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The distribution and abundance of small mammals in second rotation Sitka spruce plantations in Hamsterley Forest, south west county Durham.

by

S. A. VADHER.

A Dissertation submitted in partial fulfilment
of the requirements for the degree of
Master of Science in Ecology

Department of Biological Sciences

The University of Durham

1990

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SUMMARY

1) The populations of two species of small mammal, *Apodemus sylvaticus* and *Clethrionomys glareolus*, were censused using live traps in three types of habitat in Hamsterley Forest, county Durham.

2) The three habitats, Mature Sitka spruce plantations of the first rotation, Young and clear felled plantations of the second rotation were classified using an ordination method.

3) *Apodemus sylvaticus* occured in all habitats and reached maximum densities (c. 11 ha^{-1}) in young plantations.

4) *Clethrionomys glareolus* occured in all habitats but it was not common in clear felled areas where only one individual was captured during the study. It achieved maximum densities (c. 12 ha^{-1}) in young plantations.

5) The abundance of wood mice (*A. sylvaticus*) and bank voles (*C. glareolus*) appeared to be influenced by the composition of vegetation in the three habitats.

6) The results indicate that in second rotation Sitka spruce plantations the younger stages (4-5 years) show greater diversity in the abundance of small mammals and in species of ground vegetation.

ACKNOWLEDEGMENTS

I would like to thank Dr. N. Dunstone for his help and supervision during this dissertation and my thanks to Dr. J. E. L. Butterfield for her advice on the vegetation analysis and providing transport during the work.

I also wish to thank Mr. F. A. S. Fernandez for the time and effort given throughout the course of this study and to Rhett Harrison who helped out in the field work.

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INTRODUCTION

The planting of conifer forests, either as first rotation or upon felling, replanting to give second rotation forest, results in extensive modifications of the local environment. The patterns of change have been well studied (Jenkins 1986) though investigations, particularly in small mammal populations have concentrated on the first rotation conifer plantations. Second rotation plantations are a relatively recent development in the managed forest cycle, but as yet have not attracted the variety of investigations that are being carried out in the first rotation areas. More importantly the habitats associated with the second rotation plantations will become an increasing feature of the managed conifer forest and will consequently affect the wildlife found there (Ratcliffe 1986).

In the conifer forests of the second rotation few small mammal studies have been done. This is perhaps surprising considering the scope for work that exits in subjects such as community ecology, population dynamics and in aspects of the environment and habitat. Gibson's (1989) and Thomson's (1986) studies on small mammals in young Sitka spruce plantations seem to be the only two investigations carried out in such a habitat. The second rotation has been found to differ in its species composition and general pattern of development from the first rotation. In particular the ground vegetation was found to be species poor in these young plantations (Miles 1986, Hill 1986).

Perhaps the most obvious consequences of the development of felling and replanting is that it fragments the environment into patches of varying size and shape. Many small mammals are restricted to patches with habitat which most closely resembles that present before the disturbance. These changes may affect small mammal populations through :

- reduced dispersal.
- local extinctions.
- increased population size.
- social disturbance.

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Some of these effects have seldom been studied in the habitats described and the causes behind them are generally, poorly known.

The small mammals studied belong to the large group of mammals in the order RODENTIA and have been intensely studied since the 1950's (Corbet & Southern 1977, Flowerdew *et al* 1985). The growth in the study of these animals also occurred simultaneously throughout Europe in particular Scandinavia, Poland, Belgium, Czechoslovakia and Germany. Therefore a considerable amount is known about the biology and ecology of these animals. The three species of rodent investigated for this study are descibed below.

a) Wood mouse (*Apodemus sylvaticus* L. 1758).

A member of the family Muridae (mice and rats) of which 10 species are known in Europe and only two which are native to Britain. The two species in Britain are the woodmouse and the yellow-necked mouse (*Apodemus flavicollis*). The woodmouse has a wide distribution throughout Britain and Ireland and can be found in nearly all types of woodland, and scrub except in coniferous areas of the north and some islands.

b) Bank vole (*Clethrionomys glareolus* Schreber 1780).

Family Cricetidae, the bank vole is one of the most common species of vole occuring in Britain but in Ireland it is introduced and mostly confined to the south and west. It is one of three species of vole found in the British Isles the others are the field vole and the Orkney vole (*Microtus orcadensis*). The bank vole also prefers woodland and scrub habitats and usually areas where thick cover is present in such as hedges, banks and sometimes grasslands.

c) Field vole (*Microtus agrestis* L. 1761).

There are about 50 species of the genus *Microtus* but only one, the field vole, is found on the British mainland. Like the bank vole, the field vole is common preferring rough grasslands including grassy areas in young plantations but is also found in woodland, hedgerow and moorland.

This study continues the work done by Susan Gibson in 1989, in some of the young second rotation plantations of Hamsterley Forest, county Durham. This study has five aims. I attempt to ;

i) Describe and classify the characteristic features of three habitats - Mature Sitka spruce plantations, young Sitka spruce plantations and recently clear felled areas.

ii) Investigate the distribution of three species of wild small mammals within the habitat types.

iii) Measure the abundance, movements and home ranges of each species.

iv) Investigate the characteristics of the habitat types which influence the observed patterns of distribution and abundance.

STUDY SITE AND METHODS.

Hamsterley forest, (longitude 01° 55' W, latitude 54° 39' N) is located in southwest county Durham, some 40 kilometres from the city of Durham. It is a commercially run coniferous woodland owned by the Forestry Commission. The area, originally a shooting estate and grouse moor, was purchased by the Forestry Commission in 1927 after which extensive planting of European larch (*Larix decidua* Miller), Scots pine (*Pinus sylvestris* L.), and Sitka spruce (*Picea sitchensis* Carriere), was carried out. Records of planting of the first rotation extend up to 1951, but intensive planting 10 to 15 years after purchase of the land has left large areas of forest of uniform age. Current land use estimates (Walker,1989) of Hamsterley forest indicate three main categories:

Coniferous woodland	86%
Broadleaved woodland	4%
Pastures, rides and roads	8%

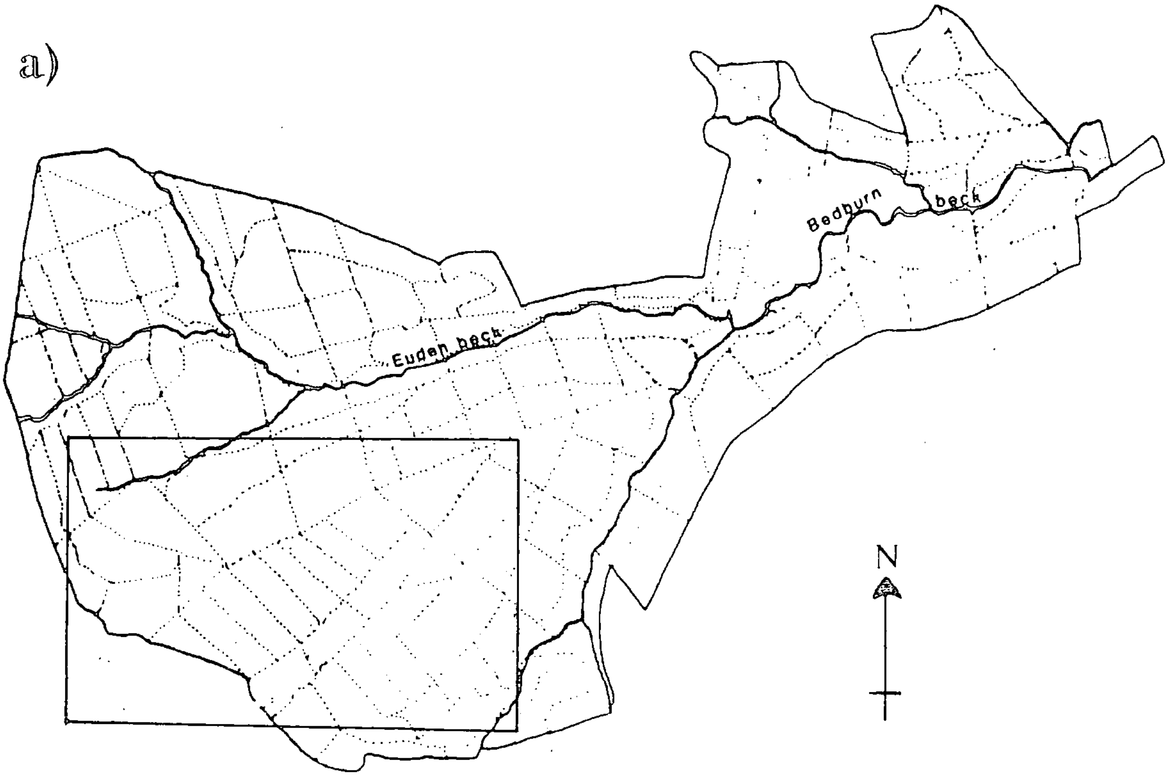
Planting and felling cycles vary from 40-50 years on higher ground to 50-60 years on lower ground, where thinning is also carried out. Thus felling and replanting of the first rotation compartments is underway and young plantations of the second rotation are beginning to develop. As a result there has been an increase in both the variety and abundance of habitats in the forest.

Sites.

