimated over the year inevitably involved losses and gains within the population; this is shown by the probability of survival and dilution parameters.

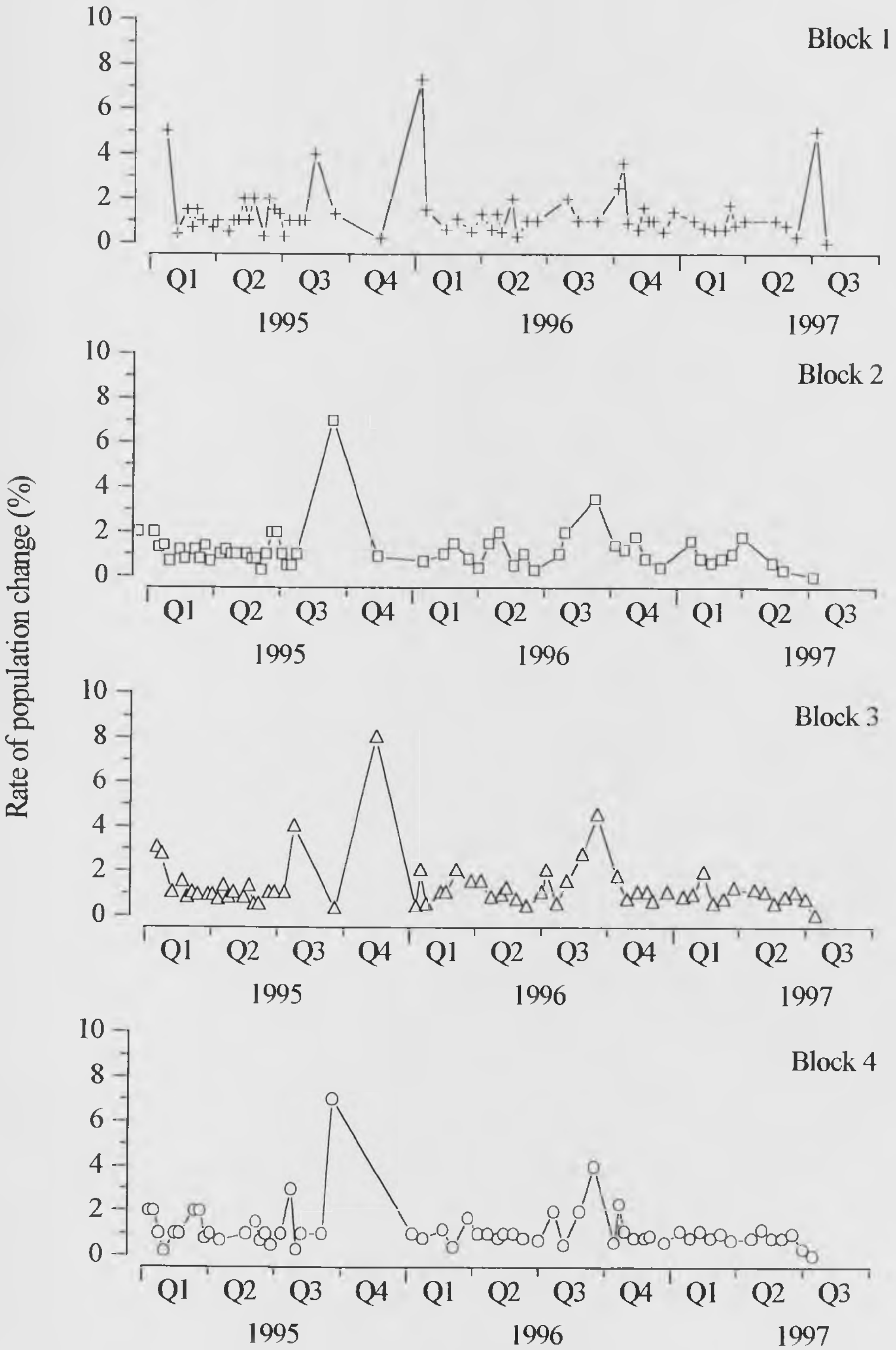


Figure 5.4 Rate of population change (%) of *A. sylvaticus* in each of the agroforestry replicate blocks.

5.3.5 Survival rate and dilution

Minimum survival rates were low during the second and third quarter of 1995 but reached 84% to 86% at the end of the year in Blocks 1, 2 and 3 (Table 5.4). In 1996 survival rates increased earlier in the Summer and stayed high over the Autumn and Winter. There was no evidence of differences in survival rates between males and females ($P \ll 0.05$).

Table 5.4 Survival rate calculated from the minimum number of animals known to be alive on a weekly basis and averaged for each quarter of the year (% / week).

		Survival rate (%/week)			
1995		Block 1	Block 2	Block 3	Block 4
Quarters	Weeks(1)				
Q1	1 to 13	45	76	77	48
Q2	14 to 26	39	54	40	64
Q3	27 to 39	54	43	44	53
Q4	40 to 52	85	86	84	*(2)
1996					
Q1	53 to 65	69	62	42	70
Q2	66 to 78	41	56	67	69
Q3	79 to 91	74	79	66	64
Q4	92 to 104	39	66	60	53
1997					
Q1	105 to 117	66	62	65	60
Q2	118 to 130	68	84	65	57

(1) = Week dates are in the appendix.

(2) = Unable to calculate survival rate in Block 4 during Q4 due to lack of data.

A considerable number of animals was added to the population each year. This fraction consisted mainly of new juveniles joining the population. Recruitment generally began at the end of the third quarter (late in the Summer) (Figure 5.5) and could explain the increased number of captures each Autumn, particularly in 1996. In 1995 numbers increased by the end of September and stayed high until the new year, when they started declining until they reached their minimum level during the breeding period in June 1996. By the end of September 1996, numbers had increased again, showing a similar pattern to 1995. Changes occurred from one week to the next and on average from one quarter to the next. Chi-square tests show a highly significant departure from homogeneity between the different quarters of the year. The main period of recruitment, the Autumn, was significantly different from that at other times of the year in each of the four replicate blocks ($\chi^2_{\mathrm{Block1}} = 83.84$, $\chi^2_{\mathrm{Block2}} = 69.55$, $\chi^2_{\mathrm{Block3}} = 76.90$ and $\chi^2_{\mathrm{Block4}} = 75.52$, d.f. = 9 at $P << 0.05$ in each case).

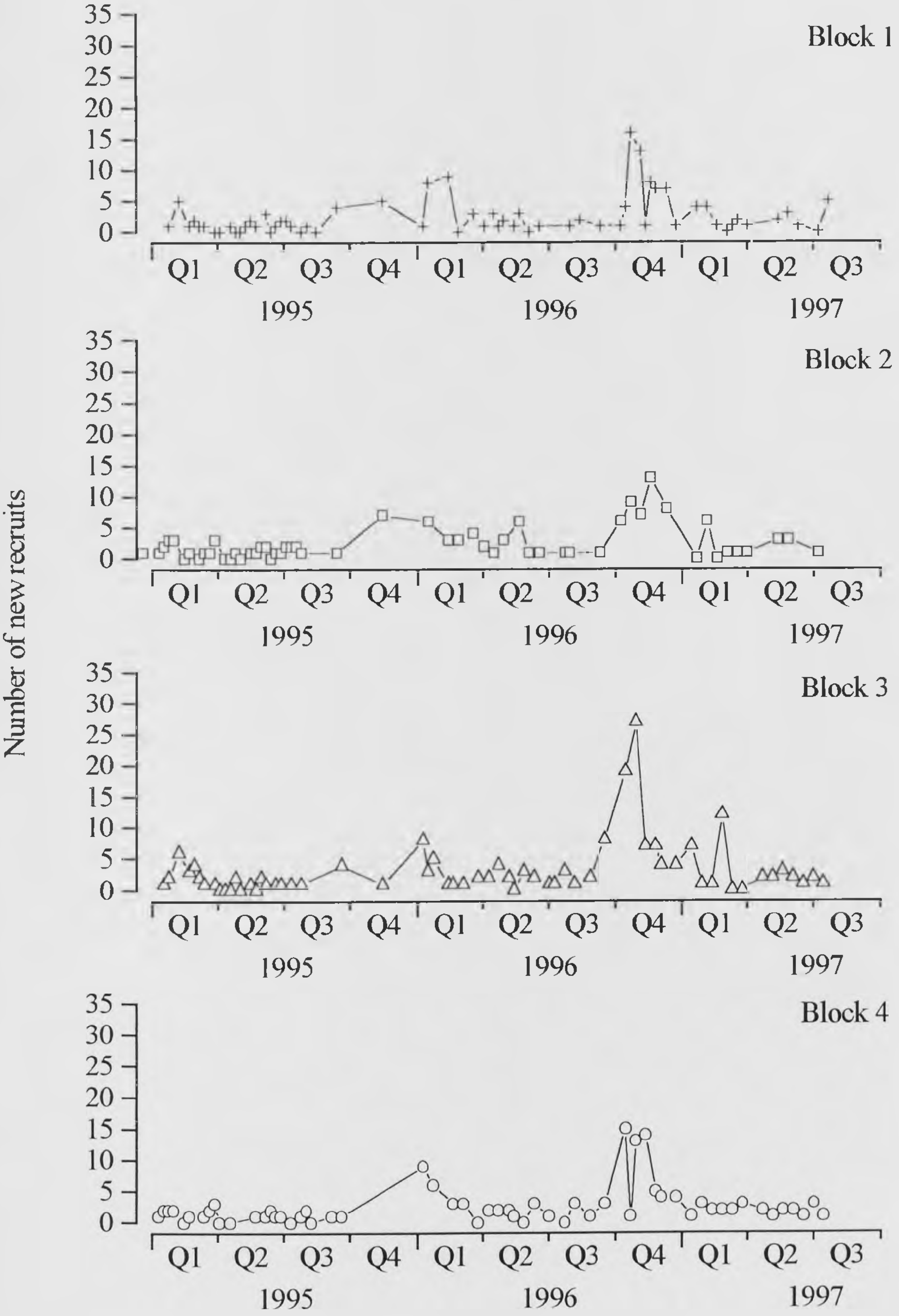


Figure 5.5 The dilution (added population) of *A. sylvaticus* in the four replicate blocks.

5.3.6 Trappability estimates

Krebs and Boonstra (1984) and Nichols and Pollock (1983) suggested that the Jolly trappability method was the most appropriate. Unfortunately, Leslie's test of equal catchability showed that the population of *A. sylvaticus* was not randomly sampled. Since this is an assumption of both the Jolly and the minimum trappability methods, neither could be applied here. Both tend to overestimate the true trappability when this assumption does not hold. Trappability estimated by the maximum trappability method (Krebs and Boonstra, 1984), summarised in table 5.5, showed that the mean seasonal pattern is different from year to year and between sex. The highest overall correlations were registered for males in 'Block 3' and for females in 'Block 4'. Trappability tended to be depressed during Summer.

Although very variable between blocks, male trappability was on average particularly high during the Winters 1995 and 1996 and the Spring of 1997. The lowest average estimate for all blocks was during Summer 1996 (39%) (influenced by the null trappability within 'Block 1'), whilst the highest was in Spring 1997 (73%).

The estimates of female trappability were also variable between blocks. They were particularly high during Winter 1996. There appeared to be little overall pattern except that trappability was particularly low during the two Autumns (25% in 1996 and 35% in 1997).

The growing density of the population sometimes affects the trappability of the individuals. However, there is no evidence here of influence of population size (MNA method) on the mean trappability calculated for each season (quarter) for each sex; the correlations were all weak (Table 5.5). A weak negative correlation is found between trappability and population density ($r_s = -0.47$). Data was combined for sexes and averaged for blocks over seasons (Figure 5.6).

Table 5.5 Estimates of trappability (%) (using the maximum trappability method of Krebs and Boonstra (1984)) of *A. sylvaticus* for each of the four blocks, averaged over quarters. r_s is the coefficient of correlation between mean trappability and the estimated population size.

	Male				Female			
	Block 1	Block 2	Block 3	Block 4	Block 1	Block 2	Block 3	Block 4
Winter 1994/95	65.0	43.9	52.0	92.2	50.0	40.6	83.3	33.3
Spring 1995	54.0	31.6	31.2	92.0	33.3	43.0	20.0	17.9
Summer 1995	46.4	37.5	100.0	28.6	71.4	70.8	0	50.0
Autumn 1995	50.0	100.0	50.0	0	50.0	0	50.0	0
Winter 1995/96	48.0	77.0	50.0	77.0	80.0	100.0	49.0	75.0
Spring 1996	40.9	77.4	48.0	56.6	42.9	80.0	47.9	71.4
Summer 1996	0	50.0	66.7	40.0	100.0	56.3	87.5	36.8
Autumn 1996	35.8	66.8	26.2	50.9	37.7	53.4	30.7	18.1
Winter 1996/97	57.5	30.4	42.6	60.0	45.8	71.6	50.4	38.0
Spring 1997	83.3	75.0	63.2	70.3	43.8	41.7	58.4	40.2
Summer 1997	0	0	0	0	0	0	66.5	0
r_s	0.02	0.19	– 0.34	0.20	– 0.12	0.09	– 0.06	– 0.29

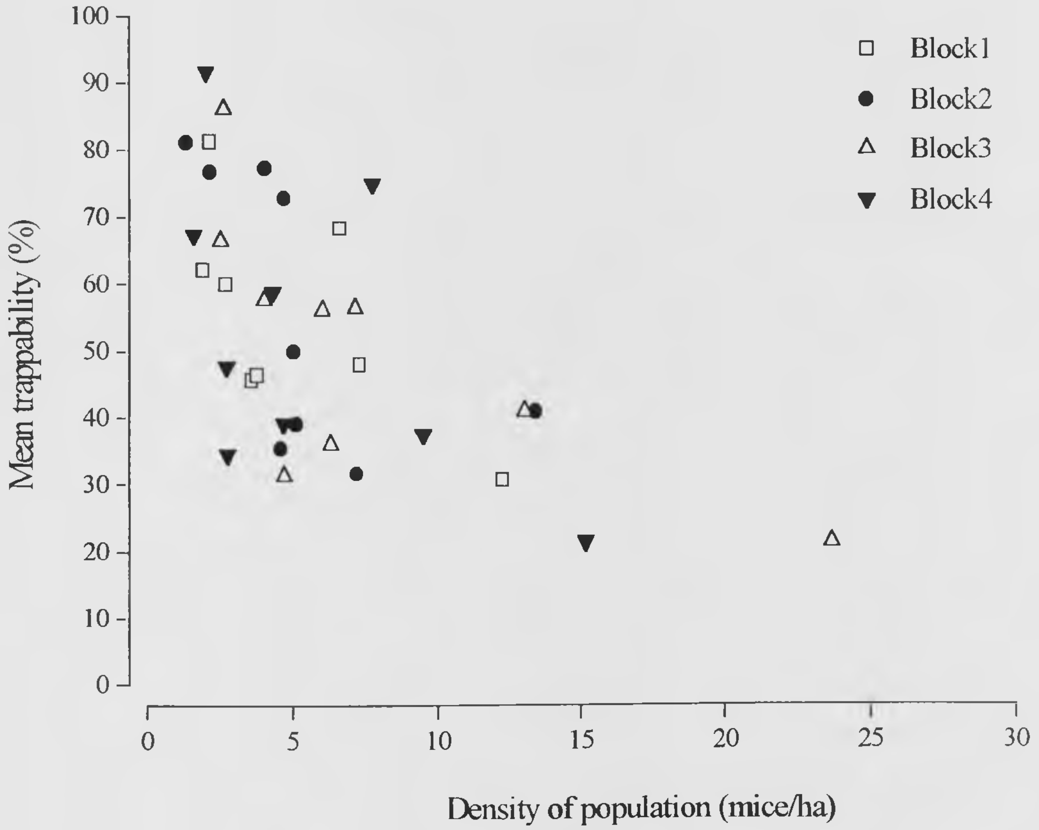


Figure 5.6 Trappability of *A. sylvaticus* in relation to the estimated population size (MNA method). Each value is the mean corresponding to the estimate for all animals (sexes combined) for one block over one season.

5.3.7 Breeding activity

The onset and length of the breeding season were much more closely defined for males than for females (Figures 5.7 and 5.8). The first breeding male was recorded around late February in 1995 and in mid-February in 1996 and 1997. The period in which most of the males caught were in breeding condition (50% of the catches and more) was much the same during the three years (Figure 5.7), lasting from mid-February to early July. Very few breeding males were caught in Autumn or early Winter. The proportion of breeding males was high during all three years in comparison with the sample size. In 1995, 84.5% of males caught during the breeding season were mature showing scrotal testes ($\chi^2 = 28.95$, d.f. = 7, $P < 0.05$), in 1996, 80% of males were in breeding condition ($\chi^2 = 55.19$, d.f. = 7, $P < 0.05$) and in 1997 this figure reached 93%. Homogeneity could not be tested for the full year in 1997 because of the lack of data during the last part of the year.

The female cycle was not as clearly defined (Figure 5.8). There were many females in breeding condition over a more prolonged period. This is because the breeding period in the female included either perforated, pregnant or lactating individuals. In 1995, the proportion of the population that was in breeding condition (78.6%) was significantly greater between early February and early July than between the other months ($\chi^2 = 23.00$, d.f. = 7, $P < 0.05$). The non-breeding period started in early September each year. However, the gap registered between July and September in 1995 might be due to the very low density of captures during this period.

In 1996 the breeding period started earlier than in 1995 with many females in oestrus in early January. Despite the scattering of breeding females throughout the year, the proportion caught between March and July 1996 was significantly higher than between the other months ($\chi^2 = 62.29$, d.f. = 3, $P < 0.05$). 71.4 % of the females caught in 1997 were also perforated, pregnant or lactating but, as for males, no test for homogeneity over the year was possible.