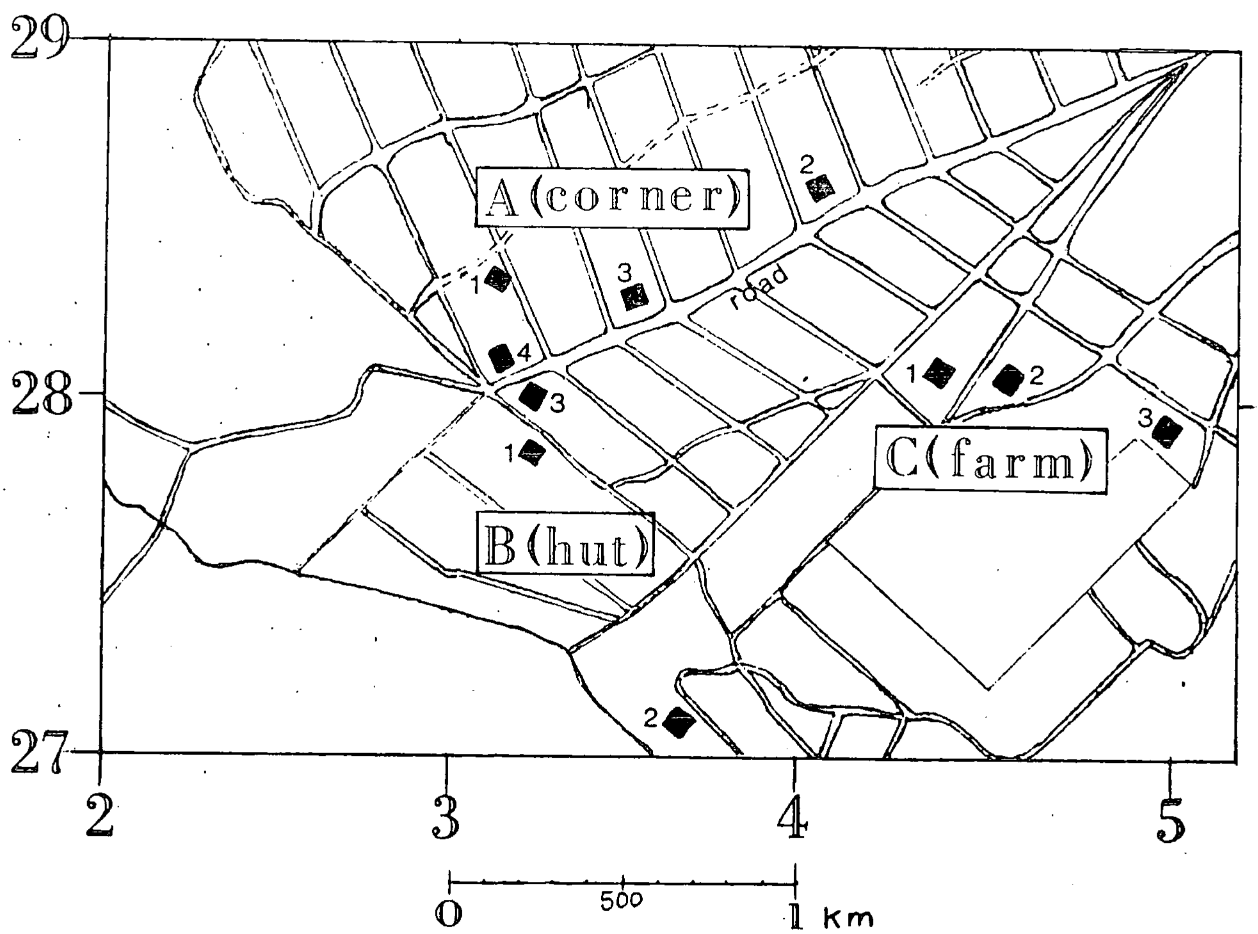
The study of small mammal populations was carried out in three types of habitat representing particular stages in the development of managed sitka spruce forests. The three habitat types selected in Hamsterley forest are listed below.

Figure. 1 a) A map of Hamsterley forest with b) inset of study area.

a)



b)



a) Clear felled sitka (1-2years after felling)

b) Young plantation (6-7 years of age)

c) Mature plantation (40 years of age)

Areas in the forest were inspected and the sites for trapping grids chosen using two main criteria. Firstly, the habitats had to be large enough to minimize any influence on the small mammals, by factors such as vegetation differences, or immigration by individuals, from the surrounding area. Secondly the areas and their sites needed to be close enough to one another to save time during trapping. Table 1 lists all nine sites studied together with their age, altitude and geographic position.

The three areas and their sites have certain characteristics which distinguish them from each other and these features are summarised below. Figure 1 shows the location of the sites in Hamsterley forest.

Area A (Corner): The three sites, near the main road, are the most northerly of all with the felled and young grids exposed on a gentle north facing slope. There is sparse vegetation of Buckler ferns (*Dryopteris dilatata*) and grasses (e.g. *Nardus stricta*) on the felled site, while on the young plantation Sitka spruce seedlings of 1 to 1.5m high grow amongst lines of brash and patches of heather (*Calluna vulgaris*), Willowherb (*Epilobium angustifolium*) and grass. The mature grid is in a compartment of Sitka spruce 150m from the road. There are rides bordering it and several drainage ditches run through it.

Area B (Hut) : The felled grid is mainly covered by brash and leaf litter with small patches of grass, young heather and bedstraw (*Gallium saxatile*). Two rides pass through the mature grid. These are overgrown with spruce, heather and mosses, in particular *Sphagnum* species. Open patches, created by windthrow offer areas where mosses, grasses such as *Deschampsia flexuosa*, spruce and herbaceous vegetation grow. The young plantation is situated on a southeast facing slope. A variety of vegetation from sedges (*Carex spp.*), rushes (*Juncus spp.*) and grasses to heather and Willowherb is found there.

Table 1. The age, position and altitude of trapping grids in the three areas studied.

Site / Type		Grid reference	Altitude (m)	Age (Years)
A1	Mature	NZ 031 283	350	44/SS
A2	Young	NZ 040 286	350	4/SS
A3	Felled	NZ 035 283	360	1/SS
A4	Mature	NZ 031 281	385	44/SS
B1	Mature	NZ 032 278	380	42-45/SS-SP
B2	Young	NZ 036 271	335	4/SS
B3	Felled	NZ 032 280	389	1/SS
C1	Mature	NZ 044 281	340	36/SS-SP
C2	Young	NZ 045 281	330	5/SS
C3	Felled	NZ 049 280	290	1/SS

(Note: Grid A4 was trapped by Mr. F. Fernandez to survey and monitor the long term changes in populations of small rodents, but is associated with work done here, on their movements.

KEY: SS = Sitka spruce SP = Scots pine

In felled areas the tree species prior to felling is indicated.

Area C (Farm) : Lines of brash 2.5m to 3.0m wide and up to 1m deep divide the felled grid whose sparse vegetation of ferns and grasses is influenced by roadside plants and a small stream. Dense Sitka spruce, 1.5 to 2.5 m in height, heather and rushes are prominent on the young plantation and amongst the brash Willowherb and Bedstraw persist. The mature site has mosses, ferns, Bilberry (*Vaccinium myrtillus*) and grassy areas where decaying trees promote open patches.

METHODS.

Trapping Grids.

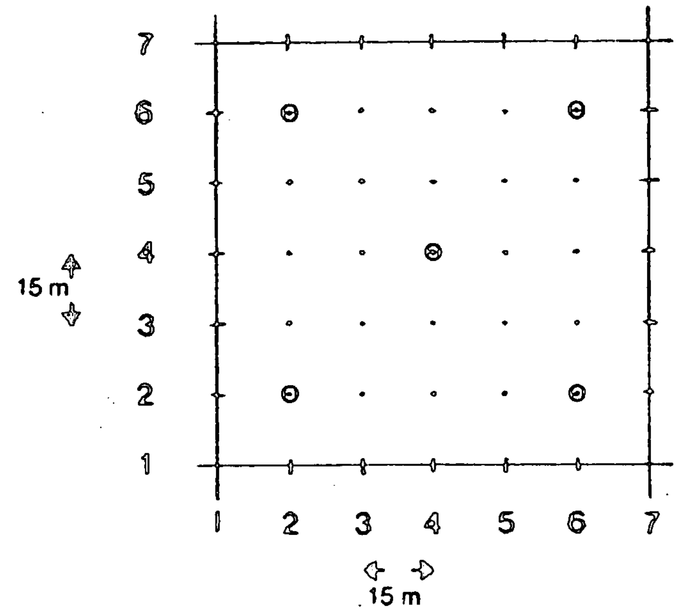
The grids for trapping were marked out using a hand- compass, measuring tape and markers. A total of 49 points arranged in a square (7x7) with approximately 15 metres between each point constituted a grid (Figure 2). Trapping points were marked with either coloured tape or bamboo canes, the latter being more suitable for young plantations and felled areas. The grid size and layout was chosen according to the method outlined by Flowerdew (1982) for the Mammal Society survey of woodland small rodents.

Soil analysis.

The nature of the soil in particular its acidity can have a profound effect both on the variety and abundance of developing ground flora. Miles (1986) describes the effects of soil acidity changes under conifer plantations and their promotion of podzolisation and litter accumulation. Therefore soil pH levels were measured in each of the grids in order to determine whether major differences existed between the areas.

Soil cores were taken from five trap points in each of the grids, Figure 2 illustrates their positions. The points were selected on the basis that their distribution would provide pH values

Figure 2. The dimensions of a trapping grid indicating the points where soil core samples were taken.



representative of the whole grid. Measurements of depth of leaf litter were made and then a 10g sample taken from a depth of 10cm was removed to determine soil pH. A standard technique was followed (Hesse 1971) dissolving the sample in 25cm^3 of distilled water, mixing and leaving for two hours before measuring the pH on a direct reading meter.

Vegetation survey.

The vegetation survey was carried out over a period of four days in August, and involved sampling using one metre square quadrats. An assessment of the vegetation was made following a modified version of the Continental Phytosociological method (Muller-Dombois *et al* 1974).

Four to five quadrats were taken in each grid and in total forty samples from the nine grids were obtained for the vegetation data base. The Domin Scale of cover and abundance (Poore 1962) was applied to each species of plant identified in a quadrat and, additionally, notes on plants present outside the quadrat were made. Finally a sketch of each grid was made noting lines of tree stumps, brash, rides, fallen trees, vehicle tracks and drainage ditches. Height of vegetation was studied mainly in the young plantations where shrubs and Sitka spruce contributed to some layering.

During trapping plant specimens were collected and identified not only from the grids but also from grass verges, ditches and roads which bordered some of the grids. This allowed the compilation of a list of the species available on the study area as a whole (see Appendix 1).

Habitat Analysis.

The aim of this analysis was to determine the major sources of variation within the three habitat types. This was achieved by classifying the vegetation data set firstly by the samples (*i.e* the quadrats) and then by the species on the basis of the sample classification. The "Twinspan" Fortran programm (Hill 1979) was used to carry out the classifications.

The program identifies the direction of variation by the method of reciprocal averaging and this "primary ordination" is used to divide the samples into major groups. A "refined ordination" is then used to produce a dichotomy of all samples and hence show the major differences between groups. At each level of the dichotomy positive and negative scores are used to divide the samples and plant species depending on the likelihood of their occurrence in the negative (left) or positive (right) side of the dichotomy. Plant species that are listed on the negative side have a "negative preferential" which is to say that they are at least twice as likely to occur on the negative side than on the positive side. Furthermore only those species that occur in at least 20% of the samples are noted in the analysis. "Positive preferentials" are exactly like negative preferentials except they select on the positive side. The program also indicates non preferential species which relate to the more commonly occurring species in the samples.

Small mammal trapping.

Longworth traps (Chitty and Kempson 1949), were used for live trapping small mammals having been prepared with hay for bedding and a mixture of crushed oats and wheat for bait. The three grids within an area were trapped, using one trap at each point, for three nights. The traps were checked for captures every morning. This constituted one trapping session or cycle. Three cycles of trapping were carried out for each of the nine areas during the summer. The only exception to this plan was grid A1 which had been partially felled just before the last cycle so trapping was not carried out. Therefore a period of at least two weeks separated the trapping sessions in each of the areas. This is the minimum time period required in order for such intensive trapping not to influence the normal activity of the small mammals (Gurnell & Flowerdew 1982).

Captured animals were identified to species. Their sex, age (adult/juvenile) and reproductive condition (visible testes, perforated vagina, lactant/pregnant) were noted. All individuals were weighed using a 50g Salter spring balance and ear-tagged with individually numbered "Michel" tags (Boulenge-Nguyen and Le Boulenge 1986). Upon release of the captured animal the trap was reset with replacement bait and returned to it's original position at the trap point. The traps were also washed and air dried to remove waste and smells that could affect the capture of the rodents (Gurnell & Flowerdew 1982).

Estimating population size.