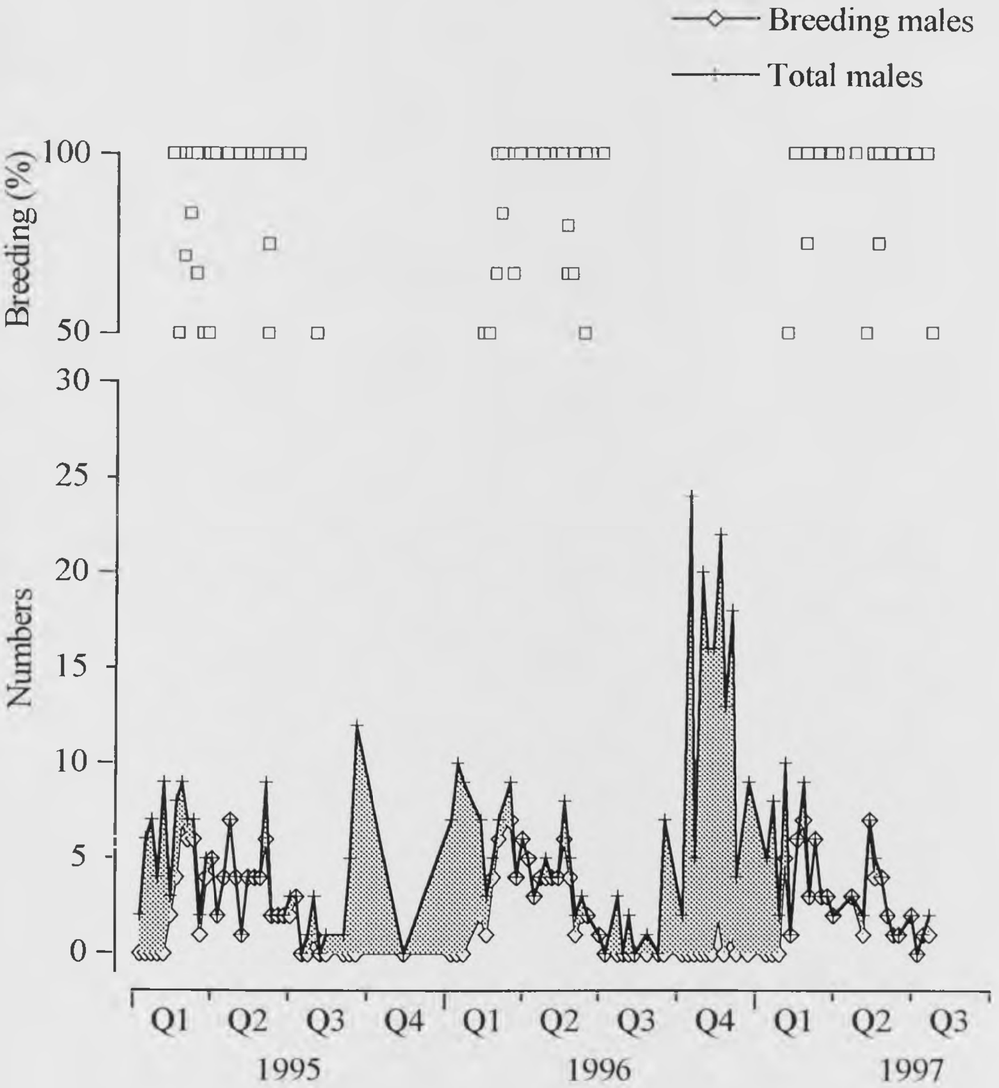


Figure 5.7 The number of male *A. sylvaticus* (breeding and overall) in relation to the onset and duration of breeding over the period of study. The shaded area shows the fraction of non-breeding males; squares represent the proportion of individuals in breeding condition. All four replicate blocks were combined.

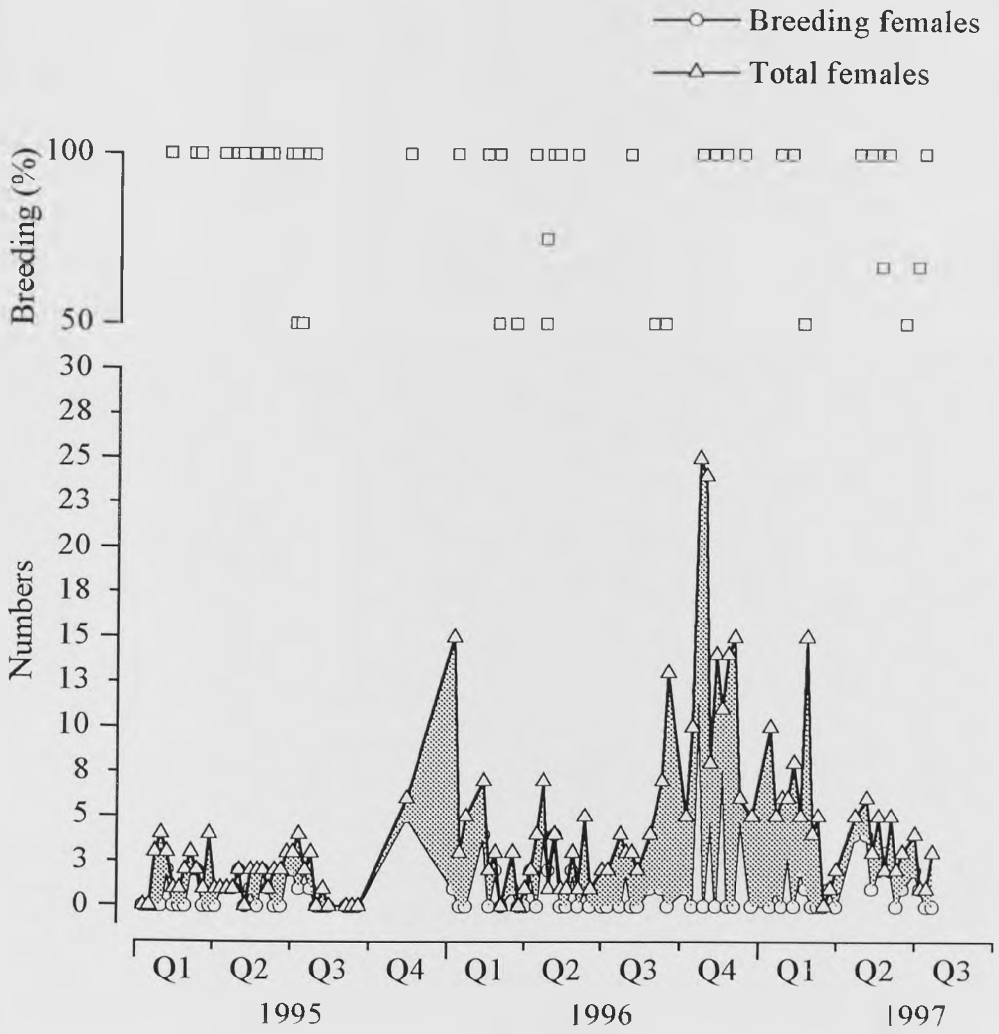
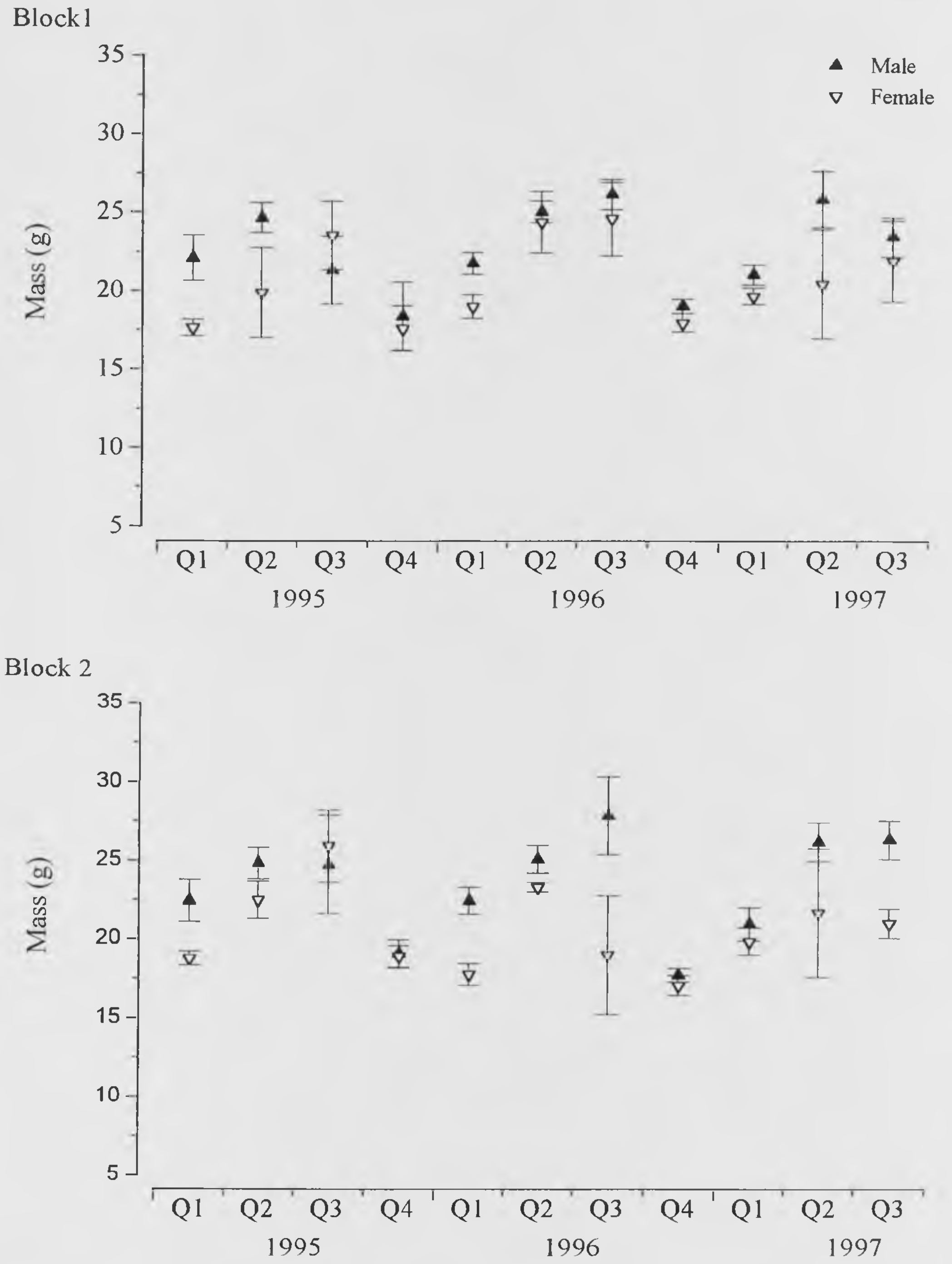


Figure 5.8 The number of female *A. sylvaticus* (breeding and overall) in relation to the onset and duration of breeding over the period of study. The shaded area shows the fraction of non-breeding females; squares represent the proportion of individuals in breeding condition. All four replicate blocks were combined.

5.3.8 Body mass distribution

Body mass was analysed over the population as a whole without distinguishing between class of age. There were no statistically significant differences in mass with season, despite the apparent differences registered, notably between the Spring/Summer and Autumn/Winter seasons (Figures 5.9 and 5.10).Certainly, animals caught during the warm season showed a more healthy appearance, probably because of food availability and mild weather. The Mann-Whitney U-test showed that males were on average heavier than females over the year in 'Block 2' ($\text{median}_{\text{male}} = 24.75$, $\text{median}_{\text{female}} = 19.85$ with $U_{\text{min}} = 0.06$ at $P = 0.04$) but not in the other blocks (Figure 5.9). However, females caught in 'Block 3' showed higher body mass during the Autumn 1995 (Figure 5.10), probably because of the large number of overwintering females with high body mass caught during this season. However, no Block effect on body mass variation was revealed by the Mann-Whitney U-test at $P = 0.05$.



Block1

Block 2

Figure 5.9 Body mass (g) (mean ± 1 S.E.) of *A. sylvaticus* adults (pregnant females excluded) within the agroforestry replicates 'Block 1' and 'Block 2' over the period January 1995 to August 1997.

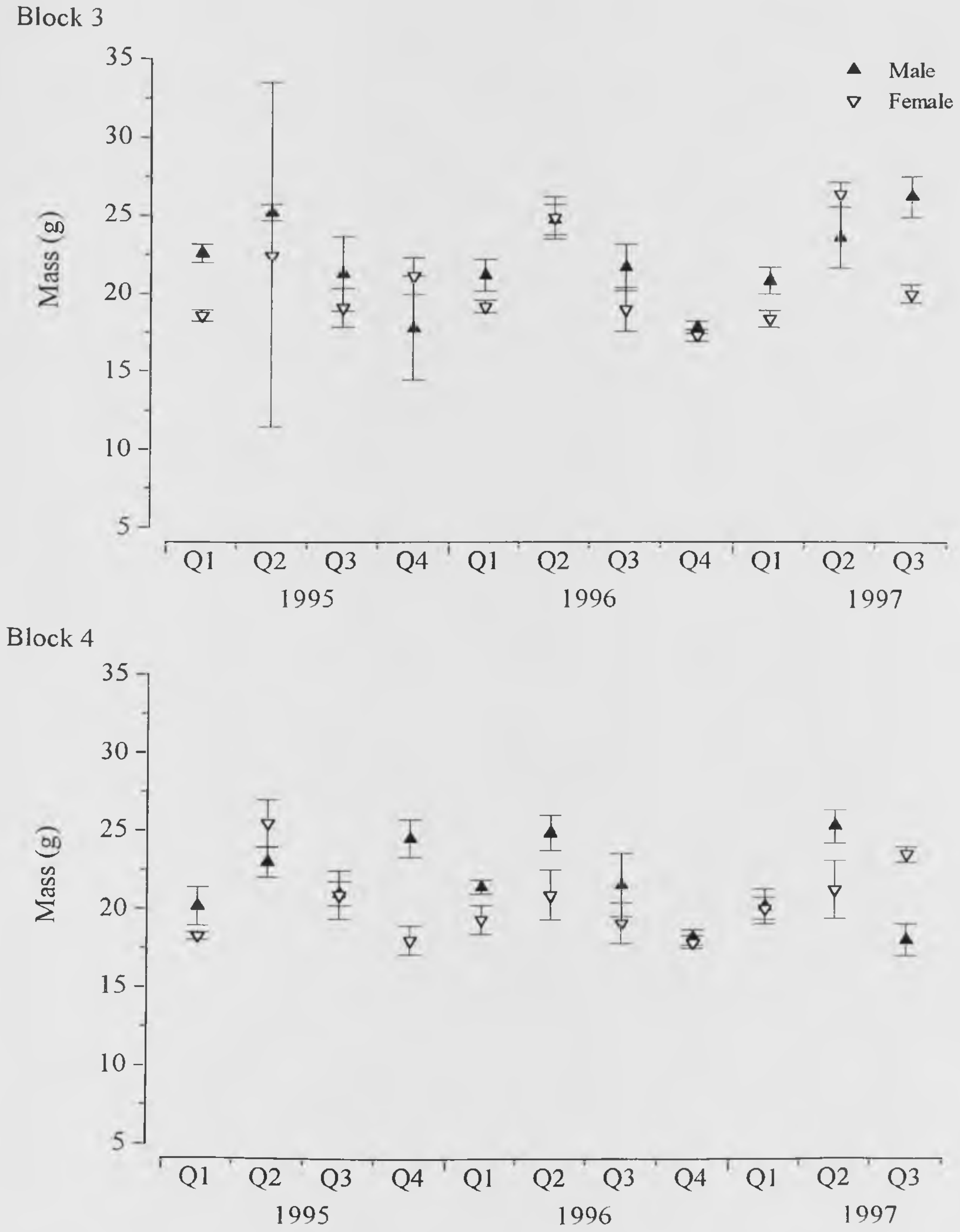


Figure 5.10 Body mass (g) (mean ± 1 S.E.) of *A. sylvaticus* adults (pregnant females excluded) within the agroforestry replicate 'Block 3' and 'Block 4' over the period January 1995 to August 1997.

5.4 Discussion

This research aimed to test the ability of small mammals such as *A. sylvaticus* to occupy an agroforestry system and to see how the population is distributed throughout the year in relation to the changes that occur in the habitat. It is well known that *A. sylvaticus* is entirely dependent on crops and tree row understorey cover, and thus is very sensitive to any variation in the quantity of food that these habitats supply; Thus it is likely that changes in animal numbers will occur during the year. The density of population seemed very low particularly at the beginning of the third quarter each year corresponding to the harvesting period. In fact population numbers suffer not only from casualties caused by the machines (particularly the young in the nest) but also from the lack of food following the harvesting.

Two sources of bias would have influenced the population estimates in this investigation. A low number of unmarked captures would have increased population estimates. On the other hand, the low frequency of recaptures would have decreased them. This latter bias might have been due to the competition for traps, but it was not the case as no evidence for this effect was revealed by the trappability estimates. In fact, decrease of trappability in *A. sylvaticus* was not related to increase of its population density. The low trappability registered during the Summers and Autumns might be due to the excess of food, which makes *A. sylvaticus* less attracted to bait within traps during Summer. The high proportion of young leaving their nest during the Autumn are less trappable than adults (Krebs and Boonstra, 1984). The correlation found between density of population and trappability was not strong enough to conclude any competition for traps.

The estimates of population density and related parameters are the first made in a silvoarable agroforestry system. However, many authors have given population density estimates for *A. sylvaticus* in different habitats. French *et al.* (1975) give a full range of density estimates. Table 5.6 show densities within different habitats in the UK for comparisons with this study. Despite the fact that the different studies were carried out in different habitats using different grid sizes and also different techniques of data analyses, they give a rough idea on population dynamics related to different habitats. The actual densities were generally higher than those found in set-aside and sand dune which are of low productivity and certainly lower than those of deciduous woodland which is a habitat of high productivity. The results were mostly comparable with those of Rogers and Gorman (1995) in farmland. However, the other studies included in table 5.6 did utilise different techniques from those of Rogers and Gorman (1995) and this study.

Table 5.6 Density estimates of *A. sylvaticus*. Comparison with previous studies. Lowest and highest numbers of mice/ha are given.

	Habitat				
	Woodland	Farmland	Set-aside	Sand dune	Agroforestry system
Current study					1-36
Gurnell (1978)	75-225				
Green (1979)		0.46-17.54			
Flowerdew (1985)	0.25-100				
Akbar and Gorman (1993)				1-13	
Rogers and Gorman (1995)		0-36	0-11		

Changes in the numbers of *A. sylvaticus* showed a typical annual cycle (Green, 1979; Gurnell, 1978; Rogers and Gorman, 1995; Watts, 1969). The number of males known to be present in the agroforestry system during the Spring and early Summer was high. The numbers increased steadily during the Spring and early Summer. This was probably due to individuals immigrating during the breeding period (mostly males looking for mates). In fact, the period in which a high proportion of males was registered coincided with the duration of breeding.

Population density increased sharply during the Autumn and early Winter, primarily because of the new offspring added to the population. Indeed, high numbers of young were recorded at this period. However, there was no increase in population density until almost the end of the breeding period each year, whereas Green (1979) and Watts (1969) registered differences between years, with the increase starting some years at the beginning of the breeding period.

At this stage, it is rather early to draw a final conclusion concerning the fluctuation of the population density because of the short duration of the research (two and a half years). However, there were some observations worthy of note. The high probability of survival in the Autumn/Winter period of 1995/96 was a prediction of the high population density registered in 1996. In general, male numbers in each block were higher than those of females (except Block 4) but this is not typical of microtines (Krebs and Myers, 1974; Southern, 1973).This might be a sign of the beginning of an increasing phase that the population is going through on its way to reaching peak density. To increase the reproductive output, high numbers of females are necessary (Williams, 1966). However, as for other microtines (Myers and Krebs, 1971), no correlation was detected between the density of population and the sex ratio to confirm this statement or otherwise.

The rate of population change is yet another parameter which could be used to detect increasing population density. In 1996, the rate of population change of *A. sylvaticus* slowed down whilst the population density was growing, i.e. the inverse of 1995. There is an inverse relationship between these two parameters shown by the way in which they increase (Davis and Golley, 1963; this study). The increasing phase was also detected for particular seasons to avoid variation in the population numbers due to environmental and hence reproductive changes. All the Blocks showed an increase in numbers between quarters 3 and 4 of 1995 and 1996 when the population was growing.

A continuous breeding activity was almost absent during the Winter period, as shown by Green (1979) and Rogers and Gorman (1995). Evidence from pregnant females caught in the first quarter of each year suggests a breeding season starting in the first quarter and finishing in late Summer and early Autumn (Rood, 1965, Rogers and Gorman, 1995). Most of the females caught in the Autumn - Winter period were in anoestrus, showing no sign of sexual activity. However, a few animals were caught showing signs of sexual activity in early January. This does not correspond to the findings of Smyth (1966), who recorded continuous breeding throughout the Winter, which he associated with a high Winter food supply.

There were differences between body masses registered over the year, with heavier animals caught during the Spring/Summer seasons and lighter ones during the Autumn and Winter, but this was not significant enough to confirm an annual cycle in body mass as shown by Montgomery (1980) and Rogers and Gorman (1995) and even less to relate these changes to population densities (Krebs and Myers, 1974).

6. RADIOTRACKING OF *Apodemus sylvaticus*

6.1 Introduction

Radio-location studies of *A. sylvaticus* or any other small mammal in an agroforestry system have not been reported previously. although, a detailed review by Harris *et al.* (1990) pointed out that many authors have previously shown an interest in home range analysis based on radio tracking data collected on mammals. However, these were concerned with animals living either in woodland or in farmland.

The basic problem facing researchers interested in home range analysis is to find an adequate method for estimating size and shape of home ranges and then analyse any related parameters. Although the term ‘home range’ is used by many ecologists, there is disagreement over its meaning and how to measure it (Anderson, 1982). All the methods used in home range analysis have a number of disadvantages (Don and Rennolls, 1983; Ford and Krumme, 1979; Kenward, 1987) and the true home range size is, therefore, difficult to determine (Kikkawa, 1964). Thus, researchers have often used more than one method to get as much information as possible from sets of location data and to facilitate comparisons between studies, as it is difficult to transform home range estimates calculated with different methods, to a common base for comparison (Worton, 1989; Anderson, 1982; Harris *et al.* 1990).

Home range is defined as an area visited by an animal within which normal activities of food gathering, mating and caring for young are performed (Burt, 1943), and exclusive of immigration, emigration or any unusual erratic wanderings (Brown and Orians, 1970). A more theoretical definition was given by Jennrich and Turner (1969), that the home range of an individual is the area of the smallest sub-region which accounts for a specified proportion ‘p’ of its total utilisation. The authors consider that this area accounts for 95% (which is an arbitrary value) of the animal's utilisation of a habitat. Using a similar equation for defining home ranges, Calhoun and Casby (1958), cited by Jennrich and Turner (1969), suggested an estimate at 99% of the utilisation of the habitat by an animal. In this research home range is assessed using different methods.

A. sylvaticus is a species living in a community where individuals can intermix whilst active. Its area of activity may or may not be shared with others and thus measures of exclusiveness are needed. This leads to an estimate of the degree of overlap of two territories, which is defined as the relative area in common between the two 'utilisation distributions' (Adams and Davis, 1967; Anderson, 1982), and to the probability that two animals can meet by chance (Jorgensen, 1968).

6.2 Methods

6.2.1 Site of radio tracking

Only movements within the confines of Block 3 were used in the analyses. Although many animals were tracked moving outside the agroforestry enclosure these data were not used because of the absence of an accurate survey of the surrounding area and hence of precise grid references from which the radio-fixes' co-ordinates would have been generated.

Only 'Block 3' was surveyed and mapped (Figure 6.1) with the help of students from Leeds College of Building under the supervision of Mr Chris Wales. The co-ordinates of each feature were generated for use in the habitat analysis. Thus 'Block 3' was chosen for monitoring the activity pattern and behaviour of *A. sylvaticus* in the agroforestry system. The design of the block and its different habitats were described in a previous chapter (section **3.1.1**).

To optimise the use of the radio-fixes recorded in the habitat analysis, all records registered within the whole arable area and not just within the arable alleys (as was done for the trapping data in the previous Chapters), were grouped. Three major habitats were defined as sharing an area of 1.23 hectares: forestry control (FC) covering 0.2 hectares (or 16.3% of the total surface of the block); four tree rows (TR) with a total of 0.07 hectares (5.7%) and arable area (AA), comprising the largest area at 0.96 hectares (78%).

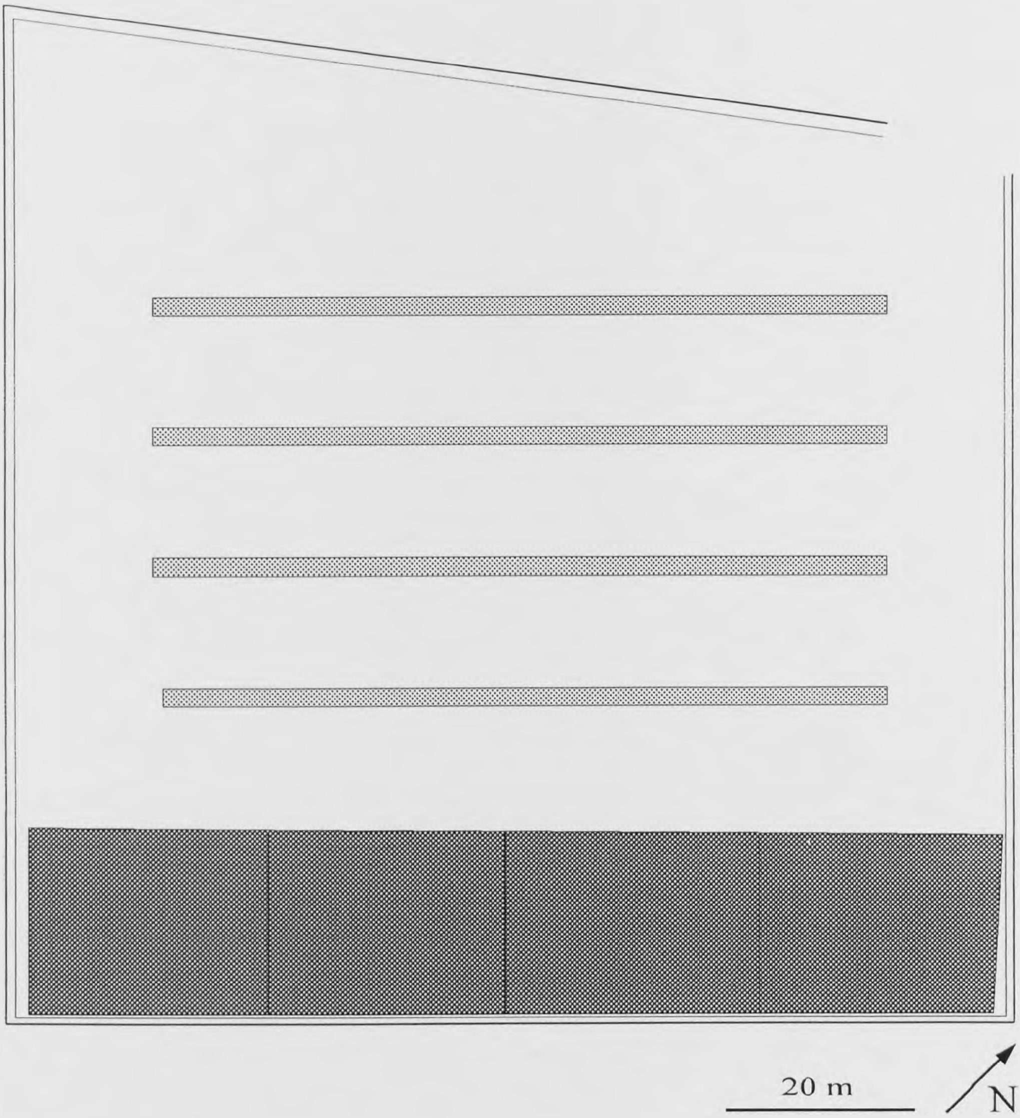


Figure 6.1 Layout of the radiotracking site showing in dark shading the forestry control (FC), in lighter shading the four tree rows (TR) and the arable area as unshaded space. The surrounding boundary is hedge.

6.2.2 The animals

20 animals from those caught during the weekly trapping sessions were fitted with collars containing radio-transmitters between the end of May 1996 and early June 1997. The animals were equipped with the collar on a Friday and released to get accustomed to it for the next three days. The first tracking session of the following week was always held on the Monday night. Three days are recommended because for forty eight hours after the attachment of a collar, mice show less activity than without a collar (Pouliquen *et al.*, 1990). Once they are accustomed to the collar it appear not to have any affect on their movement (Wolton, 1985). However, some scars on the neck of the animal might appear after few weeks due to friction of the collar against skin (Figure 6.2). To minimise the impact of the radio collar on the welfare of animals, Mackay (1974), suggested the use of a harness which automatically releases the radio collar after a prescribed period.

Five animals gave only limited data. Two of these lost their collars, one was found dead by strangulation (his right foreleg was found stuck between his neck and the collar apparently whilst he was trying to get rid of it), one disappeared and was never found, and one was predated by a tawny owl. The signal from the transmitter on the last one was still picked up from the bird's nest two months later.

The tracking of the other 15 animals involved healthy animals from both sexes (10 males and 5 females) which have been trapped in the experimental area on three or more occasions, thereby confirming their residency. The selected animals weighed 20 g or more and hence were able to carry a relatively heavy load imposed by the collar. Some of the animals were in breeding condition. Sexually mature males for instance, with a distended scrotum weighed between 22.5 and 25 g and pregnant or lactating females weighed up to 24 g. Tracked animals were individually identified and numbered: males from number 101 to 110 and females from 202 to 206 (Table 6.1).

Figure 6.2 Effect of radio collar on the skin of mouse *A. sylvaticus*, 9 weeks after the fitting.

Table 6.1 Inventory of radiotracking periods according to season and sex of animals.

	Sex	
Season	♂	♀
Summer 1996	101, 102, 103	
Autumn 1996	105, 106, 110	202, 203
Winter 1996/97	107, 108	204
Spring/Summer 1997	104, 109	205, 206
Total	10	5

6.2.3 Processing of tracking data

The procedures of data collection are described in section **3.2.2.3.** The raw data consisted of radio-fixes plotted in the field on a hand drawn grid square (Figure 6.3), where each pixel represents 2 m × 2 m (2 m is the arbitrary resolution of a radio-fix). An arbitrary co-ordinate system was created from this grid to enable the radio-fix data to be transformed into a digital format which was later transformed into co-ordinates (x and y) that matched the local map.

Digitised data were entered into a spreadsheet (Microsoft Excel) and saved as a CSV file. This was rather time consuming as the observations constituted 84 plans to be processed, each of which contained observations for a single mouse at a specific date. Data consists of :

1. Range Variables : The individual ID, age, sex, the date when recording started and the fix co-ordinates;
2. Fix Qualifying Variables (FQV's) which are the recording time and the type of habitat present at the site of the fix (tree row, arable alley or forestry control).

The co-ordinate information contained in the spreadsheet was generated using GIS facilities to create a coverage which matches the site map. The intention was to use both programs ARC/INFO (to transform the co-ordinates into a point coverage) and ARC/VIEW (for performing analysis and displaying the output) but an analysis system for this type of data was more appropriate. RANGES 5 was used to analyse the tracking data. This is a Geographic Information System (GIS) for analysing biological location data (Kenward and Hodder, 1996).

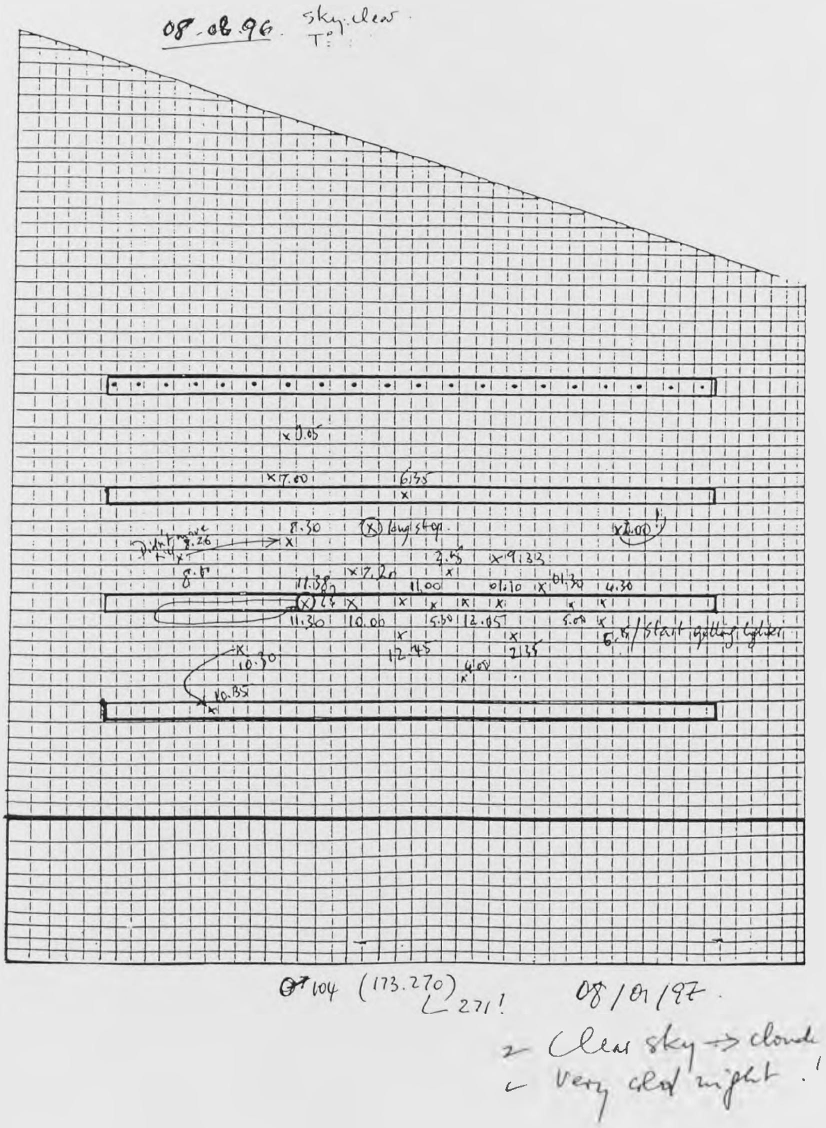


Figure 6.3 An example of data recording showing radio-fixes recorded for male 104 in the field during the night of 13/08/1997.

6.2.4 Data analysis

The utilisation distribution (UD) is a way of describing the home range as the distribution of an animal's probability of occurrence at each point in space (Van Winkle, 1975) and therefore provides a description of an individual's pattern of utilisation of space. At the population level, the average individual UDs could be considered as common for the population (PUD) if the animals have the same space use behaviour. A technique was developed by Ford and Krumme (1979) which makes it possible to decide on the percentage of fixes which define a core range and therefore to select areas with high density of fixes and excursive activity. The authors defined the UD "as a continuous or discrete function which represents the intensity with which an individual utilises each point in its habitat". The probability of distribution of the radio fixes is described using a non-parametric index; the Simpson Index of diversity:

$$D = \frac{1}{C}$$

where $C = \sum_{i}^{T} p_i^{2}$

p_i being the number of fixes (N_i) in each core (e.g. one or more high areas of high fix density in a range) as a proportion of the total number of fixes in the range (N_T). Once the proportion of radio fixes is defined, the assumption regarding the minimum number of radio-fixes necessary to estimate correctly each home range is tested. Range area is plotted against the cumulative number of radio fixes to ascertain home range asymptotes. In fact, for any method of home range analysis what matters is the stability of the home range estimate with increasing numbers of radio locations (Aebischer *et al.*, 1993). An outline is drawn around the first three fixes and as each new fix is plotted a new outline is drawn until all fixes in the range are included (Kenward and Hodder, 1996).

Six of the variety of different methods of range analysis were used here to estimate home range sizes. Three of them were non-parametric methods, based on ranking process, forming outlines that encompass linked locations (Kenward and Hodder 1996).These are: minimum concave polygons, convex polygons (MCPs) and cluster analyses. The three others were parametric methods (estimating fix density distributions). These are: probability ellipse, harmonic mean and Kernel contours.

Two-dimensional cluster analysis (Kenward, 1987) was used to define range cores because it eliminates the outlying fixes and identifies the areas most used by the animal. This method starts the first cluster by identifying the two fixes which are closest together and then adding the nearest third fix. The next fix is formed only when the mean distance between fixes within it is less than the distance between the first cluster and its nearest neighbour. If the nearest neighbour is assigned to another cluster, the two clusters merge. Convex polygons are drawn around each cluster.

The index of patchiness, which defines the area of cluster polygons as a proportion of the area of a single polygon around all the nuclei, is called the partial area. This is used as an index to assess the patchiness of the sites of activity. A patchy range has an index smaller than 1.

As most mice show patchy home ranges, cluster analysis contours were used to estimate the size of core areas. This method is particularly useful for eliminating outliers (excursive fixes) and therefore designating range cores. This method is also less sensitive to the effects of the autocorrelation of the data. In fact, most of the statistical methods of home range analysis tend to ignore a basic assumption, i.e. the independence of successive locations. These methods tend to under-estimate the true home range size (Harris *et al.*, 1990).

"The study of spacing patterns in animals is a field in which ecology and ethology complement each other" (Brown and Orians, 1970) and thus cluster analysis will identify patchiness in range use, i.e. whether the animal forages in several separate areas. Overlap analysis is performed to see whether or not there is overlap between ranges and to what extent. Interaction analyses examine spatial relationship between animals or between patterns of locations. We know that *A. sylvaticus* shares space with conspecifics both in arable lands and woodlands (Crawley, 1969; Kikkawa, 1964; Wolton, 1985) and hence we may expect the same to occur in the agroforestry system. However, space sharing is constrained by interactions between animals. The estimation of dynamic interactions for instance is based on the comparison of the observed distances between animals (revealed by the distances between fixes) and the expected distances of the 'N x N' possible distances between two animals from any of their positions. Jacobs (1974) determined an index (D_J) for comparing food selection and relative abundance which might be applied here to compare observed and expected distances. This index has symmetrical values ($-1 \leq D_J \leq 1$). Negative values of the index indicate a tendency of the animals to avoid each other, whereas positive values indicate that animals are attracted to each other (Kenward *et al.*, 1993).