The estimation of population size in the grids was carried out using three different methods, all of which were suited to the mark and recapture procedure. In all cases the accuracy of the result was dependent on sampling a sufficiently large proportion of the population.

1) Minimum number known alive (MNKA) (Krebs 1966).

This simple method involves enumeration of the individuals captured for each trapping session. The estimate for a given trapping session is the sum of a) the actual number of individuals caught in a trapping session and b) the number of previously marked individuals caught before and after the trapping session but not during it. The method assumes that these individuals were in the population at the time of sampling, but were not caught.

2) Lincoln/Petersen estimate, Petersen 1896.

The general method is well known and has been widely used in the estimation of animal abundances. The "Petersen estimate" operates on a closed population of animals which have undergone just one event of mark and release.

If the estimate N_E is to be suitable then the following assumptions must hold (as for most closed population estimates).

a) All marks are permanent.

b) The capture and handling of individuals does not affect their subsequent chances of recapture.

c) The chances of dying and emigrating are unaffected for individuals being caught and handled one or more times.

d) The population is sampled randomly which infers equal chance of capture without regard to age, sex or physiological condition.

e) The sampling period is short relative to the total time.

f) That no births or immigrations or deaths and emigration occur during the interval between the first and the second events of capture.

Upon capture individuals are marked, released and assumed to remix with the unmarked animals randomly. Under the given assumptions the proportion of marked to unmarked animals remains the same. On a second capture a random sample is again obtained of size 'n' and of these 'm' number of individuals are marked. The estimate of the population size is reflected in the relative proportions of marked to unmarked animals

$$\frac{r}{N_E} = \frac{m}{n} \quad \text{and therefore} \quad N_E = \frac{n.r}{m}$$

r = number of individuals in the first sample

In this study the number of small mammals captured on the first day was low and so 'r' was the sum of individuals from the first and second days. The third day therefore represents the second sample from the population. A modified equation of the Petersen method was adopted in the final analysis. Bailey (1951) showed that where numbers were low, ten or less, then the formula $N_E = \frac{r(n + 1)}{(m + 1)}$ could be used to give a more accurate less biased estimate

3) Estimating population sizes when capture probabilities vary among individuals (Burnham and Overton 1979, Model Mh, Otis *et al.*,1978).

The estimate is based on a model for multiple recapture studies on closed populations which allows capture probabilities to vary among individuals (heterogeneity of capture probabilities). In general, the equation can be said to give an estimate that includes those animals assumed to be in the area but were not captured.

Three equations were considered (Burham and Overton 1979) but on testing against each other by the simple null hypothesis the following equation was used:

$$N_E = S + \left(\frac{2t-3}{t}\right) f_1 - \left(\frac{(t-2)^2}{t(t-1)}\right) f_2$$

The terms are;

N_E Estimate of population size.

S Number of distinct individuals encountered

f_n Number of individuals captured n times. For instance f_1= number of individuals captured once.

t Number of capture events, three in this study.

RESULTS.

SOIL ANALYSIS.

Soil acidity.

Table 2 indicates differences in soil pH and depth of leaf litter amongst the sites. A plot of the pH results with limits of two standard error (SE) is shown in Figure 3 a).

The underlying trend from these results shows pH at a depth of approximately 10 cm to be acidic with values in the range 3.4 to 5.0. The plot shows that, within the same types of habitat there are no significant differences except in the case of site C1. This site is significantly different by 0.12 pH units which corresponds to 1.3 times less acid than the other mature sites. The lower organic content of this site is also indicated by its position within a boundary wall which in the past encircled the land which was then used mainly for pasture. On areas A and B the pattern is that young plantations have the highest pH values mature plantations the lowest and clear felled sites have pH values lying between the two. A 't' test on the samples showed a significant difference, in the pH, amongst the clear felled sites (A3 v B3 $t=2.897$ $p<0.01$; A3 v C3 $t=2.456$ $p<0.05$; B3 v C3 $t=5.984$ $p<0.001$: df=8 in all tests). The mature and young habitats of area 'C' also showed a significant difference against their corresponding habitats types in areas A and B respectively (A: $t=4.663$ $p<0.005$; $t=2.844$ $p<0.05$ and B: $t=5.682$ $p<0.005$; $t=2.706$ $p<0.05$; df=8 for all tests). A plot of depth of litter against the corresponding pH showed a significant negative correlation only in samples from the mature Sitka spruce plantations ($r=0.872$ $p<0.005$ df 13). The plot is shown in Figure 4.

Litter depth.

The litter found in the sites was composed of needles and brash, mostly twigs and branches. Figure 3 b) shows the mean depth of litter in the nine sites. In the felled sites large piles of brash were commonly distributed linearly along lines of stumps but in mature forest

Table 2. The pH and depth of surface litter of core samples taken from the grids in each area. (Mean ± 2 SE).

GRID	Soil pH	Depth of Litter (cm)
A1	3.69 ± 0.10	5.20 ± 0.50
A2	3.90 ± 0.08	2.60 ± 0.58
A3	3.79 ± 0.10	1.20 ± 0.92
B1	3.55 ± 0.12	6.10 ± 1.20
B2	4.25 ± 0.40	2.60 ± 0.86
B3	3.61 ± 0.08	3.10 ± 1.38
C1	4.07 ± 0.14	2.60 ± 0.58
C2	3.69 ± 0.14	3.80 ± 2.30
C3	3.92 ± 0.06	3.00 ± 0.70

Figure 3. Plots to show a) mean pH and b) mean depth of surface litter of soil samples taken from the three habitats (± 2 SE).

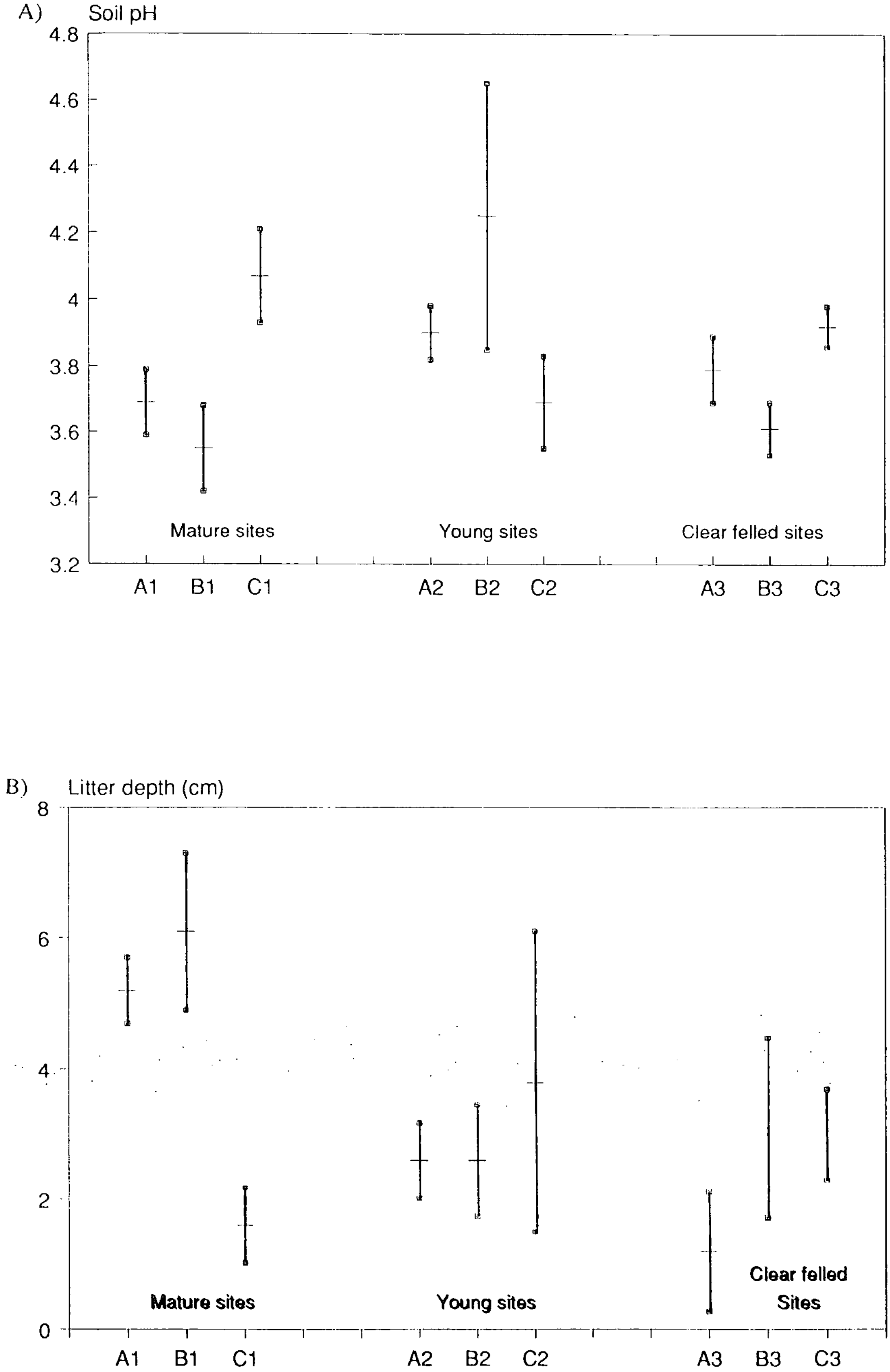
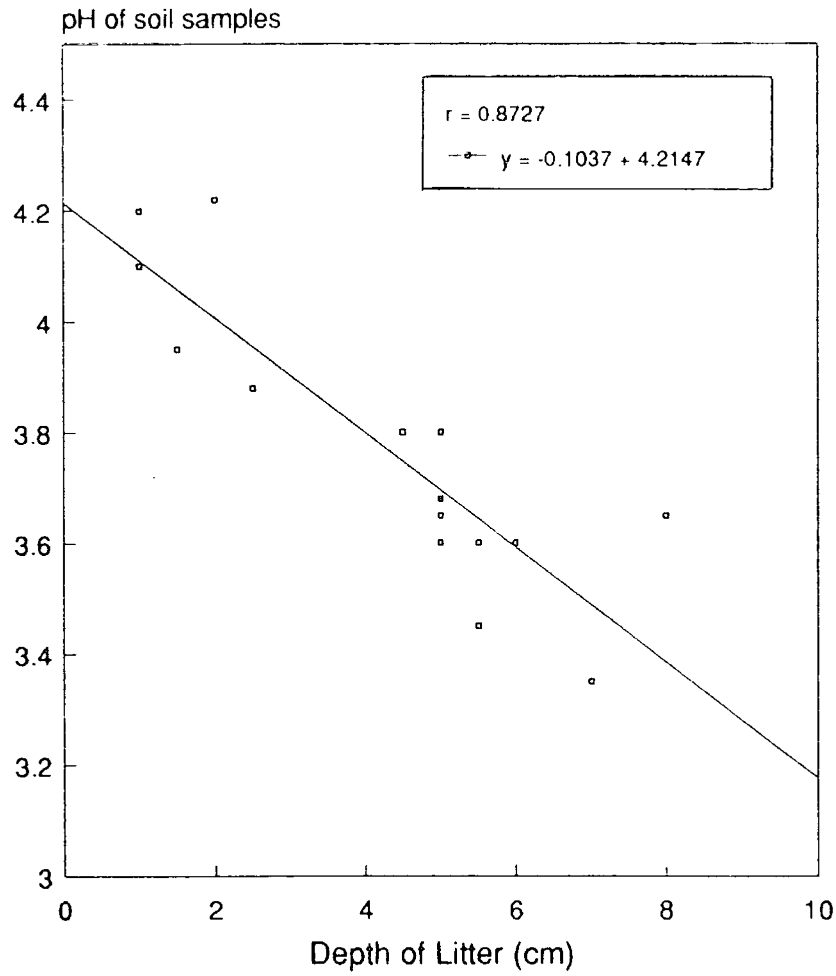


Figure 4. A plot to show the negative correlation found between litter depth (cm) and the pH of soil samples from mature Sitka spruce plantations.



brash consisted mainly of finer twigs which had been broken off by wind and rain. Young plantations had litter with patches of brash made up of larger branches produced at the time of felling.

In general clear felled areas and young plantations had less litter than mature plantations. The mature farm site (C1) however, was the exception. In this area the mature grid had on average 1.6 cm depth of litter, quite different from the 5-6 cm in the other mature sites. Area C appeared to show the most difference in soil composition, to the other two areas A and B. The young plantation (C2) in particular had a deep peaty soil which may explain the dominance of heather in the site and absence of species of grass.

Habitat Analysis.

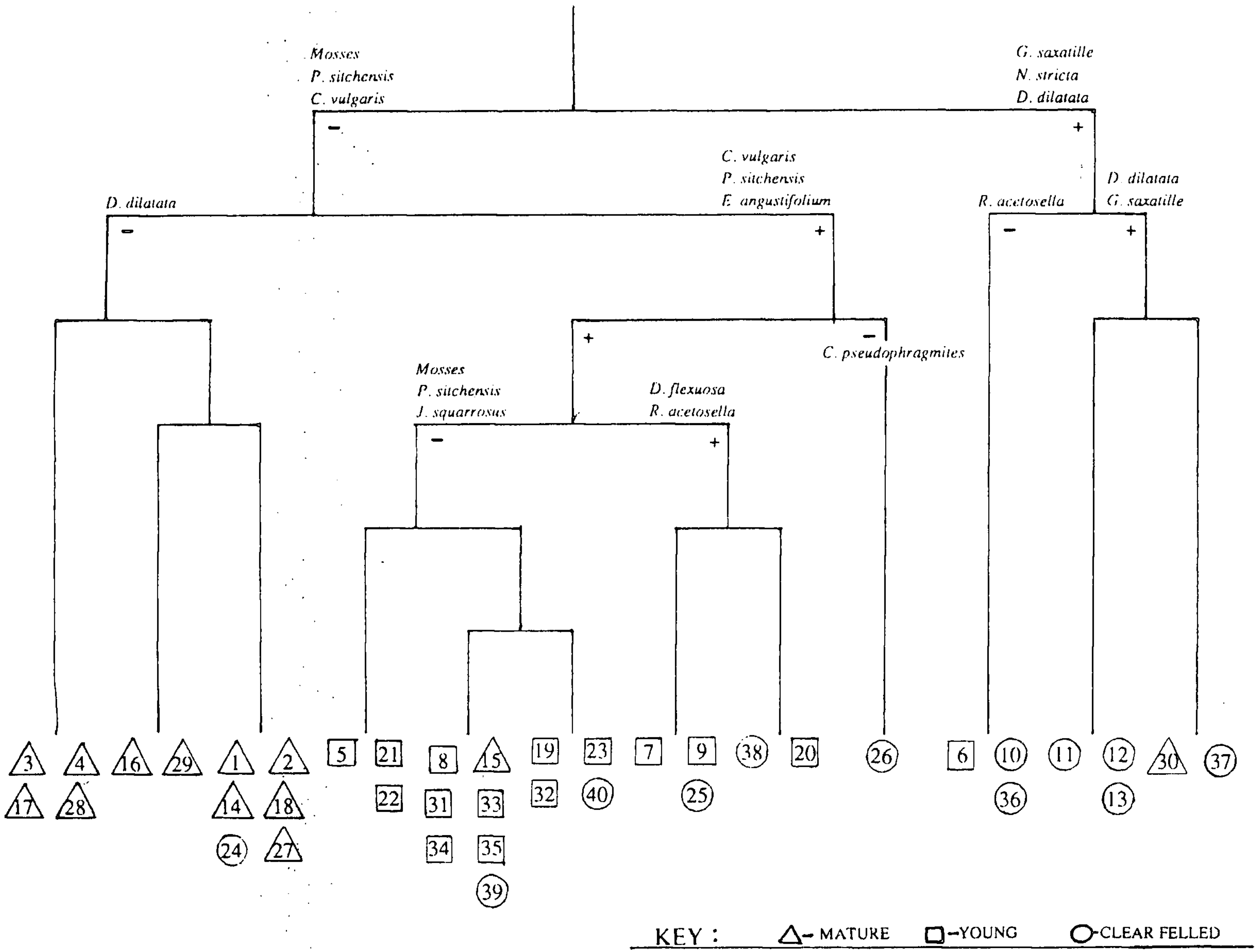
The three habitat types, mature plantations, young plantations and clear felled areas, show quite distinct ground floras. Based on simple observation some of the major differences between these sites can be determined. There are other important features to consider regarding the density of trees, their heights, species composition and as found in some sites, occurrence of surface water. However, these differences are perhaps not as important to the small mammals as the ground vegetation.

Overall a greater number of plant species are found in young plantations with herbaceous plants tending to occur more often.

Classification of quadrat samples.

A dichotomous key (Figure 5) illustrates the results of the ordination analysis and Appendix 2 identifies from which of the sites the samples originated. The first division splits the quadrat samples into a negative group of 32 and a positive group of eight samples with *Gallium saxatille, Nardus stricta* and *Dryopteris dilatata* as positive preferential species . Six of the samples in the positive group represent the felled areas A3 and C3. The other two

Figure 5. A dendrogram of the study sites, obtained by two-way indicator species analysis. Indicator species are shown for the three types of habitat classified.



samples, numbers 6 and 20, are from young plantation (A2) and mature plantation (Cl) respectively. None of the samples from the clear felled area B3 appear suggesting that this grid is different in its plant species composition.

At the second division the 32 samples, from division one, are split into two more groups of 12 and 20 samples. *D. dilatata* the only species given as the negative preferential segregates the 12 quadrat samples from the larger group which has the species *C. vulgaris, P. sitchensis* and *E. angustifolium* as positive preferentials. The samples in the negative arm of the dichotomy are predominantly from the mature forest grids. All of the quadrats from site A1 and seven out of the nine for B1 and Cl are in this group. One sample, 24, is from clear felled site B3. This sample had no vegetation in it and nearly 100 percent cover by litter and so it is not surprising to see it classified with samples from mature areas. The positive group contains all but one of the young plantation samples, four from clear felled area of which three belong to C3.

The ordination of quadrat samples produced 3 major groups whose overall structure, in terms of sites, distinguished between mature plantations, young plantations and clear felled areas. The TWINSPAN grouping indicate that the sites within each habitat type, with the exception of clear fell B3, formed valid replicates with respect to the composition of their vegetation.

THE SMALL MAMMAL STUDY

Trapping data set.

A total of 3822 trap nights were carried out between May 5th and July 19th 1990. These have resulted in a total of 782 captures of 496 individuals which belong to six species of small mammal. The distribution of captures amongst these species is shown in Table 3.

Two species of shrew were captured, common shrew (*Sorex araneus* L.) and pigmy shrew (*Sorex minutus* L.). In the early stages of trapping shrew captures were not identified to species, the numbers of these species are therefore presented as pooled data. Other species of

Table 3. Total number of individuals of the six species of small mammal captured.

SPECIES	Number of individuals	Number of captures	Percentage captures
Apodemus sylvaticus	256	511	65.3
Clethrionomys glareolus	139	260	33.3
Microtus agrestis	1	1	0.1
Sorex spp.[1]	9	9	1.2
Mustela nivalis	1	1	0.1

1 - The two species of shrew captured were:
Sorex araneus the Common shrew and
Sorex minutus the Pigmy shrew.

small mammal caught include one field vole (*Microtus agrestis* L.), trapped in a young plantation and one weasel (*Mustela nivalis* L.) which was captured on the last day of the trapping study. Only two species of rodent were caught in large numbers the woodmouse (*Apodemus sylvaticus* L.) and the bank vole (*Clethrionomys glareolus* Schreber). The distribution of small mammal captures across the three habitat types is summarised in Table 4.

A X^2 contingency test was performed in order to determine the constancy of the relative abundances of species in the different habitats. The partial X^2 (Sokal & Rohlf 1981) showed that woodmice were more abundant than expected in relation to bank voles in the felled areas, while the reverse was true in young plantations.

The sex ratio of males to females for both species of small mammal and the ratio of adults to juveniles are shown, for each habitat, in Tables 5 and 6 respectively. The number of male woodmice were significantly higher and the females significantly lower than expected in the young plantation sites ($X^2 = 6.18$, $p < 0.05$ df 2). In clear felled sites the reverse was true. There was no difference from the expected one to one ratio for bank voles. There were no significant differences in the proportions of adults to juveniles in either woodmice or bank voles between the three habitats. The adult to juvenile ratios were approximately 10:1 for *A. sylvaticus* and 7:1 for *C. glareolus*.

Population size estimates.

The three different methods used to calculate the population sizes of woodmice and bank voles in the study produced estimates that appeared to be consistent. Figure 6 shows the strong correlation ($r = 0.977$ $p<0.001$ df=24) between the MNKA (Krebs 1966) estimates and their corresponding estimates using the Burnham and Overton (1979) equation. These estimates of population size are given in Appendix 3. Table 7 indicates the mean population sizes of woodmice and bank voles, in the three habitats, by the methods described.

The mean population sizes of woodmice and bank voles were significantly greater in young than in mature plantations ($t= 2.314$ $p< 0.05$ df 11 and $t= 3.228$ $p< 0.02$ df 9

Table 4. Numbers of individuals of woodmice, bank voles and shrews captured in each session. For each kind of habitat, the three sites are pooled.

	Cycle.	SPECIES *Apodemus sylvaticus*	*Clethrionomys glareolus*	*Sorex spp.*
	1	24	5	0
MATURE	2	22	12	1
	3	13	11	0
		----	----	----
Total		59	28	1
Mean		**19.70**	**9.33**	**0.3**
S.D		5.86	3.79	0.5
		----	----	----
	1	43	28	1
YOUNG	2	48	48	2
	3	35	34	3
		----	----	----
Total		126	110	6
Mean		**42.00**	**36.70**	**2.00**
S.D		6.56	10.26	1.00
		----	----	----
	1	22	0	0
FELLED	2	27	1	1
	3	22	0	1
		----	----	----
Total		71	1	2
Mean		**23.70**	**0.3**	**0.7**
S.D		2.89	0.5	0.6
		----	----	----

$X^2 = 49.75$ ($p < 0.005$ df = 2)

Table 5. The sex ratio of individual woodmice and bank voles trapped in the three kinds of habitat.