Finally, intensive radio-tracking may give fine details on habitat preference. This is quantified in terms of the spatio-temporal use of multiple microhabitat patches such as tree rows, forestry control areas or arable areas within the home range of an animal. The animals all being adults, the data were grouped together as well as grouped by sex for analysing them. Unlike the home range analysis, habitat analysis is based on range edge and not on range fixes, and thus edge files have to be created for each home range.

As in the chapter on trapping, any relationship between distribution of captures in a trapping experiment and the season where the sessions of captures were held was looked at to see if there is any association between density of vegetation and distribution of ranges and whether any findings are related to season. The time period over which a home range is measured is one of the most important parameters needed to define home range (Morris, 1988) and the use of Summer and Winter ranges illustrates the changes over the period of study. The time period over which the animals were tracked is the same as the one described in chapter 4.

It was shown in a previous chapter (Chapter 4) how changes in the physical environment related to seasonal variations may bring about significant changes in the behaviour and distribution of *A. sylvaticus*, and thus animals were grouped by periods of tracking, each related to a season. Males 101, 102, 103, 104,109 and female 205, 206 were tracked during the Summer of 1996 and the Spring/Summer of 1997 hereafter called ‘Summer’ period when there is a dense plant cover. The second category comprises the rest of the animals (males 105, 106, 107, 108, 110 and females 202, 203, 204) tracked during the Autumn of 1996 or the Winter of 1996/1997 (referred to as ‘Winter’ period). These animals were therefore tracked when the cover was open. Hemispherical photographs were taken to show examples of the openness of cover during these two different periods.

6.3 Results

6.3.1 Home ranges estimated by different methods

The most common methods of home range analysis were used to estimate the home ranges of the 15 tracked animals. The estimates were made at a standard 95% of the density distribution of fixes. This helps to avoid the possibility of overestimation, since if 100% of the density distribution is used any outliers would be included. This is a particular problem in the case of the ellipse method, where distant outliers would cause excessive overestimation of the home range. Table 6.2 shows the total number of fixes and the total home range for each animal for the different methods used.

The evaluation of home range size for each animal using these different analytical methods shows significant differences between the areas ($P = 0.001$). It is important to note that each of these techniques relies on specific assumptions. The concave, convex and cluster polygons make more or less the same assessment (Figure 6.4a, b, c); the home range size for male 105 being 0.12-0.20 ha using these methods. The ellipse method gives an oversimplified picture (0.21 ha for mate 105) and the harmonic mean and the kernel methods (Figure 6.4e, f), which are contour models and therefore include outliers, tend to overestimate home range (0.22-0.25 ha) because of the smoothing tendency using the same proportion of radio-fixes. Thus, of the three methods which do appear not to overestimate home range, cluster analysis has the advantage that, in the system being studied, which includes different adjacent habitat types, the home range is divided into cores which enable closer relationships to be established in the utilisation of the different habitat types.

Table 6.2 Home range estimates (ha) of individual mice (*A. sylvaticus*) using different methods: Concave polygon (Cv P), convex polygon (Cx P), cluster analysis (C A), probability ellipse (P E), harmonic mean (H M) and kernel contours (K C) at 95% of density distribution. ID = identification number of the animal and N = the number of fixes.

		Method					
ID	N	Cv P	Cx P	C A	P E	H M	K C
♂							
101	36	0.20	0.17	0.16	0.34	0.21	0.25
102	14	0.14	0.18	0.15	0.54	0.03	0.18
103	63	0.36	0.36	0.19	0.53	0.34	0.35
104	48	0.55	0.54	0.30	1.13	0.55	0.68
105	78	0.20	0.16	0.12	0.21	0.25	0.22
106	73	0.19	0.16	0.12	0.24	0.16	0.17
107	34	0.14	0.12	0.12	0.21	0.14	0.17
108	183	0.45	0.28	0.21	0.49	0.44	0.41
109	117	0.40	0.33	0.29	0.43	0.38	0.35
110	20	0.27	0.27	0.09	0.75	0.14	0.34
♀							
202	61	0.32	0.29	0.11	0.58	0.32	0.37
203	60	0.14	0.12	0.07	0.20	0.13	0.13
204	166	0.21	0.20	0.12	0.20	0.22	0.17
205	9	0.02	0.06	0.06	0.21	0.01	0.07
206	48	0.06	0.04	0.04	0.09	0.05	0.05
♂ mean		0.29	0.26	0.18	0.49	0.26	0.31
♀ mean		0.15	0.14	0.08	0.26	0.15	0.16

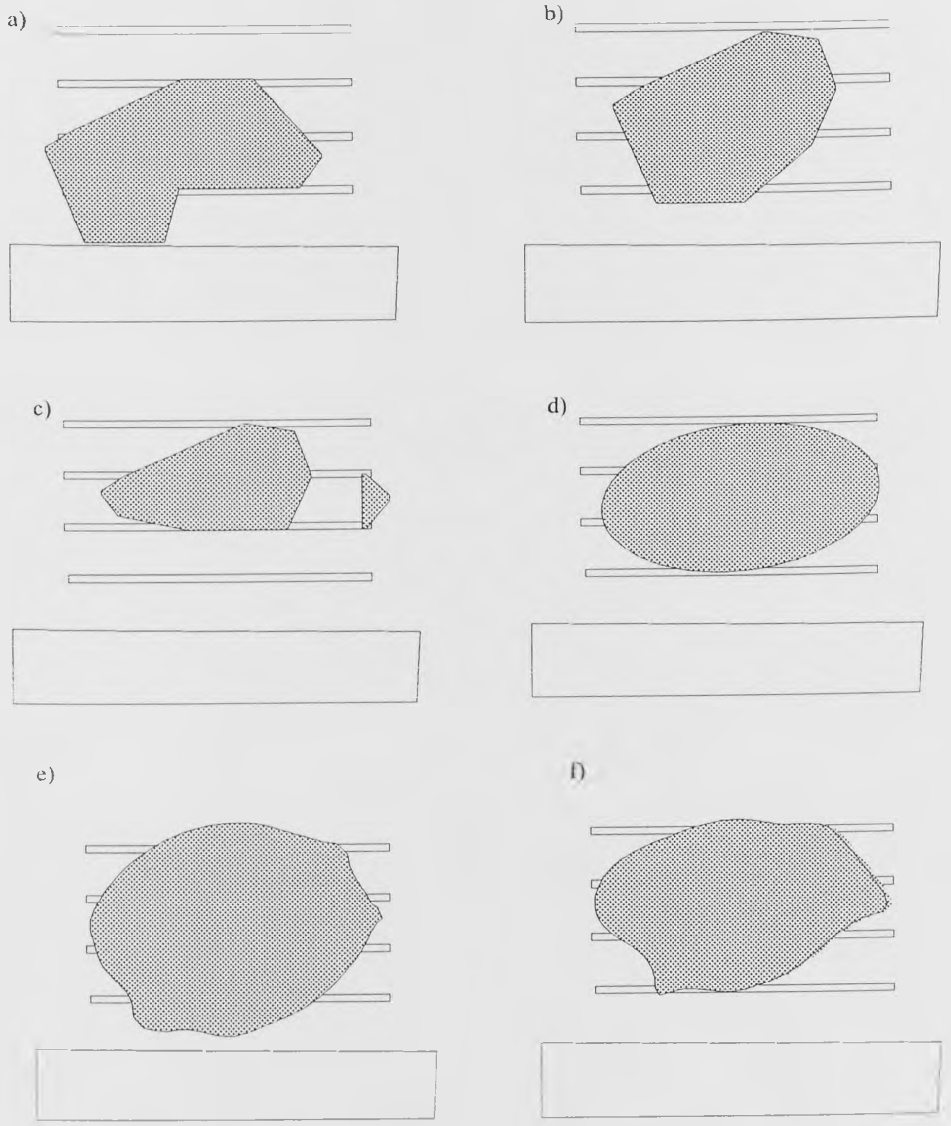


Figure 6.4 Home range polygons and contours for male 105 using different methods: a) 0.5 concave polygon, b) 95% convex polygon, c) 95% cluster analysis, d) 95% ellipse, e) 95% harmonic mean and f) 95% kernel contours.

6.3.2 Utilisation distribution and stability of home range

Incremental area analysis is a technique which assesses the assumption of home range stability. It shows how the home range area increases as fixes are added until an asymptote is approached (Figure 6.5). The 15 individual home ranges were plotted as a percentage of the maximum area against the cumulative number of radio fixes, to test whether the animals have a sufficient number of radio fixes to describe the majority of their home ranges. Only 3 out of the 15 plots did not approach an asymptote (100% polygon) within the number of radio fixes collected (Table 6.3). Sufficient data is therefore available to estimate accurately the home range sizes of twelve animals (eight males and four females).

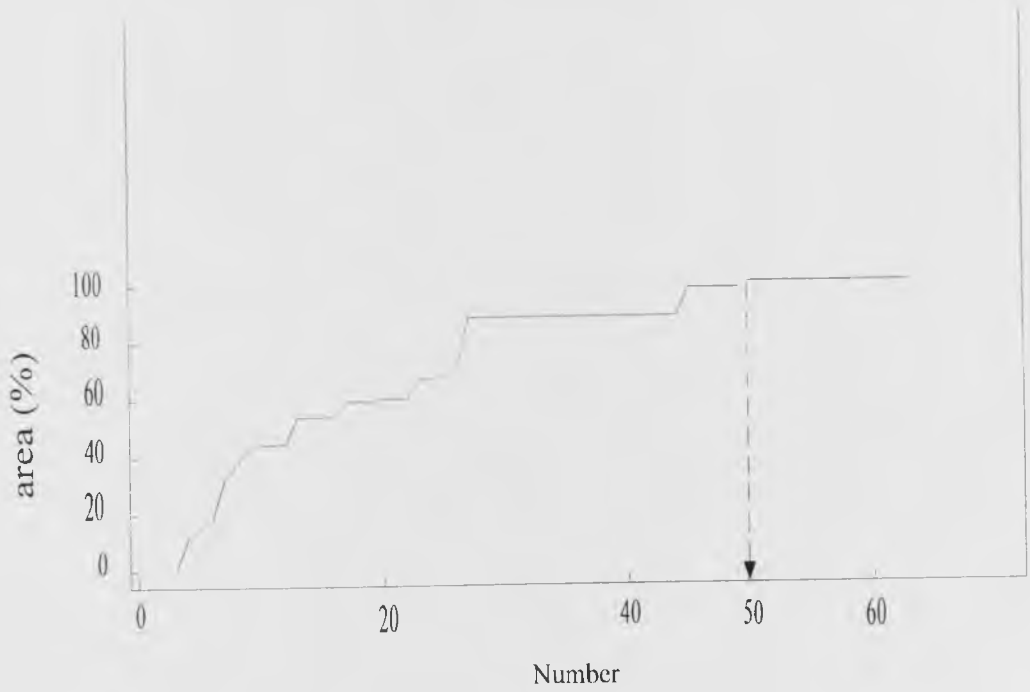


Figure 6.5 The relationship between area of home range and number of fixes included in the analysis for male *A. sylvaticus* 103. The arrow shows the number of fixes needed to define the range.

Having ascertained which animals have sufficient fixes to enable a home range to be determined with some accuracy, it is now necessary to determine the proportion of fixes required for each individual.

A multi-range utilisation plot defines the proportion of radio fixes which describe the mean magnitude of the home range of the individual in a population (population utilisation distribution (PUD)). To calculate PUD, the hierarchic cluster analysis method was chosen (Figure 6.6) for the reasons outlined above. This method shows that home range cores are determined by more than 60% of the number of fixes, with variation in home range cores reaching a minimum at this proportion of radio fixes. Above this value the variation increases due to the inclusion of outliers.

Most of the 15 individual range plots showed discontinuities in slope above 60 % of radio fixes because of the outliers. Below this value there is a smooth, shallow slope as shown in Figure 6.6. This indicates that an excursive activity was recorded for all the animals.

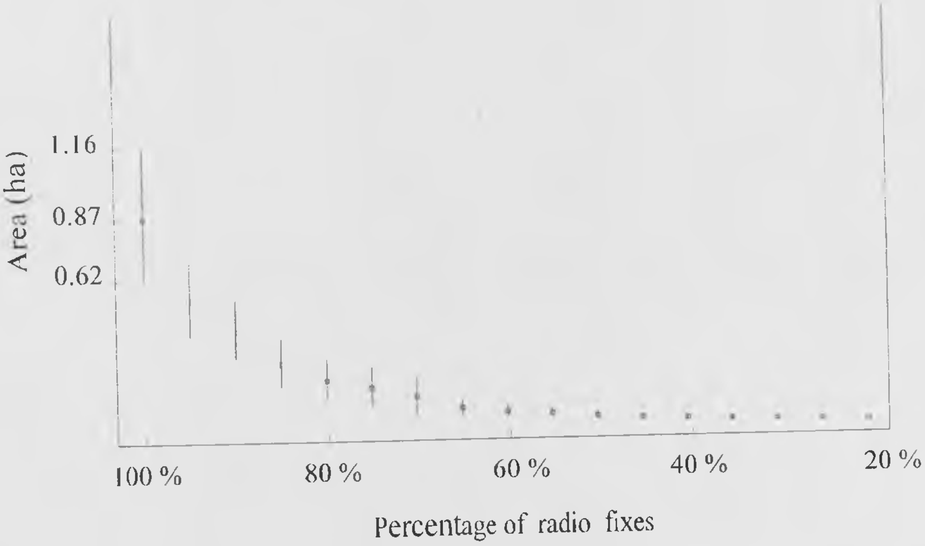


Figure 6.6 Multi-range utilisation plot of *A. sylvaticus* in the agroforestry system showing the relationship between the variation of home range area and the proportion of fixes (%).

Table 6.3 The sampling increment of home range of each animal. ID = identification number of animal, N = number of fixes and n = number of fixes required to approach the asymptote.

ID	N	n
♂		
101	36	30
102	14	No asymptote
103	63	50
104	48	35
105	78	70
106	73	65
107	34	30
108	183	90
109	117	90
110	20	No asymptote
♀		
202	61	55
203	60	25
204	166	150
205	9	No asymptote
206	48	38

6.3.3 Patchiness of the home ranges

The Simpson Index of Diversity showed different values for both fixes and areas at different core sizes, i.e. a variation in the concentration of the radio fixes is observed between clusters in the core. The highest concentration is at 65% of radio fixes (Table 6.4), which gives the maximum information on the number of clusters. At lower percentages, important fixes are omitted, giving lower values, whereas lower values at higher percentages are caused by the inclusion of outliers.

Table 6.4 Simpson Index of Diversity applied to the average number of fixes and areas in the clusters.

proportion of fixes (%)	Simpson Index (D_S)	
	For fixes	For areas
100	1.17	1.06
95	1.54	1.36
90	1.96	1.63
85	2.78	2.17
80	3.45	2.68
75	3.84	3.16
70	4.56	4.79
65	4.83	5.15
60	4.57	4.86
55	4.68	4.72
50	4.81	4.23
45	4.44	4.39
40	4.11	4.29
35	3.58	3.83
30	3.51	3.67
25	3.37	3.47

All the animals have patchy ranges comprising between 1 and 21 nuclei shown as polygons on the habitat map describing the features of the surveyed 'Block 3'. Male 108 (Winter 1996/97) has a low index of patchiness of 0.18. It shows 17 nuclei representing the range core for 65% of the 183 radio fixes collected (Figure 6.7a). The clusters are of unequal sizes as shown by the high value of the Simpson Index (D_s = 8.34) and this particular male mouse had a specific area of activity mainly situated within the forestry control. The most important range core was drawn by fixes collected around a focal site (nest) that the animal was frequently visiting. Male 107 (Winter 1996/97)has the highest index of patchiness (0.55) for 65% of fixes describing the cores. Only 2 nuclei, each with a different intensity of distribution of fixes (D_s = 1.42) occur, (Figure 6.7b), indicating that this mouse was intensively utilising two small areas. It was found mostly along tree row 3 and, to a lesser extent within the middle arable alley. The denser understorey of the tree row in the Winter could explain the preference of male 107 for this habitat. In fact this animal was tracked for 3 nights during January 1997 when the crop may have been still too low in the arable alleys to be attractive to it. The lowest index of patchiness (0.04 at 70% of radio fixes describing the cores) was registered for female 202 (Autumn 1996), which was tracked for 3 nights in October 1996. Ten clusters of unequal sizes (D_s = 7.94) are shown along tree rows 2, 3 and 4 and in the forestry control (Figure 6.7c). Even though the main activity was registered along the tree rows, incursions into the alleys were often observed.

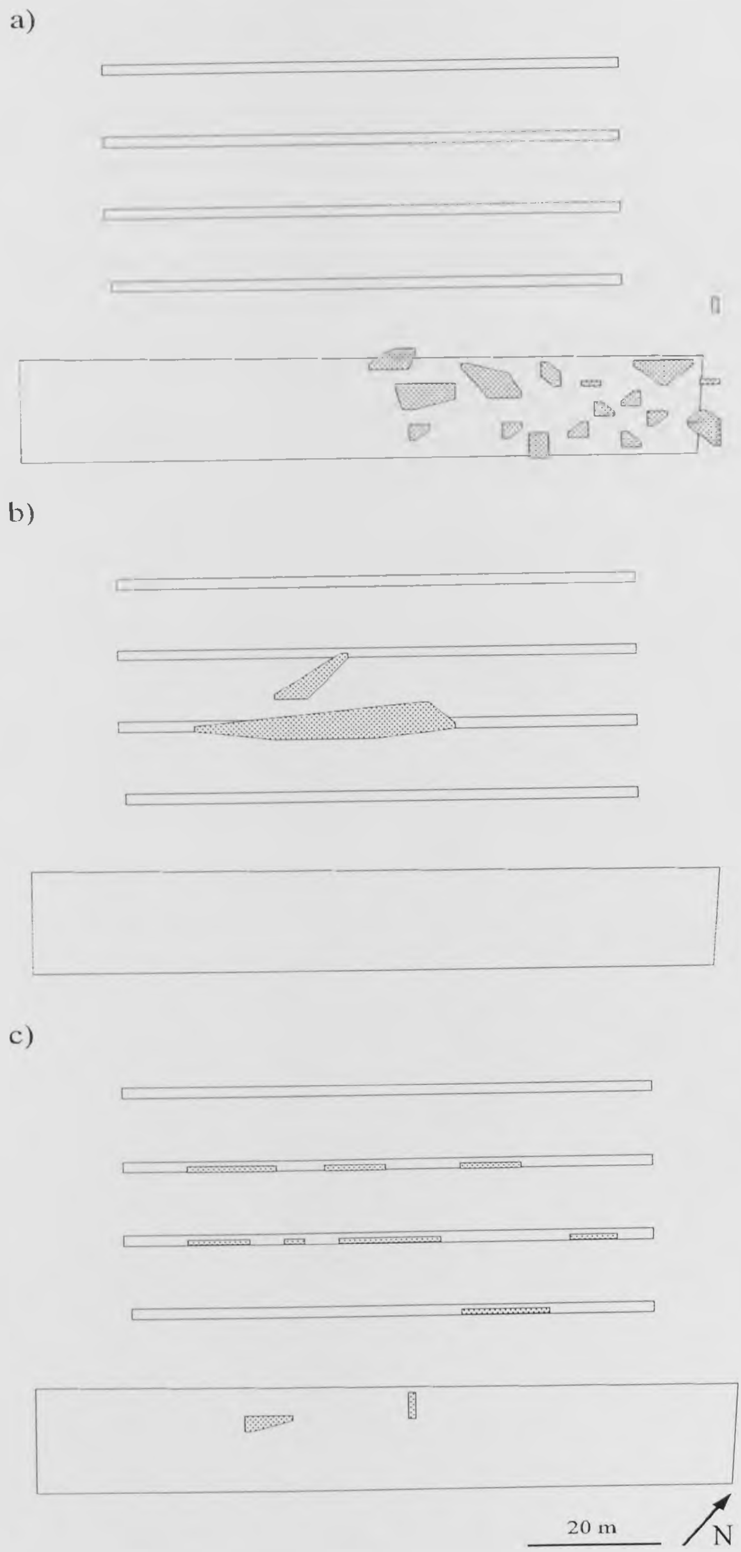


Figure 6.7 Distribution of all clusters within the home range of a) male 108 and b) male 107 at 65% utilisation of radiofixes (in Winter 96/97) and c) female 202 at 70% utilisation of radio fixes (in Autumn 96).