Habitat	*A.sylvaticus* male	*A.sylvaticus* female	*C.glareolus* male	*C.glareolus* female
Mature	33	25	14	16
Young	83	43	71	58
Felled	34	37	0	0
Total	150	105	85	74
X^2(contingency) (with Yates correction)	6.18 ($p<0.05$)		0.76 (NS)	

NS - Not significant.

Table 6. The ratio of the numbers of adults and juveniles of *A. sylvaticus* and *C. glareolus* in the three types of habitat.

Habitat	*A. sylvaticus* Adult	*A. sylvaticus* Juvenile	*C. glareolus* Adult	*C. glareolus* Juvenile
Mature	54	5	25	3
Young	114	12	96	14
Felled	65	6	1	0
Total	233	23	122	17
X^2(contingency) (with Yates correction)	0.16 (NS) df 2		0.01 (NS) df 1	

NS = Not significant

Figure 6. A plot to show the correlation in Population size estimates between the Burnham and Overton method (1979) and the MNKA methos (Krebs 1966).

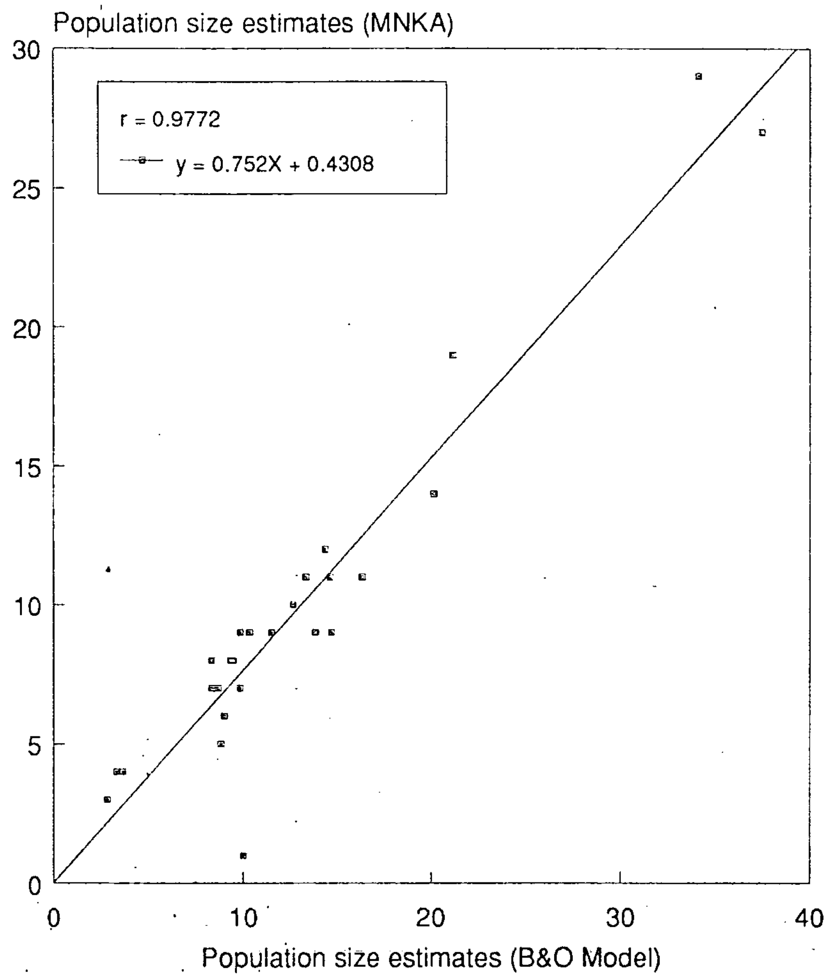


Table 7. Mean population sizes for *A. sylcvaticus* (A.s) and *C. glareolus* (C.g) in the three types of habitat.

MNKA	Minimum number known alive, after Krebs 1966.
L/P	Lincoln / Petersen (1896) estimate, using Bailey's modification (1951) for low sample numbers.
M h	Model for Heterogeneity, Burham and Overton estimate for individuals with differing capture probabilities (1979).

SITES	MNKA		L / P		M h	
	A.s.	C.g.	A.s.	C.g.	A.s.	C.g.
			MATURE PLANTATIONS			
n	8	8	8	8	8	8
MEAN	**7.50**	**3.50**	**7.53**	**3.48**	**8.99**	**4.10**
S.E	1.29	0.68	1.33	0.72	1.68	0.92
			YOUNG PLANTATIONS			
n	9	9	9	9	9	9
MEAN	**14.00**	**12.22**	**15.55**	**12.98**	**18.00**	**17.61**
S.E	3.00	2.67	3.34	3.02	3.51	4.07
			CLEAR FELLED AREAS			
n	9	0	9	0	9	0
MEAN	**7.89**	0	**8.20**	0	**10.02**	0
S.E	0.95	0	1.06	0	1.53	0

respectively). Woodmice were present in felled habitats at numbers similar to those found in mature forest, but they were the only species of mammal, besides shrews, to be captured frequently.

Density of small mammals.

The calculation of density, number of animals per unit area, would be relatively simple assuming that the area sampled by each trap was the same. However, this assumption often fails to be upheld due to the phenomenon of 'edge effect', noted in many small mammal trapping studies (Kikkawa 1964, Smith *et al* 1970, Gurnell 1989). The edge effect is shown by the increased frequency of capture by traps on the periphery of a trapping grid, which are usually visited by animals moving from the area surrounding the grid. So the external traps sample a greater area than the internal traps. Table 8 shows the differences in numbers of captures between the outside 24 traps and the inside 25. The percentage captures for both species are shown in Figure 7.

A X^2 analysis on the total numbers of captures of both species within the three habitats showed no significant difference among the number of captures in outer and inner traps (X^2 = 2.78, df 2). Separately, woodmice showed a very significant result ($X^2 = 11.62$, $p < 0.005$, df 2) with much of the deviation being due to the pattern of captures in the mature forest. Similarly, for bank voles a significant difference ($X^2 = 5.61$, $p < 0.025$, df 1) was obtained and again most of the deviation was observed in captures in the mature plantation where more than twice the number of captures were in the inside 25 traps.

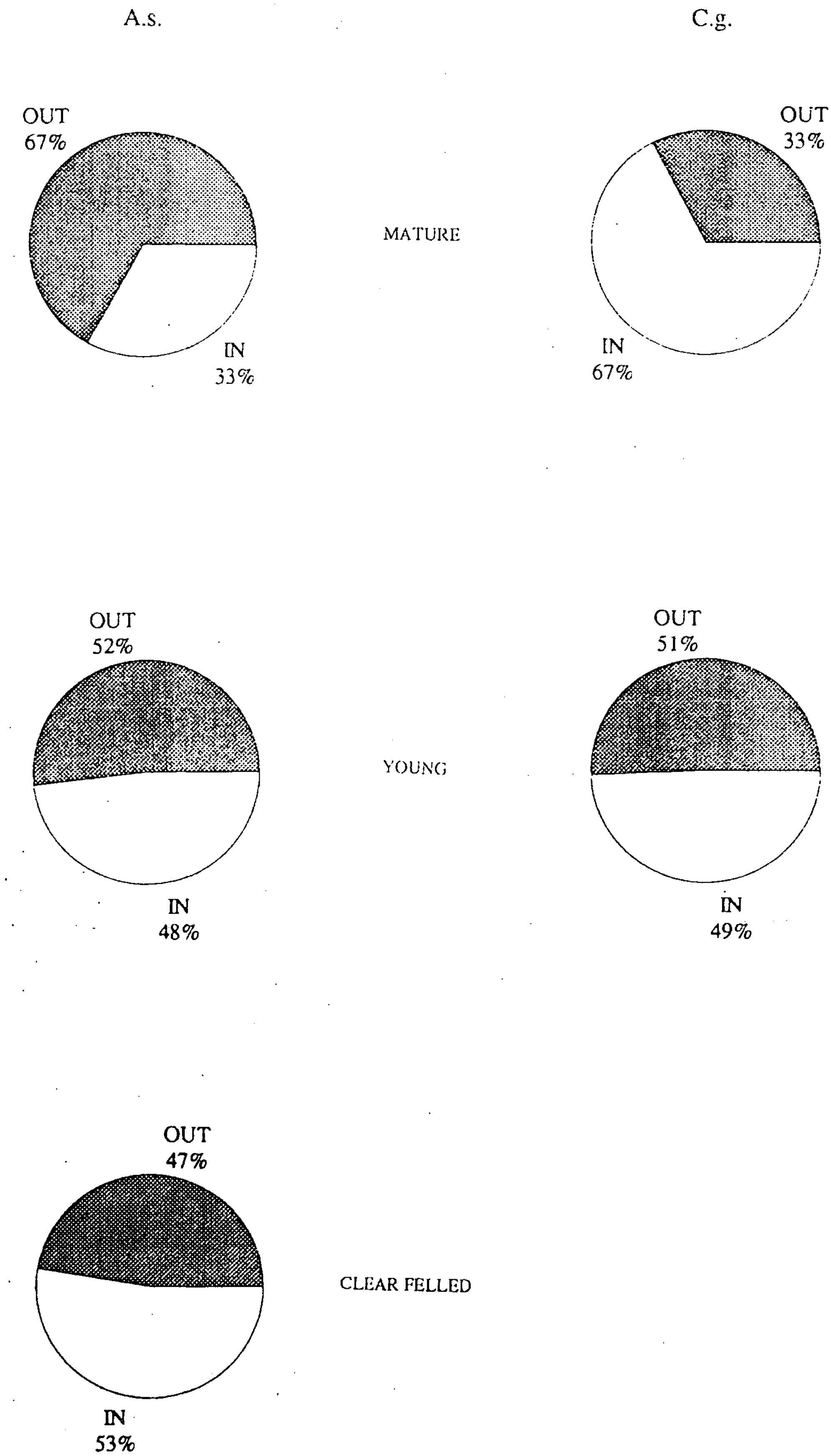
In order to ascertain approximately the size of the area sampled by the external traps, and hence determine 'effective sampling area' two methods were tested, both of which take account of the movements of the small mammals.

Either mean distance moved (MDM) (Brant 1962, Gurnell *et al* 1989a) or mean home range radius (see Wolton *et al* 1985) for each species, described in more detail in a later

Table 8. The distribution of woodmice and bank vole captures between, the 24 external traps (OUT) and the 25 inside traps (IN) of the grids

	A. sylvaticus.		*C. glareolus.*		Total.	
	OUT	IN	OUT	IN	OUT	IN
MATURE	83	41	18	37	101	78
YOUNG	140	131	99	96	239	227
FELLED	70	78	0	0	70	78
OVERALL TOTAL					**410**	**383**
X^2 (contingency) df	11.62 $p<0.005$ 2		5.02 $p<0.025$ 1		NS	

Figure 7. Analysis of edge effect : Pie charts to show the percentage of captures of *Apodemus sylvaticus* (A.s) and *Clethrionomys glareolus* (C.g) in the 24 external traps (OUT) and the 25 internal ones (IN) of the grids.



section, can be used to determine the effective area sampled by the trapping grids. If we consider animals outside the trapping grid which have a home range that encompasses a grid edge, then the likelihood of capture for the individual increases if the home range area increases, due to the increased probability of encountering a trap. The radius of home range can be estimated by the radius of a circle of area equal to the home range area estimated by the minimum convex polygon method (see Home range). The effective area sampled for the particular species would be the grid area plus the area around the grid which is a distance equal to the radius of the mean home range. Accordingly for MDM the effective area is $(L + 2MDM)^2$ where L is the length of the grid square.

Estimates for mean distance moved and home range are given in Table 9 (A to C) and 11 respectively (see Home range). These show that the MDM for both species was greater than the mean home range radius. Deciding on which data to use depends on several factors associated with the methods used for capture and release. Intensive trapping, grid size and duration of trapping may influence movement patterns of individuals and hence density estimates. Therefore Table 10 shows effective densities of *Apodemus sylvaticus* and *Clethrionomys glareolus* using mean home range radius. The decision to use the mean home range radius was based on the observation that the MDM data included distances from individuals which moved between grids (intergrid movements see later). In Burt's (1943) definition of home range these movements or sallies are not part of the animals normal activities; in this study such movements produced positive bias in the estimates especially for male woodmice.

The home ranges were found to be different between species and for woodmice between sexes as well, Table 11. The mean home range radius for a species represents the mean from all samples, male and female.

The densities of small mammals were determined using the population size estimates from the Burnham and Overton model. The greatest densities can were found in the young plantation reaching approximately 12 ha^{-1} for both mice and voles. In contrast to this, densities in mature forest were lower with woodmice, at 5.5 ha^{-1} being twice as common as bank voles.

Table 9. Mean distance moved (MDM) by males and females of woodmice and bank voles in the three habitat types. All distances are in metres (m).

A) MATURE PLANTATION SITES

	A.sylvaticus		*C.glareolus*	
	MALES	FEMALES	MALES	FEMALES
	55.2	11.4	24.8	27.0
	93.6	24.4	0.0	28.3
	83.6	33.7	68.1	0.0
	111.0	16.9	41.1	22.5
	68.4	78.3	60.0	33.7
	78.4	0.0		30.0
	16.9	51.3		
	45.7	31.9		
	121.4	39.5		
	119.3			
	21.3			
n	11	9	5	6
Mean(MDM)	74.1	31.9	38.8	23.6
SE	11.0	7.7	12.3	4.9
Students t test	t=2.991 (p<0.05) df = 18		t=1.230 (NS) df = 9	

SE - Standard Error. NS - Not Significant.

B) YOUNG PLANTATION SITES

	A.sylvaticus		*C.glareolus*	
	MALES	FEMALES	MALES	FEMALES
	7.5	16.6	16.2	18.7
	35.0	11.2	30.8	16.6
	41.9	20.0	9.1	17.7
	27.0	22.1	40.8	14.5
	24.9	33.0	30.8	17.0
	18.1	15.0	7.5	15.0
	32.8	22.5	5.3	34.0
	19.0	19.1	25.0	10.6
	26.0	18.3	16.3	15.0
	22.5	24.4	0.0	99.2
	10.0	17.1	22.5	24.1
	18.1		7.5	
	24.4		33.1	
			0.0	
n	13	11	14	11
Mean(MDM)	23.6	19.9	17.4	25.6
SE	2.6	1.7	3.5	7.6
Student's t test	t=1.122 (NS) df 22		t=1.051 (NS) df 23	

C) CLEAR FELLED SITES

	A.sylvaticus	
	MALES	FEMALES
	56.6	30.9
	26.7	21.6
	59.1	11.5
	26.6	20.6
	53.3	31.3
	16.9	16.2
	12.7	30.0
	19.7	10.6
		11.2
		15.0
n	8	10
Mean(MDM)	33.9	19.9
SE	6.8	2.6
Student's t test	t=2.098 (NS) df 16	

Table 10. Effective population densities of woodmice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*) derived from estimates using the Burnham & Overton model (1979).

Habitat	Population size	Effective area (m^2)	Density (n/ha)
		Apodemus sulvaticus	
Mature	8.99	16073	**5.59**
Young	18.00	16073	**11.20**
Felled	10.02	16073	**6.23**
		Clethrionomys glareolus	
Mature	4.10	14285	**2.87**
Young	17.61	14285	**12.33**
Felled	*	*	*

* - Only one individual captured therefore not considered in estimates

In the felled habitat, where woodmice were only present, densities were not significantly different from those in mature forest (t=0.453 df 15: using estimates of population size).

Breeding and age composition of wood mice and bank voles.

The summer season for both species of mammal corresponds to an intense period of breeding. An investigation of the breeding condition and age of individuals determined by weight, is illustrated in Figures 8 & 9. A criterion of 15g weight was selected in order to differentiate between juveniles and adults on the basis of reproductive maturity. Some reproductively active animals less than 15g were present indicating the variation in the onset of maturity. Only four male woodmice under 15g were captured, all in the young plantation. Two of these had developed testes and two were immature. Adult and juvenile females were captured in all areas with only one juvenile, in the young plantation B2, showing breeding activity. Adult breeding females (70% of the total catch) predominated in all areas, though in the felled sites females with perforated vaginas were more common than lactating or pregnant females; this pattern is in contrast with the other two habitats.

Bank voles (Figure 9) in mature and young habitats show a similar pattern to woodmice. Fourteen of the 15 juveniles captured were trapped in young plantations, interestingly one third were in active breeding condition. In both species a large majority of the adults were in breeding condition, but the numbers of juveniles of both species were low and their distribution among the habitats could not be reliably tested.

Movements and home range of small mammals.

Analysis of capture events of small mammals provided some information on their movements and home ranges. Differences between species and sexes were noted.

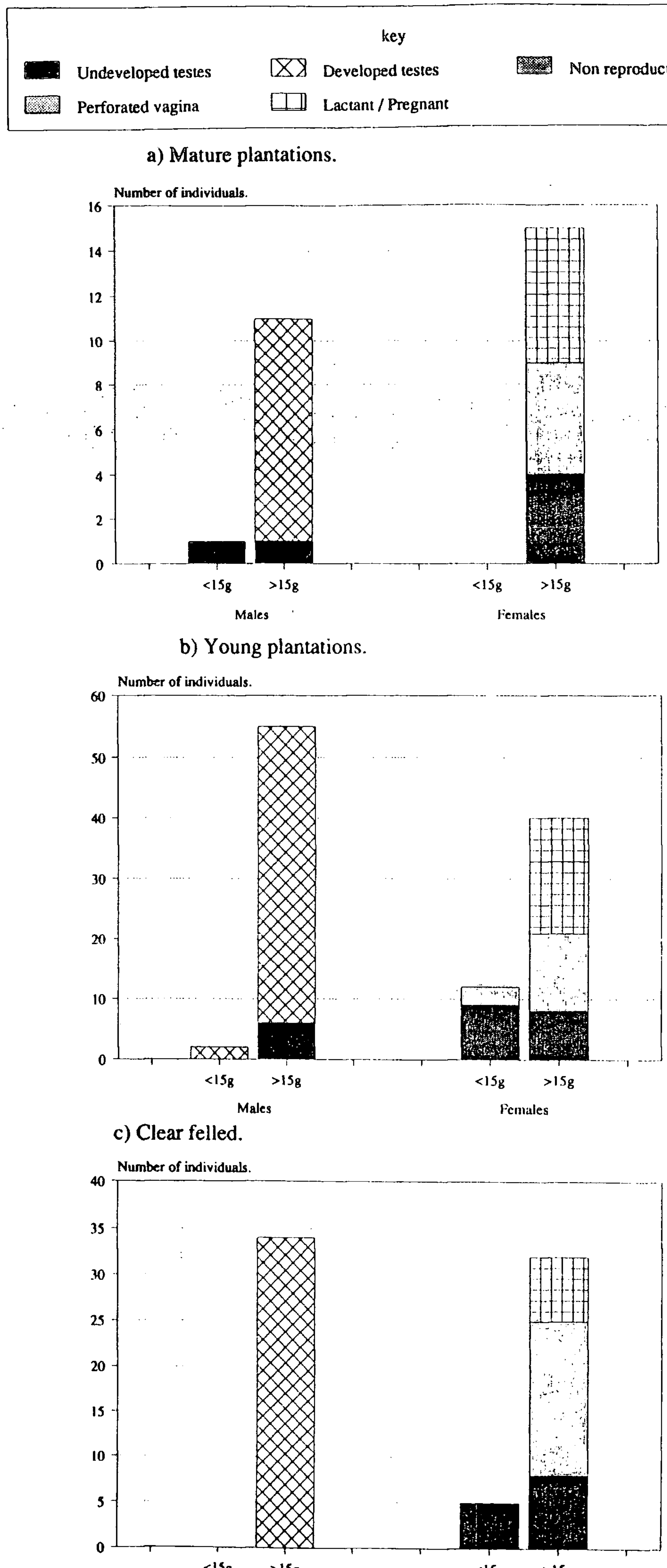
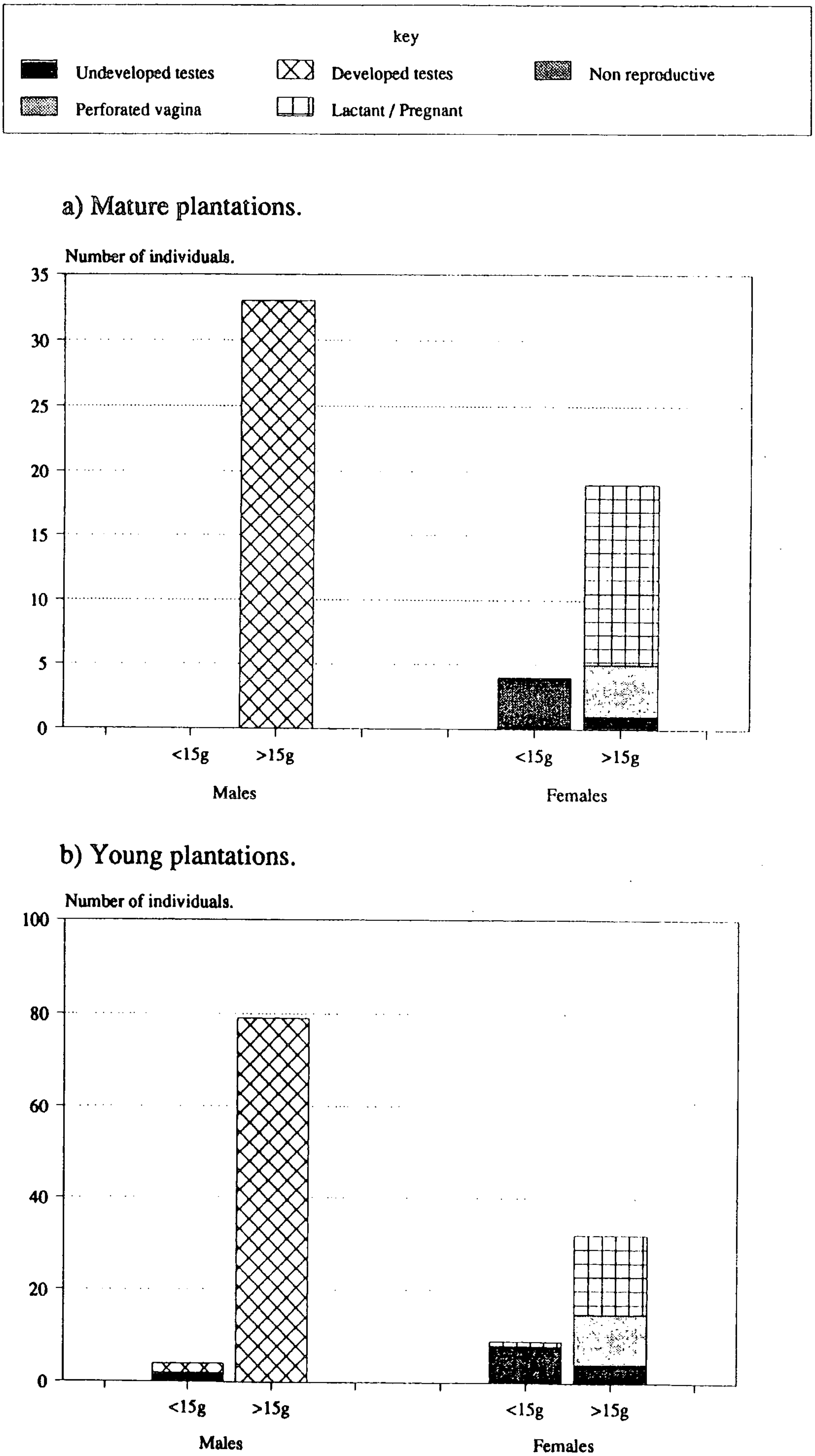