6.3.4 Estimation of core range size

Core range sizes were processed by the cluster analysis method. The estimated ranges of the twelve mice which approached the asymptote (assumption of stability) are shown in Table 6.5. The other mice did not have the minimum number of radio fixes necessary for the estimation (Section **6.3.2**). Individual core ranges were calculated using the number of fixes as a proportion of the total number of fixes recorded for each individual.

Table 6.5 Estimates of core range area using cluster analysis for male and female *A. sylvaticus* in an experimental agroforestry environment.

ID	N	Core ranges (ha)	Fixes (%)	Area (%)	Total nuclei
♂					
101	36	0.11	83	56	1
103	63	0.09	79	23	5
104	48	0.17	73	39	4
105	78	0.10	90	47	1
106	73	0.09	89	49	3
107	34	0.10	88	60	1
108	183	0.01	49	3	13
109	117	0.04	77	8	14
♀					
202	61	0.04	90	25	8
203	60	0.005	42	3	5
204	166	0.08	90	37	3
206	48	0.01	79	14	4

Male and female core ranges are shown in Figures 6.8 and 6.9. The ranges shown in these figures include mice trapped during both seasons. Male core ranges are larger than those of females. The size of these ranges tends to be larger during Spring and Summer (breeding period) compared with Autumn and Winter for males and the inverse for females. The association between sex and seasonal size of range was highly significant ($\chi^2 = 228.8$ with d.f. = 1, $P = 0.01$).

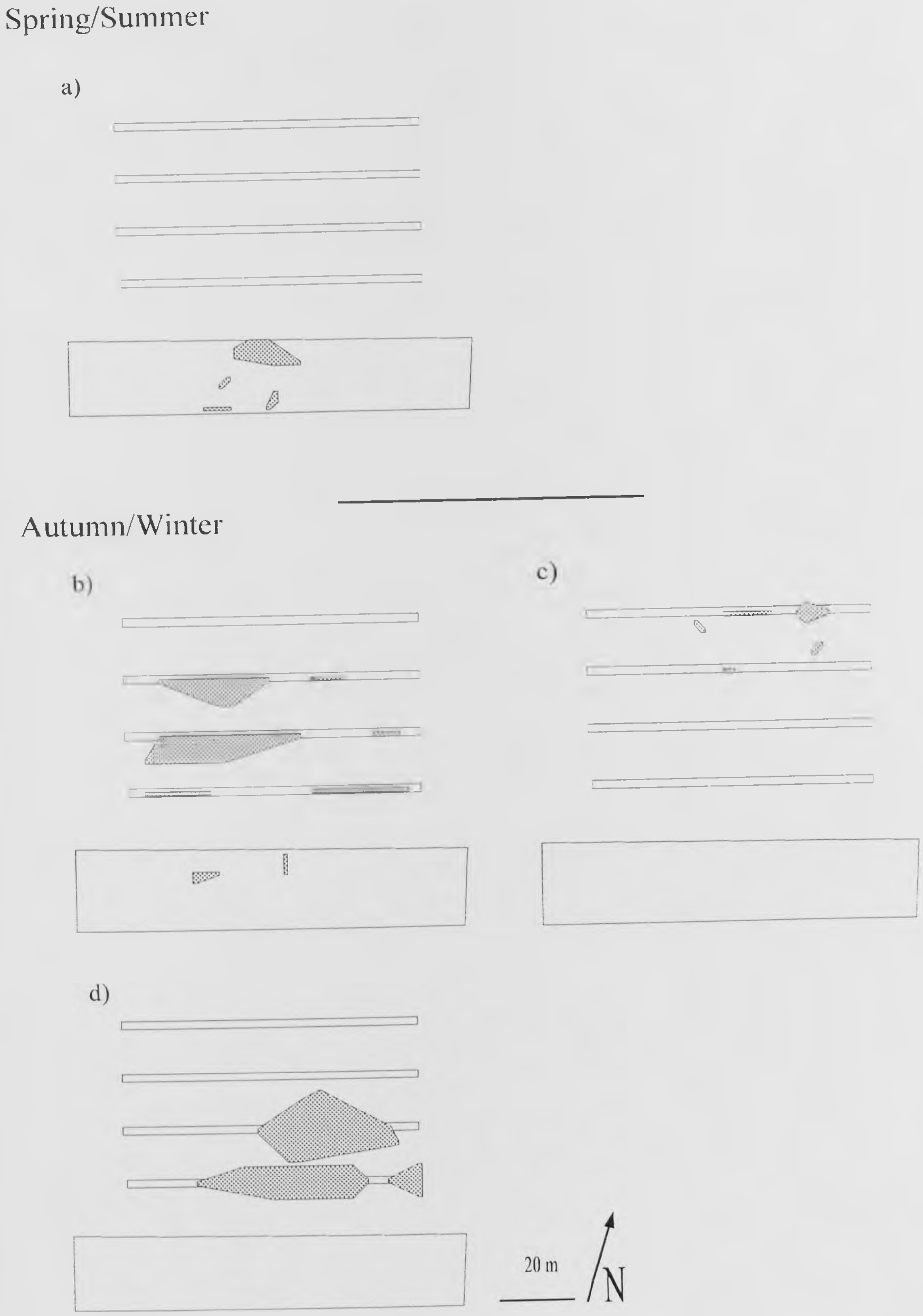


Figure 6.8 Distribution of core ranges of female *A. sylvaticus* a) 206, b) 202, c) 203 and d) 204 in agroforestry 'Block 3' in relation to habitat.

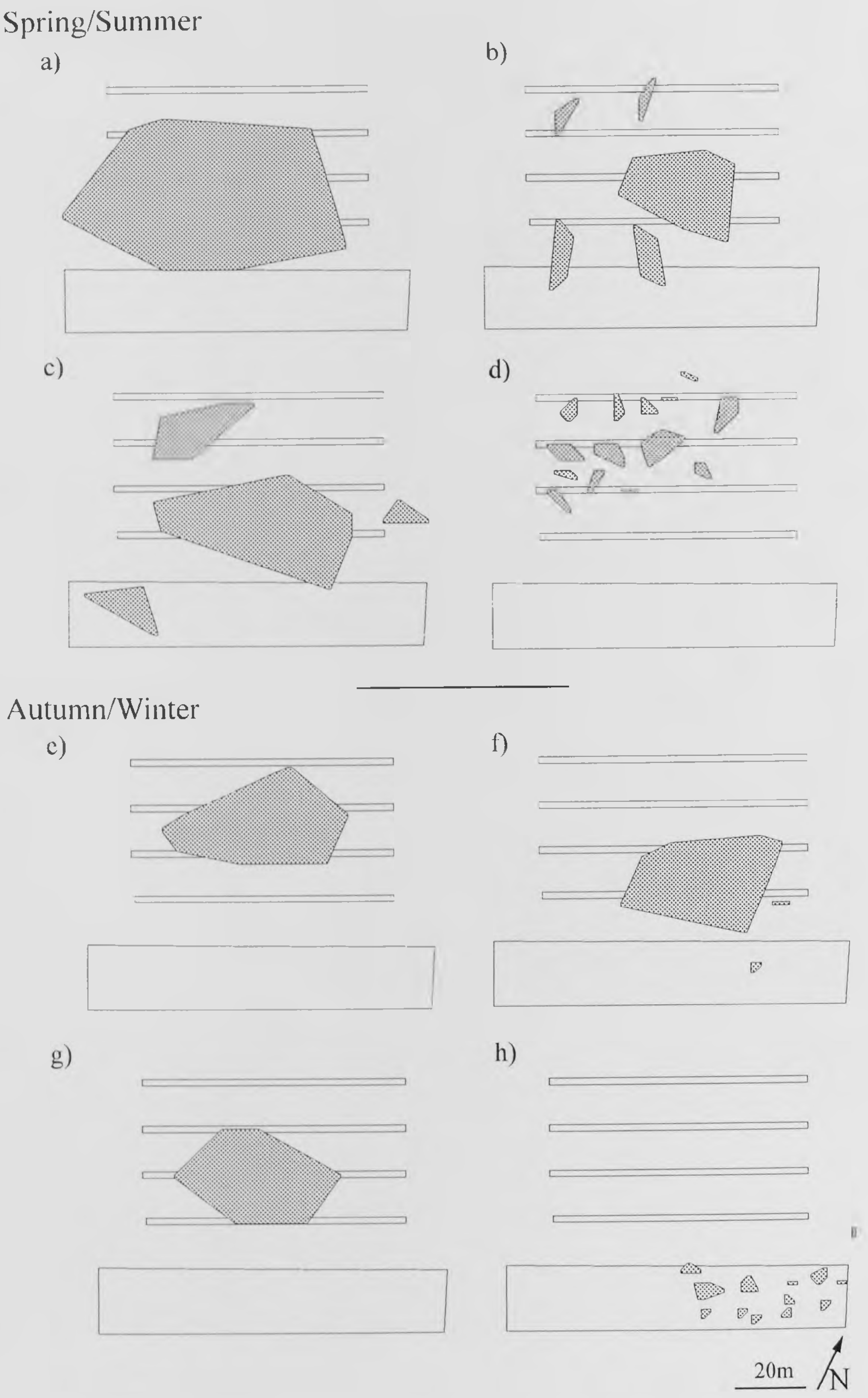


Figure 6.9 Distribution of core ranges of *A. sylvaticus* males a) 101, b) 103, c) 104, d) 109, e) 105,f) 106, g) 107 and h) 108 in agroforestry 'Block 3' in relation to habitat.

6.3.5 Range distribution and overlap

The overlap between animals tracked during the same periods, i.e. animals whose ranges could overlap, are shown in Figure 6.10.

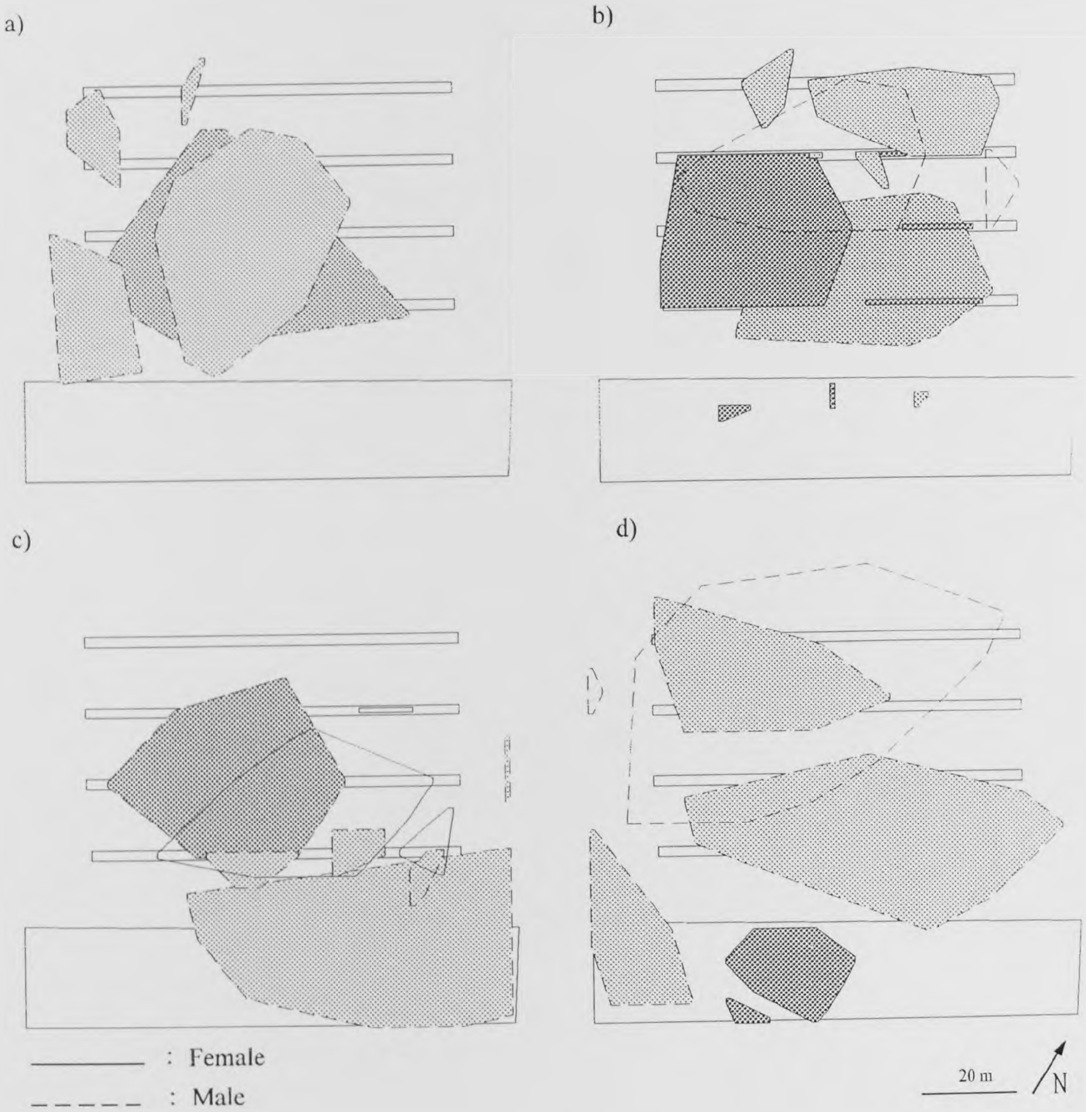


Figure 6.10 Polygons showing the extent of overlap of ranges of a) males 101 and 103, b) males 105-106 and females 202-203, c) males 107-108 and female 204, d) males 104-109 and female 206.

The plots (Figure 6.10) clearly show range overlap between males or between females as well as between animals of the opposite sex. Observed and expected distances between two animals (Table 6.6) were compared using Jacobs Index to reveal any attraction or avoidance between animals whose ranges were overlapping. Geometric distances were used to reduce the influence of distant fixes. Movement distances are often best normalised with a log-transform (though a negative exponential is sometimes better). Geometric means are means estimated with logarithms; log (x+1) was used to remove the problem of x = 0.

Table 6.6 Dynamic interaction between pairs of mice *A. sylvaticus* with overlapping ranges as shown by the mean distances between the N observed and the (N x N) expected pair of fixes for each animal (geometric mean).

		Mean distance (m)	
Pair	N (N x N)	Observed (Expected)	Jacobs Index
Single sex			
101/103	36 (1296)	48 (51)	0.05
104/109	48 (2304)	85 (76)	– 0.11
105/106	73 (5329)	48 (49)	– 0.01
202/203	60 (3600)	70 (72)	0.03
♂/♀ pair			
105/202	61 (3721)	48 (51)	0.05
105/203	60 (3600)	47 (43)	– 0.08
106/202	61 (3721)	45 (47)	0.06
107/204	34 (1156)	37 (41)	0.1

Two out of three of the male/male overlap analyses showed an avoidance tendency ($D_J = -0.11$ and $D_J = -0.01$) which might be explained by the fact that the animals were breeding and probably trying to avoid each others territory. In male/female relationships the only sign of avoidance was registered between male 105, a late mature male, and female 203 which did not show any sign of breeding, which may explain this avoidance tendency. On the other hand, this same male seemed to be accepted by female 202, which was still showing late signs of breeding. This female seemed to accept male 106 which was still in breeding condition in the Autumn. No dynamic interaction was found between male 106 and female 203 and also between male 104 and females 206 and 209.

6.3.6 Habitat analysis

For this analysis, individual edge files were used to estimate the proportion of each different habitat utilised by each mouse. Thus the proportion of fixes used to generate these files was described in the utilisation distribution and stability section (Section 6.3.2). For each habitat the space used along with the percentage of the maximum area were calculated (Table 6.7).

Association between frequency of individual distribution of ranges and habitat type were tested ($\chi^2 = 5072.9$ with 22 d.f., $P << 0.001$). There was a high discrepancy between observed and expected range sizes, mainly within the forestry control and the arable area, due to the heterogeneity of dispersion between these habitats; only two animals used the forestry control area as their preferred habitat. In general females are more confined within tree rows than males, the latter spreading all over the area. This is supported by the overall range core cluster polygons (Figure 6.11).

Table 6.7 Habitat content of ranges (m^2) for *A. sylvaticus* individuals in an agroforestry experimental plot. Values in brackets are areas as a proportion (%) of the maximum area of the range of that animal. M^2 was used instead of ha because of low values of habitat contents.

	Habitat		
I D	Tree rows	Forestry control	Arable alleys
♂			
101	175 (15.6)	0	950 (84.4)
103	100 (11.4)	0.5 (0.1)	775 (88.5)
104	225 (13)	150 (8.7)	1350 (78.3)
105	150 (13)	0	1000 (87)
106	175 (18.8)	7.5 (0.8)	750 (80.4)
107	150 (15.4)	0	825 (84.6)
108	0	137.5 (96.5)	5 (3.5)
109	75 (20)	0	300 (80)
♀			
202	200 (42.3)	22.5 (4.8)	250 (52.9)
203	25 (52.6)	0	22.5 (47.4)
204	200 (24.2)	0	625 (75.8)
206	0	100 (95.2)	5 (4.8)

Figure 6.11 Distribution of range cores of both sexes of *A. sylvaticus* in the agroforestry system experimental plot. Female ranges (4 animals) are dark shaded and male ranges (8 animals) are light shaded.