Figure 8. The breeding condition of adult (>15g) and juvenile (<15g) woodmice captured in the three kinds of habitat a) to c).

Figure 9. The breeding condition of adult (>15g) and juvenile (<15g) bank voles captured in Mature (a) and Young (b) habitats.



Movements:

Incidences of captures for individual animals were noted and the distances between capture points measured (a minimum of two capture events was required for records to be included). The mean distance moved (MDM) was obtained by dividing the sum total of distances (D) by the number of captures (n) minus 1, ie. MDM = D/(n-1). Records of mean distances moved in each habitat type were made distinguishing between sex and species. Table 9 lists the mean distance moved by bank voles and woodmice.

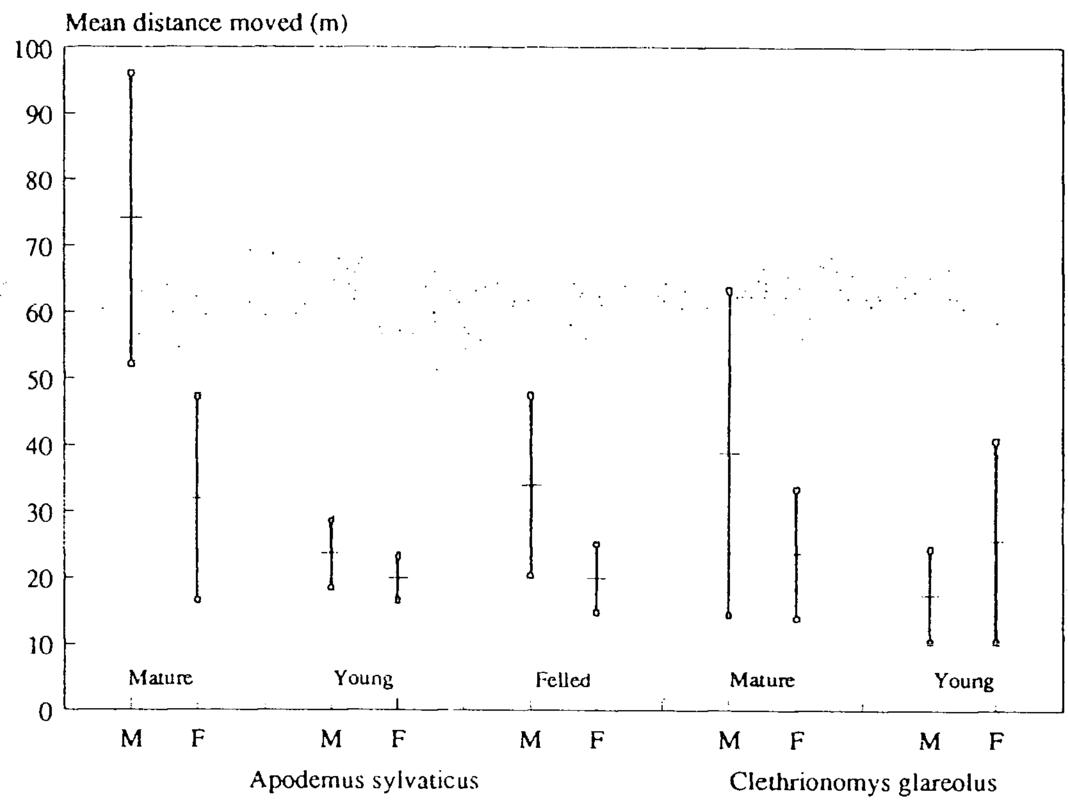
Overall the data suggest that males move further than females but a t-test showed no significant difference except in the case of male woodmice ($t=2.991$ df 18 $p<0.005$). Figure 10 shows that the male woodmice from the mature areas (mainly from A1) showed the only significance in distance moved. In the two habitats in which bank voles could be found there was no significant difference in the mean distances moved by either sex. Similarly, there was no significant difference in the MDM of female woodmice from all three habitats.

Intergrid movements:

In areas such as A and C the close proximity of grids to each other resulted in captures of some individuals in more than one habitat type. Woodmice were captured in different habitats on 16 occasions. Over the period of ten weeks only one bank vole, a female, was captured in C1 having been last caught in C2 (Table 11). The distances moved, as measured on the map, ranged between 100 and 350 metres. This reflects the distance between grids and the animals might have covered greater distances had they not been captured. It is most likely that this is the case because the distances calculated were straight line estimates from the point of capture to the grid edge, and on to the grid in which the animal was next captured. In many cases the distances covered took less than one week and about half overall were travelled in a day or less.

The main habitat type the woodmice moved into was mature forest (12 individuals) and

Figure 10. The mean distance moved (MDM ± 2SE) by males and females of woodmice and bank voles.



then felled (3) and young plantation (2). There is therefore some indication of a preference for mature forest by these travelling woodmice. Figure 11 shows the distribution of individuals of mice and voles in their MDM. The plot suggests a bimodal distribution in the distances travelled by woodmice. However a larger data set is needed in order to confirm this view.

Home range:

The estimation of home range is based on incidences of capture of an animal in the study areas. The greater the number of captures "fixes" the closer the estimate of home range will be to the true home range. The number of fixes needed to calculate a reasonable estimate of home range can be determined by plotting range size against number of fixes (Kikkawa 1964, Harris *et al* 1990). An asymptote is reached after which additional fixes result in a minimum increase in home range size (Figure 12).

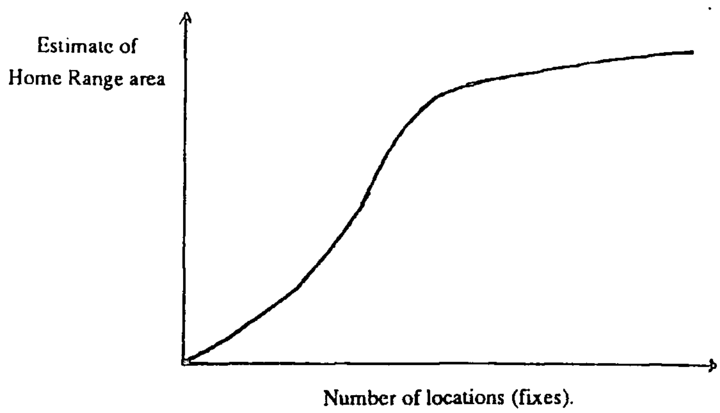


Figure 12. Diagram to illustrate the asymptotic increase in the estimate of Home Range Area with increase in number of "fixes" (Source *Harris et al* 1990)

The minimum number of captures was set at five, following Lidicker 1966, Contreras 1972 and Murúa *et al* 1986. Several methods exist for calculating home range size and most are related to the method involved in tracking or tracing the movement of animals. The minimum convex polygon method (MCP) (Mohr 1947, Southwood 1966) has been one of the most widely used and is suitable here because of its robustness particularly when the number of fixes are low (Harris *et al* 1990). Home ranges for both sexes of mice and voles were

Figure 11. A plot to show the distribution of Mean distance moved by woodmice and bank voles.

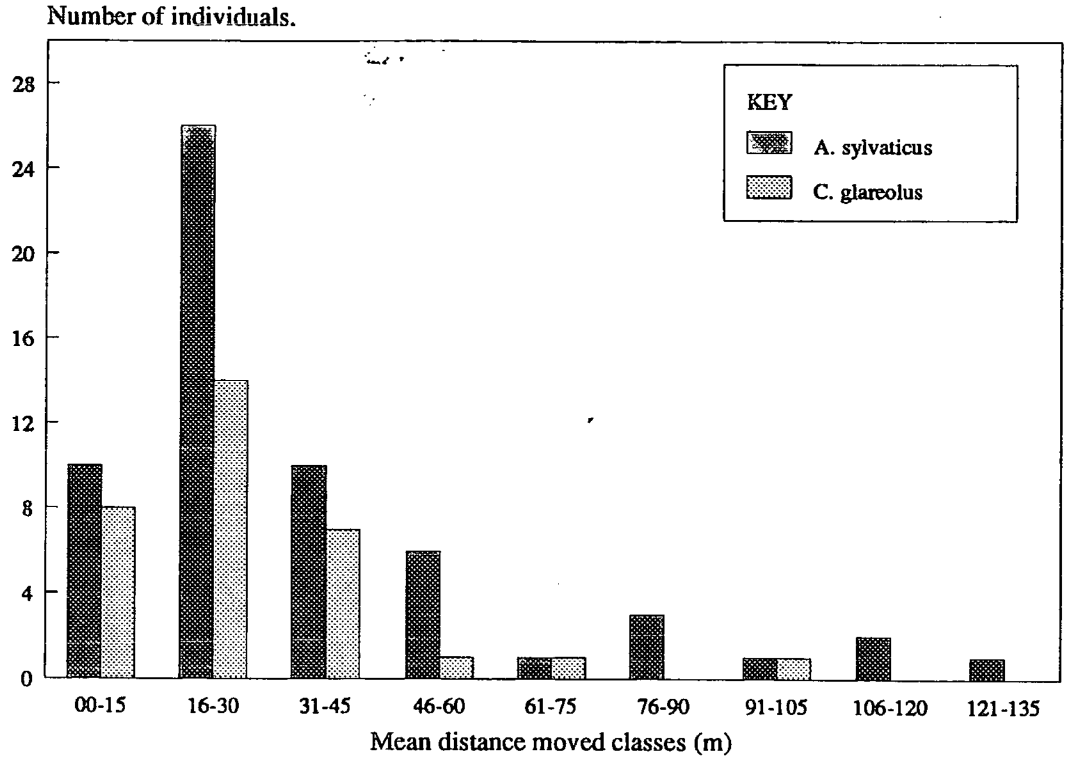


Table 11. Intergrid movements of woodmice and bank voles.