There is a highly significant association between animals grouped by sex and the habitat content of their home ranges ($\chi^2 = 53.26$ with 2 d.f., $P < 0.01$). In order to see which group of animals is associated with which habitat, the group components of χ^2 were calculated (Table 6.8). It appears that the largest χ^2 values for females are in tree rows and arable alleys. Females spread more in the tree rows than expected and thus a positive association exists between the habitat content of the female home ranges and this habitat. However, there is less space used by females within the arable alleys than expected and thus we can conclude that a negative association exists between the habitat content of females and the arable alleys. On the other hand the habitat content of male home ranges is positively associated with the arable alleys and negatively associated with the tree rows. Moreover, a positive association with the forestry control is found for males but not for females (Figure 6.11).

Table 6.8 Association between habitat content of ranges and sex of animal tracked.

	Average habitat content of range (m^2)		
	Tree rows	Forestry control	Arable alleys
♂			
Observed	131	37	744
Expected	167	48	694
χ^2	8.22	2.69	3.62
♀			
Observed	106	31	226
Expected	68	19	276
χ^2	22.29	6.79	9.12

There was no significant association between habitat content of home ranges and density of cover (Table 6.9) at the 5 % level of significance ($\chi^2 = 3.022$ with 2 d.f.). The discrepancy between the observed and the expected values was too small, and thus the density of the cover does not seem to have any influence on the habitat content of home ranges. However, it is hard to make further objective statements since animals were tracked at different periods of the year and thus under different densities of cover as shown by the hemispherical photographs of the area (Figure 6.12).

Table 6.9 Association between habitat content of ranges and density of cover in the tracking area.

	Average habitat content of range (m^2)			
Plant cover	Tree rows	Forestry control	Arable alleys	Total
Dense	129.17	41.75	667.5	838.42
Open	116.67	29.92	475.42	620
Total	245.83	69.67	1142.92	1458.42

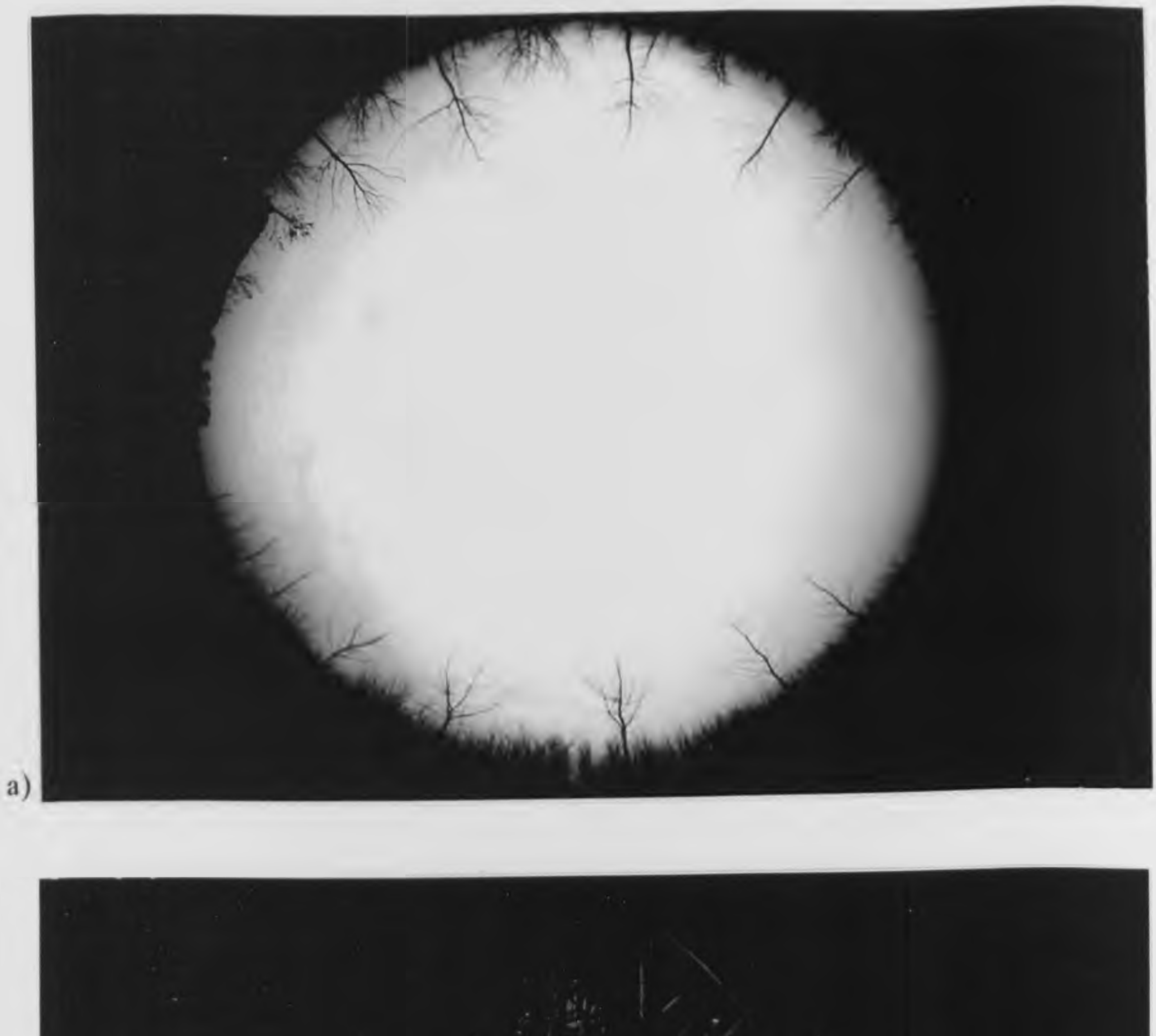


Figure 6.12 Hemispherical photographs taken in the arable alley 3 a) in November 1996 and b) in May 1997.

6.4 Discussion

Although there is no consensus about which analytical method yields results of most value in field ecology (Don and Rennols, 1983), it was important to select a home range model well-suited to the radio tracking data. The maximum polygon (Mcdonald *et al.*, 1980), even though one of the few methods that is comparable between studies (Harris *et al.*, 1990), includes peripheral fixes that strongly influence estimates of range size (Wolton, 1985). The concave polygon method might be a solution to reduce the overestimation of the maximum polygon method (Kenward, 1987) but it generates results that are not easy to compare with other methods. In the agroforestry system as it is designed, animals such as mice have discrete range boundaries limiting their expansion defined by the tree rows and the transition between them and the forestry control, and thus methods based on range depiction by isopleths such as the harmonic mean method (Dixon and Chapman, 1980) and the kernel method (Worton, 1989) would have been inappropriate. The ellipse method assesses the home range of an animal by its probability of occurrence at each point in space (Hayne, 1949). This probabilistic method has several disadvantages; it assumes that the centre of activity of the home range is derived from the arithmetic mean, which may not have any biological significance (Dixon and Chapman, 1980). This method also assumes that the fixes in a home range are independent and normally distributed around the centre of activity (Swihart and Slade, 1985), which is rarely true.

The choice of cluster analysis over the other methods was motivated by the fact that the agroforestry system and the forestry control are different habitat types in close proximity. The first was constituted with single tree rows adjacent to arable areas planted with an annual crop and the second was an area of trees planted at forestry density. The elimination of the outlier fixes and separation of range cores was important to see where mice forage and if they do so in more than one of these habitats. Most of them seemed to have preferred areas, from which a high proportion of the radio fixes were obtained. In fact home ranges were not used in an uniform manner, as is the case in most mammals (Spencer and Barrett, 1984; Jones, 1989).

Estimates, by different methods, of home ranges and overlap of home ranges can not be compared because of the differences in computational methods and in the underlying assumptions which lead to over- or under-estimates (Harris *et al.*, 1990). The maximum mice range estimated at 95% utilisation distribution is within the significant limits proposed by Gurnell (1976) and Randolph (1977), that is 0.87 - 2.18 ha for males and 0.024 - 0.3 ha for females. However, most of the ranges calculated here, using different methods, show sizes smaller than those suggested by Gurnell (1976) for both males and females e.g. 0.12-1.13 ha for males and 0.01-0.58 ha for females). In deciduous woodlands in England, Wolton and Flowerdew (1985) suggested an overall home range of 0.4-1.0 whilst Delany (1982), proposed 0.23 ha for males and 0.18 ha for females. The smaller home ranges found in the present study, are probably the result of habitat structure, as agroforestry might affect space use in so far as all the animal's needs may be available in such a system.

Male ranges are shown to be larger than female's as suggested by Kikkawa (1964), Gurnell (1978), Green (1979) and Montgomery (1979). Their ranges are larger during the breeding season, presumably so that they can maximise their chances of encountering an oestrus female (Wolton, 1985). Females use tree rows more intensively and show the spacing behaviour described by Brown (1969) as small monopolised zones established by pregnant females. In fact one of the females (202) showing activity strongly confined within this habitat, was pregnant whilst another one (204) was lactating.

The overlapping ranges between animals of the same sex might be due to a social system based on a dominance hierarchy (Brown, 1969). Whether a male has dominance over more than one female has yet to be proven as the interactions found between males and females are inconclusive. The overlap registered between animals of same sex (males 101 and 103) and (females 202 and 203) could be accepted if they were related as siblings.

It has been shown that the agroforestry area attracted more *A. sylvaticus* than did the forestry control. Most of the females were found within the tree rows and only one female was tracked within the forestry control. The reason for that may be that tree rows and forestry control areas are never ploughed and so suitable nest sites develop and are never destroyed. Males ranged more widely than females, using both tree rows and arable areas, whatever the period of the year and under open or dense plant cover. Males increased their range size in the breeding season whereas females reduced them.

7. GENERAL DISCUSSION

Live trapping and radiotracking are important in studies related to the ecology of small mammals particularly because of the difficulty of carrying out direct observations. However, quantification of patterns of movements such as habitat preference or size and shape of home range is difficult at best (Lemen and Freeman, 1985). Moreover, data collected by these methods are not free from bias and the following facts must be stressed: firstly, trapped animals that spend the night, or part of it, confined within a trap are prevented from carrying out their normal activities, such as mating, feeding and keeping intruders away from their territory, which is of high importance in social communities. Secondly, the presence of people within an experimental area for radiotracking purposes is obviously disturbing and may affect the normal behaviour of tracked animals. However, there is no better way for studying such animals at the present time, and estimation of the density of a population and the way the individuals use the habitat are key concerns for this investigation.

Both trapping and radiotracking data have given much information regarding the activity of animals across seasonal and annual cycles. However, radiotracking even though more time consuming than trapping, does allow observations concerning activity over twenty-four hours. It gives much finer detail, allowing habitat preference to be quantified in terms of the spatio-temporal use of multiple habitat patches (Tew et al., 1992) within the home range.

The present study was carried out on a silvoarable agroforestry trial system at the University of Leeds farm, where the most common small mammal was *Apodemus sylvaticus*.

Agroforestry is an approach to integrating conservation into common arable farming. The design of the replicate blocks in the system studied, and their proximity to mature hedges, made exchanges between habitats easy. However, there is no evidence to indicate that either blocks or mature hedges exerted any influence on the overall number of captures. The differences in numbers caught are not necessarily habitat related. There must be some other factors such as disturbance influencing the density of population. There were differences in numbers captured along mature hedges which were probably the results of disturbance, as one of the mature hedges borders a main road. Harvesting and ploughing (particularly the later) may also have a serious effect on the animals' distribution. It may reduce their activity in the arable areas for a short time (Pollard and Relton, 1970). This could explain why the numbers caught in the undisturbed areas increased sharply, i.e. because of a large immigration from the disturbed regions, notably the arable control where the number of animals was very low in Autumn when cover was sparse. The physical factors, such as the orientation of blocks and exposure to wind, do not seem to have any influence unlike the situation with insect pests and their predators (Naeem, 1996).

The species richness within the agroforestry system was not as high as that suggested by earlier work of Wright (1994). Neither *Microtus agrestis* nor *Micromys minutus* were caught during this study, although, Wright (1994) described them at low density of captures. The data confirm that areas located in the agroforestry such as tree rows and arable alleys have a greater concentration of animals than the controls.

Densities of captures were generally low. The number of traps used may have had an effect on numbers of animals caught. But this was not shown by the results of a test run in July 1997, as twice as many traps than that usually used caught only a slightly larger number of animals. Thus, captures gave the impression that the whole population was sampled which corresponds to the findings of Tanton (1965) using different trap densities.

7.1 Density of captures

Overall, the highest density of captures of small mammals was found in the agroforestry system, particularly within the tree rows. This habitat of four single lines of trees, although planted at a low density of trees (250 trees/ha) seems to be more attractive than the control planted at a forestry density (2020 trees/ha). Tree rows are typical habitat fragments. They are used by small mammals, notably *A. sylvaticus* and *Sorex araneus* as refuges, especially during Winter (Ylönen *et* al., 1991). However, *Clethrionomys glareolus*, which is usually a forest species (Hansson and Zejda, 1977), was mainly found along mature hawthorn hedges. This may be because *C. glareolus* is under competition pressure exerted by the more numerous *A. sylvaticus* within the narrow tree rows. However, appearance in 'marginal' habitats may not be a sign of subordinance, and similar situations of *C. glareolus* as well as many other rodents have occurred for many years in northern Scandinavia (Hansson, 1979a).

The microtine cycle of abundance has a typical periodicity of three or four years, though there are some populations that regularly, or occasionally, display a two- or five-year cycle (Begon *et al.*, 1986). The low density of captures of *C. glareolus* suggests that this species was going through the decreasing phase of its cycle (Krebs and Myers, 1974). This is supported by the data of Wright (1994) which for the same site in 1991 - 1994 (Figure 7.1) show that the density of captures of *C. glareolus* was far higher than during 1995-1997 (the period of the current research). The densities of *C. glareolus* in 1991-1994 were even similar to those of *A. sylvaticus*. However, many authors support the idea that *C. glareolus* declined in numbers in farmlands because of habitat destruction (Moore *et al.*, 1967; Pollard and Relton, 1970). *Sorex araneus* converse to the situation with *C. glareolus*, the population has increased in comparison with 1991-1994. This species occurs even within the open field, where many animals were caught.

It is possible that *C. glareolus* numbers are reduced by the presence of *Mustela erminea* in the area. Even at low population densities of, *C. glareolus* may constitute the favoured prey for *M. erminea* (Fitzgerald, 1977) even though an alternative prey (*Oryctolagus cuniculus*) was abundant in the area. This predator may exercise control over the fluctuation in abundance of *C. glareolus* by maintaining its density at a low level over a long period of time (Pearson, 1966). Predator-prey relationships and their role in the regulation of microtine populations in an agroforestry environment require a great deal of research.

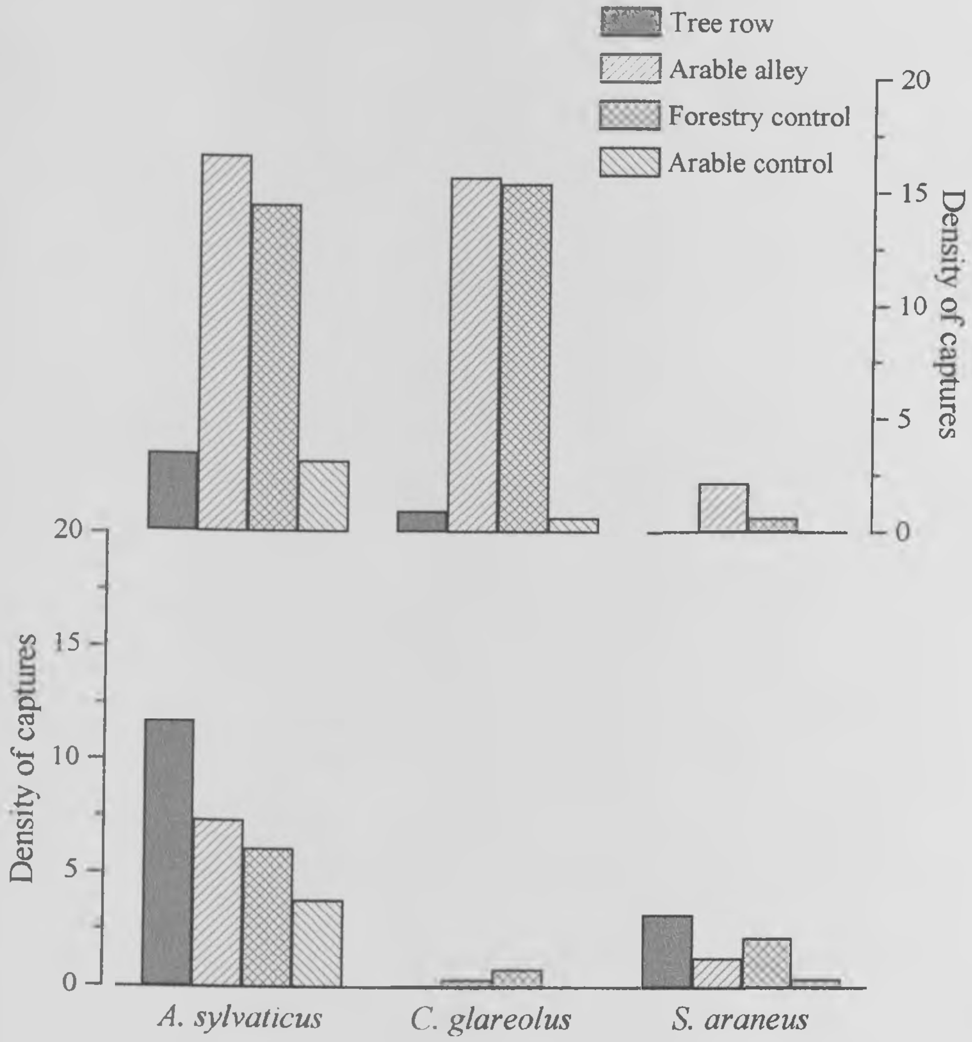


Figure 7.1 Densities of capture (Klaa, this work) compared with those of Wright (1994) (upper layer).

Captures of *A. sylvaticus* suggest that it exploits all the habitats found in the area (arable areas, tree areas and hedgerows). It showed a habitat generalist behaviour with, however, preference for habitats within the agroforestry system rather than the controls. Unlike for arthropods (Peng *et al.*, 1993), tree rows attracted more mice than trees planted at forestry density.

This species had a wider distribution in Winter, moving from and to each of the agroforestry habitats, whilst in Summer it moved mainly within tree rows, where relatively high number of captures were made each year. Similar observations were revealed by Kikkawa (1964) in a woodland surrounded by a wheat field in Berkshire (UK). Although season, and to a lesser extent temperature were seem to influence the density of capture, there was no evidence of environmental factors such as rainfall or wind speed affecting the results. The present results disagree with those of Gentry and Odum (1957) on old-field rodents.

7.2 Population dynamics

A high fraction of the population of *A. sylvaticus* was trapped, suggesting accurate estimates of the population size (Krebs and Boonstra, 1984), but it has to be accepted that no population size can ever be specified exactly (Begon, 1979)

No clear seasonal variations in trappability were shown in this study, even though this was mentioned by Pollard and Relton (1970). Trappability was modestly related to the density of population whilst density of captures and density of population were strongly correlated (Figure 7.2), and the patterns of their annual cycle were identical to those described by Tanton (1965) and Flowerdew (1985) in woodland and those of Green (1979) and Rogers and Gorman (1995) in farmland.

In general, small mammal populations show two types of cycles: a seasonal cycle within each year and a longer cycle with peaks occurring at intervals of several years (Morris, 1955). The annual cycle of *A. sylvaticus* in the agroforestry had three phases: the increase of the Winter followed by a decrease starting early in the Spring and lasting till the end of the Summer, and then the increase in early Autumn. In part this is related to the onset and duration of the breeding period, but also to losses in the population due to death, as mentioned by Zyadi and Benazzou (1992).

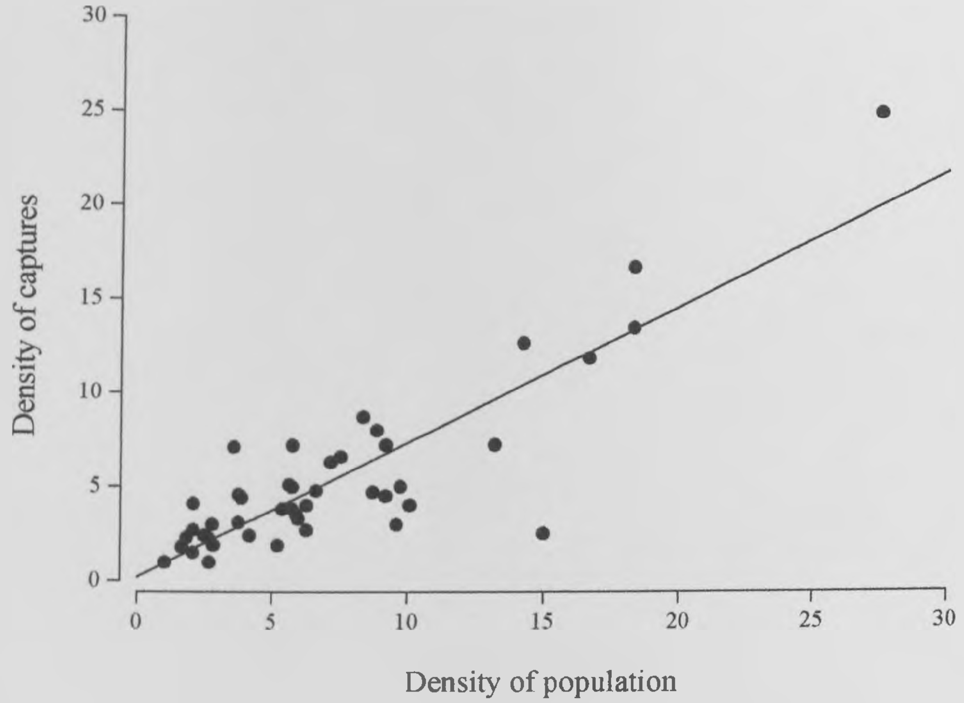


Figure 7.2 Mean density of captures of *A. sylvaticus* within the agroforestry system in relation to estimated density of population (using MNA). Data grouped for the four replicate blocks over the seasons ($r_s = 0.86$).

The highest rate of changes of the population were found during Autumn and Winter, suggesting an addition to the population at this period of the year. This added fraction to the population was mainly offspring, but a few adults were also present. Adult males, for instance, were present in low numbers in the Autumn/Winter period even though their proportion in the population did not follow a clear seasonal pattern. Periodicity in numbers of males does not match periodicity of the whole population. Thus there were more males caught in the Spring, corresponding to the breeding period, than in the Autumn. The high proportion of males in the population during Spring may have generated interference between individuals within the population (Krebs and Myers, 1974) which could have led to the observed sharp decline in their numbers, either because of death or emigration. The most important losses seemed to be during the Summer, resulting in a decrease in population density. Adults, notably males, were rarely caught in Autumn. Thus, the added population was mainly of young animals (Gurnell, 1978) that will overwinter. Indeed, high survival was registered during the Winter, as suggested by Rogers and Gorman (1995).

Food availability seems to have affected many parameters of the population, notably the distribution of the animals, their density, survival and breeding as was described by Smyth (1966) and Hansson (1971). It is tempting to believe that with different cropping systems involving, for example, Spring crops, the annual cycles would follow different patterns, or that if environmental factors can be manipulated this will help to understand how population numbers are modified and cycles shifted because of these factors (Flowerdew, 1987).

In the agroforestry systems, breeding stopped in early Autumn; this was mainly shown for male *A. sylvaticus* as females had a longer and sporadic breeding period. However, no continuous breeding was registered over the Winter as suggested by Smyth (1966). It has been suggested that the period of reproduction of this species was related to day length (Brown, 1955). For such a nocturnal species, the period of activity above ground is reduced as days get longer. This may explain why radiotracking showed that the tracked animals spent more time off the nest in the Winter. The seasonal pattern clearly shown by the male breeding cycle, may also have a link with food supply as has been suggested by many authors (e.g. Flowerdew, 1972; Gurnell, 1978; Hansson, 1971). Smyth (1966) even made a series of hypotheses concerning the effect of food abundance on Winter breeding. Winter wheat in the arable alleys and controls was harvested in 1995 and 1996 late in July and Winter barley in 1997 was harvested in early Summer (June) coinciding with the end of breeding in male *A. Sylvaticus*. Moreover, Flowerdew and Gardner (1978) showed that if food availability is abundant, survival of the animals must be good and the population density must increase from Winter to Summer. This was not the case for *A. sylvaticus* in the agroforestry system as the estimated survival rates were at their lowest values at this period, corresponding to the decline of the population density.

7.3 Movement and use of space

Despite the fact that the arable areas are more likely to be serious obstacles to movement of many small mammals (Mader, 1984; Henderson *et al.*, 1985), radiotracking of *A. sylvaticus* has shown, on several occasions, animals travelling between blocks using routes across arable fields. However, Zhang and Usher (1991), stressed the importance of ground cover for the dispersal of small mammals and accordingly most movements of *A. sylvaticus* within the open field were recorded when wheat and barley crops were high enough to provide a thick cover. Recaptures in the fields (arable controls) of animals previously caught within the Agroforestry enclosure tend to support the above observation.

Short range movements were observed in *A. sylvaticus* between the agroforestry system and the surrounding habitats such as the controls, because of their proximity (Flowerdew, 1976). This may have had an effect on the population dynamics (Green, 1979). Migration into the agroforestry system happened during ploughing, increasing the density of the population there. Tree rows were then used as an alternative habitat. Moreover dispersal as defined by Berndt and Sternberg (1968), within tree rows and arable areas showed seasonal patterns which ceased when the field was bare. Wegner and Meriam (1979) described similar movement patterns between cropped fields and woodlands.

This study, the first to apply radiotracking to experimental agroforestry habitats, supports the view that *A. sylvaticus* switch from one habitat to another under different circumstances. These shifts were most probably brought about by changes in abundance of food. The tendency of this animal to shift the centre of its activity was reported by Randolph (1977) and Green (1979). However, the main problem was to define the real home range from the overestimated space used by each animal due to sporadic excursions (Macdonald, 1978).

Home ranges of male *A. sylvaticus* were larger than those of the females, showing a seasonal pattern particularly during the breeding period corresponding to the Spring. Increasing the home range is probably a way of compensating for the few mating opportunities, as the average males:females ratio for the four agroforestry experimental blocks during this period was 9:5. This corresponds to the findings of Myllymäki (1977) and Nelson (1995), working on *Microtus agrestis*. They noted that home ranges of males were related to the density of females. Food availability may also have contributed to an increase in the activity of this species, and thus home range increase may also be related to searching for food (Taylor and Quy, 1978).

Most of the fifteen mice intensively studied had overlapping ranges. Overlaps were registered between animals of same sex as well as animals of opposite sexes. No rivalry was detected from the pattern of dispersion of the animals, notably between males. This is probably due to the low risk for a conspecific to be detected, as the animals were ‘patrolling’ in relatively large areas which minimised their chance to meet a rival (Nelson, 1995).

8. Bibliography

Adams L. and Davis S. D. 1967. The internal anatomy of home range. Journal of Mammalogy, **48**, 529-536.

Aebischer N. J., Robertson P. A. and Kenward R. E. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology, **74**, 1313-1325.

Akbar Z. and Gorman M. L. 1993. The effect of supplementary feeding upon the sizes of the home ranges of wood mice *Apodemus sylvaticus* living on a system of maritime sand-dunes. Journal of Zoology, **231**, 233-237.

Alibhai S. K. and Gipps J. H. W. 1985. The population of bank voles. Symposia of the Zoological Society of London, **55**, 277-305.

Altieri M. A., Trujillo F. J. and Farrell J. 1987. Plant-insects interactions and soil fertility in agroforestry systems: Implications for the design of sustainable agroecosystems. In: Agroforestry: realities, possibilities and potentials. 89-108, (H. L. Gholz), Martinus Nijhoff, Florida (USA).

Amlaner Jr. C. J. 1978. Biotelemetry from free ranging animals. In: Animal marking, recognition marking of animals in research. 205-228, Stonehouse B., Bradford.

Anderson D. J. 1982. The home-range: a new non parametric estimation technique. Ecology, **63**, 103-112.

Atta-krah A. N. and Francis P. A. 1987. The role of on-farm trials in the evaluation of composite technologies: the case of alley farming in southern Nigeria. Agricultural Systems, **23**, 133-152.

Beddall J. L. 1957. Hedges for farm and garden. Faber and Faber, London.

Begon M. 1979. Investigating animal abundance. Edward Arnold, London.

Begon M., Harper J. L. and Townsend C. R. 1986. Ecology. (M. Begon, J. L. Harper and C. R. Townsend), Blackwell Scientific Publications, London.

Bernard J. 1969. Les mammifères de Tunisie et des régions voisines. Bulletin de la faculté d'Agronomie, Univ. Tunis, **24**, 41-172.

Berndt R. and Sternberg H. 1968. Terms studies and experiments on the problems of bird dispersion. Ibis, **110**, 256-269.

Berry R. J., Evans I. M. and Sennitt B. F. C. 1967. The relationships and ecology of *Apodemus sylvaticus* from the small isles of the inner Hebrides, Scotland. Journal of Zoology, **152**, 333-346.

Blower J. G., Cook L. M. and Bishop J. A. 1981. Estimating the size of animal populations. George Allen and Unwin Limited, London.

Brewbaker J. L. 1987. Significant nitrogen fixing trees in agroforestry systems. In: Agroforestry: realities, possibilities and potentials. 31-35, (H. L. Gholz), Martinus Nijhoff, Florida (USA).

Brown J. L. 1954. Small mammal population at Silwood Park Field Centre, Berkshire, England. Journal of Mammalogy, **35**, 161-176.

Brown J. L. and Orians G. H. 1970. Spacing patterns in mobile animals. Annu. Rev. Ecol. Syst., **1**, 239-262.

Brown L. E. 1969. Field experiments on the movements of *Apodemus sylvaticus* L. using trapping and tracking techniques. Oecologia, **2**, 198-222.

Buck L. E. 1995. Agroforestry, policy issues and research directions in the United States and less developed countries. Insights and challenges from recent experience.

In: Agroforestry: science, policy and practice. 57-73, (F. L. Sinclair), Kluwer Academic Publishers, Bangor (UK).

Burt W. H. 1943. Territoriality and home-range concepts as applied to mammals. Journal of Mammalogy, **24**, 346-352.

Callow N. L. 1995. Interactions among predators, parasitoids and aphids in relation to a Silvoarable Agroforestry Environment. (M.Sc. Thesis), University of Leeds.

Chapman D. G. 1954. The estimation of biological populations. Ann. Math. Stat., **25**, 1-15.

Chitty D. and Kempson D. H. 1949. Prebaiting small mammals and a new design of live trap. Ecology, **30**, 536-542.

Churchfield S. 1986. Shrews. Mammal Society Series, 20pp.

Clancy J. 1991. Site surveying and liveling. Edward Arnold, London.

Corbet G. B. and Harris S. 1991. The handbook of British mammals. Third edition. (G. B. Corbet and S Harris), Blackwell Science, Oxford.

Corry D. 1990. The Silvoarable Group. Agroforestry in the U.K., **1**, 11-12.

Crawley M. C. 1969. Movements and home ranges of *Clethrionomys glareolus* Schreber and *Apodemus sylvaticus* L. in north-east England . Oikos, **20**, 310-319.

Crowcroft P. 1957. The life of shrew. Max Reinhart, London.

Current D. and Scherr S. J. 1995. Farm costs and benefits from agroforestry and farm forestry projects in Central America and the Caribbean: implications for policy. In: Agroforestry: Science, policy and practice. 87-103, (F. L. Sinclair), Kluwer Academic Publishers, Bangor (UK).

Davis D. E. and Golley F. B. 1963. Principles in mammalogy. (Peter Gray), Chapman and Hall, London.

Delany M. J. 1974. The ecology of small mammals. Edward Arnold, London.

Delany M. J. 1982. Mammal ecology. Blackie, London.

Dixon K. R. and Chapman J. A. 1980. Harmonic mean measure of animal activity areas. Ecology, **61**, 1040-1044.

Don B. A. C. and Rennolls K. 1983. A home-range model incorporating biological attraction points. Journal of Animal Ecology, **52**, 69-81.

Dupraz C. and Newman S. M. 1997. Temperate agroforestry: The European way. In: Temperate agroforestry systems. 181-236, (A. M. Gordon and S. M. Newman), CAB International, Ontario (Canada), Buckingham (UK).

Eisenberg J. F. and Harris L. D. 1987. Agriculture, forestry and wildlife resources: a brief review for the western hemisphere . In: Agroforestry: Realities, possibilities and potentials. 47-57, (H. L. Gholz), Martinus Nijhoff, Florida (USA).

Ellenbroeck F. J. M. 1980. Interspecific interactions of the common shrew (*Sorex araneus*) and the pygmy shrew (*Sorex minutus*). Netherlands Journal of Zoology, **30**, 532-532.

Evans F. C. 1942. Studies of small mammal population in Bagley woods, Berkshire. Journal of Animal Ecology, **11**, 182-197.

Fisher R. A. and Ford E. B. 1947. The spread of a gene in natural conditions in a colony of the moth *Panaxia dominula* L. Heridity, **1**, 143-174.

Fitzgerald B. M. 1977. Weasel predation on a cyclic population of the mountain vole *Microtus montanus* in California. Journal of Animal Ecology, **46**, 367-397.

Fitzgibbon C. D. 1997. Small mammals in farm woodlands: the effects of habitat isolation and surrounding land-use patterns. Journal of Applied Ecology, **34**, 530-539.

Flowerdew J. R. 1976. The effect of a local increase in food supply on the distribution of woodland mice and voles. Journal of Zoology, **180**, 509-513.

Flowerdew J. R. 1985. The population dynamics of wood mice and yellow-necked mice. Symposia of the Zoological Society of London, **55**, 315-338.

Flowerdew J. R. 1987. Mammals. Their reproductive biology and population ecology. Edward Arnold, London.

Flowerdew J. R. 1972. The effect of supplementary food on a population of wood mice (*Apodemus sylvaticus*). Journal of Animal Ecology, **41**, 553-566.

Flowerdew J. R. 1974. Field and laboratory experiments on the social behaviour and population dynamics of the wood mouse, *Apodemus sylvaticus*. Journal of Animal Ecology, **43**, 499-511.

Flowerdew J. R. and Gardner G. 1978. Small rodent populations and food supply in a Derbyshire ash wood. Journal of Animal Ecology, **47**, 725-740.

Ford R. G. and Krumme D. W. 1979. The analysis of space use patterns. Journal of Theoretical Biology, **76**, 125-155.

French N. R., Stoddart D. M. and Bobek B. 1975. Patterns of demography in small mammal populations. In: Small mammals: Their productivity and population dynamics. 73-102, (F. G. Golley; K. Petrusewicz and L. Ryszkowski), Cambridge University Press, Cambridge.

Gentry J. B. and Odum E. P. 1957. The effect of weather on the winter activity of old-field rodents. Journal of Mammalogy, **38**, 72-77.

Gholz H. L. 1987. Agroforestry: Realities, possibilities and potentials. (H. L. Gholz), Martinus Nijhoff, Florida (USA).

Golley F. B., Ryszkowski L. and Sokur J. K. 1975. The role of small mammals in temperate forest, grassland and cultivated fields. In: Small mammals: their productivity and population dynamics. 223-242, (F. G. Golley, K. Petrusewicz and L. Ryszkowski), Cambridge University Press, Cambridge.

Gordon A. M., Newman S. M. and Williams P. A. 1997. Temperate agroforestry: An overview. In: Temperate agroforestry systems. 1-8, (A. M. Gordon and S. M. Newman), CAB International, Ontario (Canada), Buckingham (UK).

Green R. 1979. The ecology of wood mice (*Apodemus sylvaticus*) on arable farmland.. Journal of Zoology, **188**, 357-377.

Grewal S. S., Juneja M. L., Singh K. and Singh S. 1994. A comparison of two agroforestry systems for soil, water and nutrient conservation on degraded land. Soil Technology, **7**, 145-153.

Gurnell J. 1982. Index to theses and dissertations relevant to the biology of *Apodemus sylvaticus*, *Apodemus flavicollis* and *Clethrionomys glareolus* held in British Universities. Mammal review, **12**, 143-145.

Gurnell J. 1978. Seasonal changes in numbers and behavioural interaction in wood mice *Apodemus sylvaticus*. Journal of Animal Ecology, **47**, 741-755.

Gurnell J. 1976. Studies on the effects of bait and sampling intensity on trapping and estimating wood mice, *Apodemus sylvaticus*. Journal of Zoology, **178**, 91-105.

Gurnell J. and Flowerdew J. R. 1982. Live trapping small mammals. A practical guide. The Mammal Society, Berkshire.

Hansson L. 1971. Small rodent food, feeding and population dynamics. A comparison between granivorous and herbivorous species in Scandinavia. Oikos, **22**, 183-198.

Hansson L. (a) 1979. Condition and diet in relation to habitat in bank voles *Clethrionomys glareolus*: population or community approach? Oikos, **33**, 55-63.

Hansson L. (b) 1979. Food as a limiting factor for small rodent numbers. Oecologia (Berlin), **37**, 297-314.

Hansson L. and Zejda J. 1977. Plant damage by bank voles (*Clethrionomys glareolus* Schreber) and related species in Europe. EPPO Bulletin, **7**, 223-242.

Harris S., Cresswell W. J., Ford P. G., Trewhella W. J., Woollard T. and Wray S. 1990. Home-range analysis using radio-tracking data: a review of problems and techniques particularly as applied to the study of mammals. Mammal Review, **20**, 97-123.

Hayne D. W. 1949. Calculation of size of home-range. Journal of Mammalogy, **30**, 1-18.

Hayward G. P. and Phillipson J. 1979. Community structure and functional role of small mammals in ecosystems. In: Ecology of small mammals. 135-211, (D. M. Stoddart), Chapman and Hall, London.

Henderson M. T., Merriam G. and Wegner J. 1985. Patchy environments and species survival: Chipmunks in an agricultural mosaic. Biological Conservation, **31**, 95-105.

Herubin C. A. 1991. Principles of surveying. IV edition. (Charles A. Herubin), Englewood Cliffs, New Jersey.

Hilborn R., Redfield J. A. and Krebs C. J. 1976. On the reliability of enumeration for mark and recapture census of voles. Can. J. Zool., **54**, 1019-1024.

Jacobs J. 1974. Quantitative measurement of food selection. A modification of the forage ratio and Ivlev's Electricity Index. Oecologia (Berlin), **14**, 413-417.

Jarvis P. G. 1991. Agroforestry: Principles and practice. (P. G. Jarvis), London.

Jennrich R. I. and Turner F. B. 1969. Measurement of non-circular home-range. Journal of Theoretical Biology, **22**, 227-237.

Jolly G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika, **52**, 225-247.

Jolly G. M. and Dickson J. M. 1983. The problem of unequal catchability in mark-recapture estimation of small mammal population. Can. J. Zool., **61**, 922-927.

Jones W. T. 1989. Dispersal distance and the range of nightly movements in Merriam's kangaroo rats. Journal of Mammalogy, **70**, 27-30.

Jorgensen C. D. 1968. Home range as a measure of probable interactions among populations of small mammals. Journal of Mammalogy, **49**, 104-112.

Kenward R. 1987. Wild life radio tagging. Academic Press, London.

Kenward R. E. and Hodder K. H. 1996. Ranges V. An analysis system for biological location data I.T.E., Dorset, UK.

Kenward R. E., Marcström V. and Karlbom M. 1993. Post-nestling behaviour in goshawks, *Accipiter gentilis*: II. Sex differences in sociability and nest-switching. Animal Behaviour, **46**, 371-378.

Kikkawa J. 1964. Movement, activity and distribution of the small rodents *Clethrionomys glareolus* and *Apodemus sylvaticus* in woodland. Journal of Animal Ecology, **33**, 259-299.

Kowalski K. 1985. Annual cycle of reproduction in *Apodemus sylvaticus* in Algeria. Acta Zoologica Fennica, **173**, 85-86.

Krebs C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecol. Monogr., **36**, 239-273.

Krebs C. J. 1989. Ecological Methodology. Harper and Row, London, New York.

Krebs C. J. and Boonstra R. 1984. Trappability estimates for mark-recapture data. Can. J. Zool., **62**, 2440-2444.

Krebs C. J. and Myers J. H. 1974. Population cycles in small mammals. Advances in Ecological Research, **8**, 267-399.

Lemen C. A. and Freeman P. W. 1985. Tracking mammals with fluorescent pigments: a new technique. Journal of Mammalogy, **66**, 134-136.

Leslie P. H., Chitty D. and Chitty H. 1953. The estimation of population parameters from data obtained by means of the capture-recapture method. iii: an example of the practical applications of the method. Biometrika, **40**, 137-169.

Macdonald D. W. 1978. Radio-tracking: some applications and limitations. In: Animal marking, recognition marking of animals in research. 193-204, B. Stonehouse, Bradford.

Mader H. J. 1984. Animal habitat isolation by roads and agricultural fields. Biological Conservation, **29**, 81-96.

Mallorie H. C. and Flowerdew J. R. 1994. Woodland small mammal population ecology in Britain. A preliminary review of the Mammal-Society survey of wood mice *Apodemus sylvaticus* and bank voles *Clethrionomys glareolus*, 1982-87. Mammal Review, **24**, 1-15.

Manly B. F. J. 1984. Obtaining confidence limits on parameters of the Jolly-Seber model for capture-recapture data. Biometrics, **40**, 749-758.

Manly B. F. J. and Parr M. J. 1968. A new method of estimating population size, survivorship, and birth rate from capture-recapture data. Transactions of the Society for British Entomology, **18**, 81-89.

Montgomery W. I. 1980. Population structure and dynamics of sympatric *Apodemus* species (Rodentia: Muridae). Journal of Zoology, **192**, 351-377.

Montgomery W. I. 1979. An examination of interspecific, sexual and individual bias affecting rodent captures in Longworth traps. Acta Theriologica, **24**, 35-45.

Montgomery W. I. 1978. Studies on the distribution of *Apodemus sylvaticus* (L.) and *A. flavicollis* (Melchior) in Britain. Mammal Review, **8 (4)**, 177-184.

Moore N. W. 1987. The bird of time. The science and politics of nature conservation. Cambridge University Press, Cambridge.

Moore N. W., Hooper M. D. and Davis B. N. K. 1967. Hedges. I. Introduction and reconnaissance studies. Journal of Applied Ecology, **4**, 201-220.

Morris P. A. 1988. A study of home range and movements in the hedgehog (*Erinaceus europaeus*). Journal of Zoology, **214**, 433-449.

Morris R. F. 1955. Population studies on some small forest mammals in Eastern Canada. Journal of Mammalogy, **36**, 20-33.

Myers J. H. and Krebs C. J. 1971. Sex ratio in open and enclosed vole populations: demographic implications. Am. Nat., **105**, 325-344.

Myllymäki A. 1977. Intraspecific competition and home range dynamics in the field vole *Microtus agrestis*. Oikos, **29**, 553-569.

Naeem M. 1996. Responses of Aphids and their natural enemies to a silvoarable agroforestry environment. (Ph.D. thesis), University of Leeds.

Nair P. K. R. 1987. Soil productivity under agroforestry. In: Agroforestry: Realities, possibilities and potentials. 21-30, (H. L. Gholz), Martinus Nijhoff, Florida (USA).

Nair P. K. R. 1984. Soil productivity, aspects of agroforestry. (P. A. Huxley), ICRAF, Nairobi (Kenya).

Negus N. G. and Berger P. J. 1977. Experimental triggering of reproduction in a natural population of *Microtus montanus*. Science, **196**, 1230-1231.

Nelson J. 1995. Determinants of male spacing behaviour in microtines: an experimental manipulation of female spatial distribution and density. Behavioural Ecology and sociobiology, **37**, 217-223.

Newman S. M. and Gordon A. M. 1997. Temperate agroforestry: Synthesis and future directions. In: Temperate agroforestry systems. 251-266, (A. M. Gordon and S. M. Newman), CAB International, Ontario (Canada), Buckingham (UK).

Nichols J. D. and Pollock K. H. 1983. Estimation methodology in contemporary in small mammal capture-recapture studies. Journal of Mammalogy, **64**, 253-260.

Nicholson A. J. 1954. An outline of the dynamics of animal populations. Austr. J. Zoology, **2**, 9-65.

Ong C. K., Corlett J. E., Singh R. P. and Black C. R. 1991. Above and below ground interactions in agroforestry systems. In: Agroforestry: Principles and practice. 45-57, (P. G. Jarvis), Elsevier, London.

Palm C. A. 1995. Contribution of agroforestry trees to nutrient requirements of intercropped plants. In: Agroforestry: Science, policy and practice. 105-124, (F. L. Sinclair), Kluwer Academic Publishers, Bangor (UK).

Pearson O. P. 1966. The prey of carnivores during one cycle of mouse abundance. Journal of Animal Ecology, **3**, 217-233.

Peng R. K., Incoll L. D., Sutton L. S., Wright C. and Chadwick A. 1993. Diversity of airborne arthropods in a sylvoarable agroforestry system. Journal of Applied Ecology, **30**, 551-562.

Peng R. K., Sutton S. L. and Fletcher C. R. 1992. Spatial and temporal distribution patterns of flying Diptera. Journal of Zoology, **228**, 329-340.

Pollard E. and Relton J. 1970. Hedges. V: a study of small mammals in hedges and cultivated fields. Journal of Applied Ecology, **7**, 549-557.

Pouliquen O., Leishman M. and Redhead T. D. 1990. Effect of radio collars on wild mice, *Mus domesticus*. Can. J. Zool., **68**, 1607-1609.

Price C. 1995. Economic evaluation of financial and non-financial costs and benefits in agroforestry development and the value of sustainability. Agroforestry Systems (Kluwer Academic Publishers, Netherland), **30**, 75-86.

Randolph S. E. 1977. Changing spatial relationships in a population of *Apodemus sylvaticus* with the onset of breeding. Journal of Animal Ecology, **46**, 653-676.

Rocheleau M. D. E. 1987. The user perspective and the agroforestry research and action agenda. In: Agroforestry: realities, possibilities and potentials. 59-87, (H. L. Gholz), Martinus Nijhoff, Florida (USA).

Roff D. A. 1973. On the accuracy of some mark-recapture estimators. Oecologica, **12**, 15-34.

Rogers L. M. and Gorman M. L. 1995. The population dynamics of small mammals living in set-aside and surrounding semi-natural and crop land. Journal of Zoology, **236**, 451-464.

Rood J. P. 1965. Observations on the life cycle and variation of the long tailed field mouse *Apodemus sylvaticus* on the isles of Scilly and Cornwall. Journal of Zoology, **147**, 99-107.

Sargent C. and Bass S. 1992. Plantation politics. Forest plantations in development. (C. Sargent and S. Bass), Earthscan Publications Ltd, London.

Seber G. A. F. 1965. A note on the multiple recapture census. Biometrika, **52**, 249-259.

Seber G. A. F. 1986. A review of estimating animal abundance. Biometrics, **42**, 267-292.

Seber G. A. F. 1973. The estimation of animal abundance and related parameters. Charles Griffin Publications, London.

Smith M. H. 1971. Food as a limiting factor in the population ecology of *Peromyscus pelionotus* (Wagner). Annals Zoologici Fennici, **8**, 109-112.

Smyth M. 1966. Winter breeding in woodland mice, *Apodemus sylvaticus*, and voles, *Clethrionomys glareolus* and *Microtus agrestis*, near Oxford. Journal of Animal Ecology, **35**, 471-485.

Southern H. N. 1973. A yardstick for measuring populations of small rodents. Mammal Review, **3**, 1-23.

Spencer W. D. and Barrett R. H. 1984. An evaluation of the harmonic mean measure for defining carnivore activity areas. Acta Zoologica Fennica, **171**, 255-259.

Stoddart M. D. 1982. Does traps odour influence estimation of population size of the short-tailed vole, *Microtus agrestis*? Journal of Animal Ecology, **51**, 375-386.

Sutherland W. J. 1996. From individual behaviour to population ecology. Oxford University Press, Oxford.

Swihart R. K. and Slade N. A. 1985. Testing for independence in animal movements. Ecology, **66**, 1176-1184.

Tanton M. T. 1965. Problems of live trapping and population estimation for the wood mouse, *Apodemus sylvaticus* (l). Journal of Animal Ecology , **34**, 1-22.

Taylor K. D. and Quy R. J. 1978. Long distance movements of a common rat (*Rattus norvegicus*) revealed by radio-tracking. Mammalia, **42**, 63-71.

Tew T. E. 1994. Farmland hedgerows: habitat, corridors or irrelevant? A small mammal's perspective. In: Hedgerow management and nature conservation. 80-94, (Watt T. A. and Buckley G. P.), Wye College Press, Wye.

Tew T. E. and Macdonald D. W. 1993. The effects of harvest on arable wood mice *Apodemus sylvaticus*. Biological Conservation, **65**, 279-283.

Tew T. E., Macdonald D. W. and Rands M. R. W. 1992. Herbicide application affects microhabitat use by arable wood mice (*Apodemus sylvaticus*). Journal of Applied Ecology, **29**, 532-539.

Van Winkle W. 1975. Comparison of several probabilistic home-range models. Journal of Wildlife Management, **39**, 118-123 .

Vergara N. T. 1987. Agroforestry: a sustainable land use for fragile ecosystems in the humid tropics. In: Agroforestry: Realities, possibilities and potentials. 7-19, (H. L. Gholz), Martinus Nijhoff, Florida (USA).

Watson C. A., Atkinson D., Newbould P., Birley M. A. B. and Hooker J. E. 1991. Environmental impact of silvopastoral systems. Agroforestry in the UK, **2**, 43-45.

Watts C. H. S. 1969. The regulation of wood mouse (*Apodemus sylvaticus*) numbers in Wytham woods, Berkshire. Journal of Animal Ecology, **38**, 285-304.

Wegner J. F. and Merriam G. 1979. Movements by birds and small mammals between a woodland adjoining farmland habitats. Journal of Applied Ecology, **16**, 349-357.

Williams G. C. 1966. Adaptation and natural selection. Princeton Univ. Press, Princeton.

Wolton R. J. 1985. A possible role for faeces in range-marking by the wood mouse, *Apodemus sylvaticus*. Journal of Zoology, **206**, 286-291.

Wolton R. J. and Flowerdew J. R. 1985. Spatial distribution and movements of wood mice, yellow necked mice and bank voles. Symposia of the Zoological Society of London, **55**, 249-275.

Worton B. J. 1989. Kernel methods for estimating the utilisation distribution in home-range studies. Ecology, **70**, 164-168.

Wright C. 1994. The distribution and abundance of small mammals in a silvoarable agroforestry system. Agroforestry Forum, **5 (2)**, 26-28.

Ylönen H., Altner H. J. and Stubbe M. 1991. Seasonal dynamics of small mammals in an isolated woodland and its agricultural surroundings. Annals Zoologici Fennici, **28**, 7-14.

Zhang Z. and Usher M. B. 1991. Dispersal of wood mice and bank voles in an agricultural landscape. Acta Theriologica, **36**, 239-245.

Zyadi F. and Benazzou T. 1992. Dynamique de population de *gerbillus campestris* (Rodentia, Gerbillidae) dans la plaine du gharb, Maroc. Rev. Ecol. (terre vie), **47**, 245-258.

9. Appendix

Week number	Start to finish	Month	Year
1	20 to 26	December	1994
2	27 to 02	December	1994
3	03 to 09	January	1995
4	10 to 16	January	1995
5	17 to 23	January	1995
6	24 to 30	January	1995
7	31 to 06	January	1995
8	07 to 13	February	1995
9	14 to 20	February	1995
10	21 to 27	February	1995
11	28 to 06	February	1995
12	07 to 13	March	1995
13	14 to 20	March	1995
14	21 to 27	March	1995
15	28 to 03	March	1995
16	04 to 10	April	1995
17	11 to 17	April	1995
18	18 to 24	April	1995
19	25 to 01	April	1995
20	02 to 08	May	1995
21	09 to 15	May	1995
22	16 to 22	May	1995
23	23 to 29	May	1995
24	30 to 05	May	1995
25	06 to 12	June	1995

26	13 to 19	June	1995
27	20 to 26	June	1995
28	27 to 03	June	1995
29	04 to 10	July	1995
30	11 to 17	July	1995
31	18 to 24	July	1995
32	25 to 31	July	1995
33	01 to 07	August	1995
34	08 to 14	August	1995
35	15 to 21	August	1995
36	22 to 28	August	1995
37	29 to 04	August	1995
38	05 to 11	September	1995
39	12 to 18	September	1995
40	19 to 25	September	1995
41	26 to 02	September	1995
42	03 to 09	October	1995
43	10 to 16	October	1995
44	17 to 23	October	1995
45	24 to 30	October	1995
46	31 to 06	October	1995
47	07 to 13	November	1995
48	14 to 20	November	1995
49	21 to 27	November	1995
50	28 to 04	November	1995
51	05 to 11	December	1995
52	12 to 18	December	1995
53	19 to 25	December	1995
54	26 to 01	December	1995

55	02 to 08	January	1996
56	09 to 15	January	1996
57	16 to 22	January	1996
58	23 to 29	January	1996
59	30 to 05	January	1996
60	06 to 12	February	1996
61	13 to 19	February	1996
62	20 to 26	February	1996
63	27 to 04	February	1996
64	05 to 11	March	1996
65	12 to 18	March	1996
66	19 to 25	March	1996
67	26 to 01	March	1996
68	02 to 08	April	1996
69	09 to 15	April	1996
70	16 to 22	April	1996
71	23 to 29	April	1996
72	30 to 06	April	1996
73	07 to 13	May	1996
74	14 to 20	May	1996
75	21 to 27	May	1996
76	28 to 03	May	1996
77	04 to 10	June	1996
78	11 to 17	June	1996
79	18 to 24	June	1996
80	25 to 01	June	1996
81	02 to 08	July	1996
82	09 to 15	July	1996
83	16 to 22	July	1996

84	23 to 29	July	1996
85	30 to 05	July	1996
86	06 to 12	August	1996
87	13 to 19	August	1996
88	20 to 26	August	1996
89	27 to 02	August	1996
90	03 to 09	September	1996
91	10 to 16	September	1996
92	17 to 23	September	1996
93	24 to 30	September	1996
94	01 to 07	October	1996
95	08 to 14	October	1996
96	15 to 21	October	1996
97	22 to 28	October	1996
98	29 to 04	October	1996
99	05 to 11	November	1996
100	12 to 18	November	1996
101	19 to 25	November	1996
102	26 to 02	November	1996
103	03 to 09	December	1996
104	10 to 16	December	1996
105	17 to 23	December	1996
106	24 to 30	December	1996
107	31 to 06	December	1996
108	07 to 13	January	1997
109	14 to 20	January	1997
110	21 to 27	January	1997
111	28 to 03	January	1997
112	04 to 10	February	1997

113	11 to 17	February	1997
114	18 to 24	February	1997
115	25 to 03	February	1997
116	04 to 10	March	1997
117	11 to 17	March	1997
118	18 to 24	March	1997
119	25 to 31	March	1997
120	01 to 07	April	1997
121	08 to 14	April	1997
122	15 to 21	April	1997
123	22 to 28	April	1997
124	29 to 05	April	1997
125	06 to 12	May	1997
126	13 to 19	May	1997
127	20 to 26	May	1997
128	27 to 02	May	1997
129	03 to 09	June	1997
130	10 to 16	June	1997
131	17 to 23	June	1997
132	24 to 30	June	1997
133	01 to 07	July	1997
134	08 to 14	July	1997
135	15 to 21	July	1997
136	22 to 28	July	1997
137	29 to 04	July	1997
138	05 to 11	August	1997
139	12 to 18	August	1997
140	19 to 25	August	1997
141	26 to 01	August	1997