SPECIES (sex)	DATE(1990) Dept / Arr.	LOCATIONS From to	HABITAT TYPES	DISTANCE (m)	TIME (days)
A.s (M)	25/4 to 08/5	A4 to B3	M»F	193	13
A.s (M)	25/4 to 08/5	A1 to B3	M»F	343	13
A.s (F)	10/5 to 17/5	BW to B1	M»M	134	7
A.s (M)	10/5 to 30/5	BN to A1	M»M	199	20
A.s (M)	29/5 to 30/5	BN to A1	M»M	109	1
A.s (F)	29/5 to 30/5	A4 to A1	M»M	284	1
A.s (M)	10/5 to 01/6	BN to A1	M»M	124	22
A.s (M)	01/6 to 05/6	A4 to B3	M»F	103	4
A.s (M)	05/6 to 06/6	B3 to B1	F»M	235	1
A.s (M)	13/6 to 14/6	C1 to C2	M»Y	190	1
C.g (F)	14/6 to 15/6	C2 to C1	Y»M	220	1
A.s (M)	15/6 to 15/6	C1 to C2	M»Y	220	0
A.s (M)	16/6 to 19/6	BN to A1	M»M	154	4
A.s (M)	05/6 to 19/6	B3 to A4	F»M	178	18
A.s (F)	19/6 to 19/6	A4 to A1	M»M	194	0
A.s (M)	07/6 to 20/6	BS to A1	F»M	343	13
A.s (M)	15/6 to 03/7	C2 to C1	Y»M	134	7

KEY:

A.s = *Apodemus sylvaticus* C.g = *Clethrionomys glareolus*

M = Male F = Female

1 = MATURE 2 = YOUNG 3 = CLEAR FELLED (4 = MATURE)

A = Area A B = Area B C = Area C

B = BORDERLINES (N: North, S: South, W: West) determined by recording the points of capture, plotting them, and calculating the area. The area was described by a line encompassing all the points using only extant angles. Examples of some home ranges are shown in Figure 13.

Estimates of home range are given in Table 12. A non-parametric Mann-Whitney test (Sokal & Rohlf 1981) was carried out on the data, due to the small number of samples, and showed no significant difference in the mean home ranges between the sexes. The low numbers of individuals represented in the data prevented estimates to be made separately for the three habitat types.

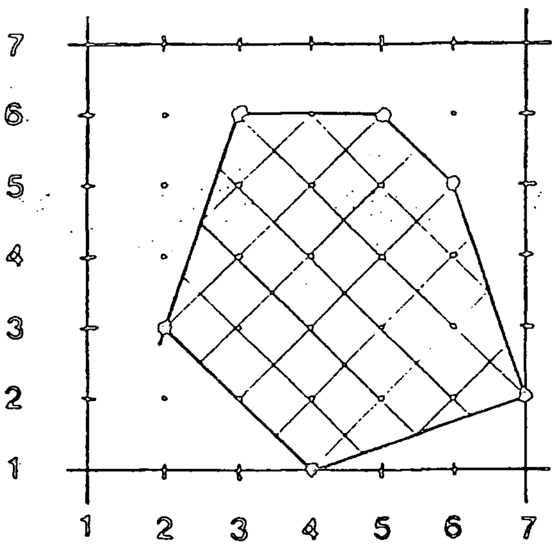
Table 12. The mean home range area estimates (m^2) from individuals which have been captured at least five times.

	A.sylvaticus		*C.glareolus*	
	MALES	FEMALES	MALES	FEMALES
	3825	450	1575	1125
	1013	225	225	1350
	900	1575	450	337
	788	1238	113	563
	1013	563	1013	225
	113	113	675	563
	1238			
	2700			
	1350			
	673			
	225			
	1125			
n	12	6	6	6
Mean(m^2)	1247	694	675	694
SE	300	238	223	182

The mean home range area (m^2)for woodmice and bank voles:

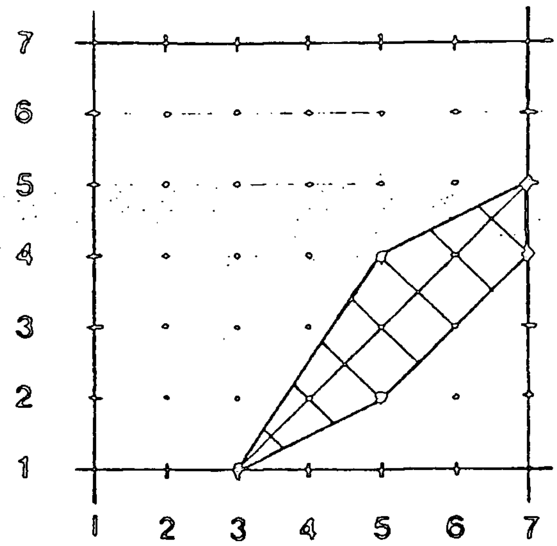
n	18	12
Mean	**1063**	**685**
SE	220	137

Figure 13. Some examples of Home Range area (m^2) estimates, using the Minimum Convex Polygon method (MCP), of woodmice and bank voles. The minimum number of captures (fixes) was set at 5.



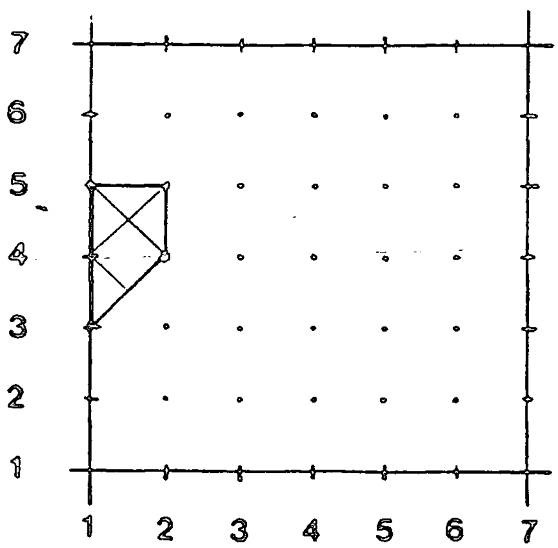
A. sylvaticus MALE

Home range = 3825 m^2



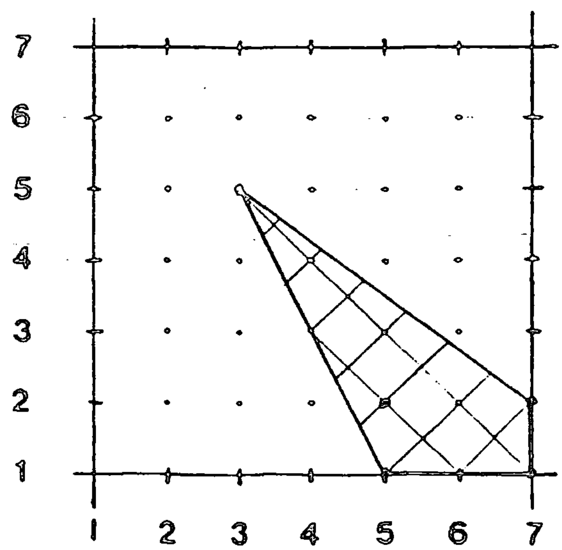
A. sylvaticus MALE

Home range = 1237 m^2



C. glareolus FEMALE

Home range = 338 m^2



C. glareolus MALE

Home range = 1575 m^2

DISCUSSION

Soil and Vegetation study.

The effects of Sitka spruce on the soil and vegetation have been shown to be very marked (Miles 1986, Hill 1986). Studies have shown, that on more susceptible soils, conifers tend to promote the accumulation of surface organic matter. Soils of the upland in Britain tend to be more peaty as a consequence of the wet oceanic climate. Some of the samples taken in Hamsterley Forest support this. A characteristic of such soils is a reduced buffering capacity.

The forest areas studied represent habitats found at the transition from first rotation mature coniferous forest to second rotation felled and young plantations. Much of the acidity has therefore resulted from the organic material left by the Sitka spruce. The patterns of change in pH and litter depth under Sitka spruce follow an oscillating trend with decrease in pH as the trees grow followed by a gradual increase as the trees mature (Miles 1986). The relationship between pH and litter depth was found to be significant only in samples from the mature plantations. This perhaps indicates the relatively stable conditions in the accumulation and decomposition of litter in these habitats. The lack of any correlation between pH and litter depth in samples from young plantations and felled areas suggests these habitats are more heterogeneous

At the beginning of the second rotation the substrate is characterised by acid soils covered with litter and brash left behind from the clear felling. This leads to a ground flora that is species poor, but shows a constancy of compositon between the felled habitat types. This similarity between replicate sites may be explained by considering the methods of seed dispersal by the plants found there. Hill (1986) noted that windborne seeds of birch, spruce, *Deschampsia flexuosa* and *Eriophorum angustifolium* were confined to the superficial layers of conifer litter, whereas seeds of most other species, bramble, sedges, heather, foxgloves, were found in layers of the soil that were present before the conifer litter started to accumulate. The ability of plants to colonise an area generally depends on their mode of dispersal and the soil environment. Therefore the flora of the felled habitats may reflect the buried viable seed component while in the young plantations the higher pH favours development of more species of plant. Additionally the smothering effect of litter is reduced by the decrease in litter depth in these areas. The disturbances by animals and increased litter decomposition could release those seeds present before litter accumulation, allowing for a greater number of plant species to colonize the area.

The classification of the vegetation data into the three habitat types showed that there was little difference between the replicates among the areas. Overall the vegetation cover, surface litter and abundance of species proved to be the main variables that described the variation between the habitats. The young plantations, as a group, were more heterogeneous than the either the felled or mature areas in terms of the abundance and diversity of the small mammals and species of plants present. In the classification the mature and young areas separated out well but quadrats from the clear felled habitats did not group well. This is perhaps an indication of the large influence of particular species of plant in these samples, namely heather (*Calluna vulgaris*) and seedlings of Sitka spruce (*Picea sitchensis*). The TWINSPAN analysis may be used to explain more subtle differences between habitats which do not appear to differ superficially from one another. A study by Dickman and Doncaster (1987) on small mammal populations in urban habitats, showed vegetation variables to be better predictors of population densities than variables characterising the urban habitat. Therefore in conifer plantations the classification may prove itself of more value when differences between plantations are not so striking.

THE SMALL MAMMAL COMMUNITY.

Of the six species of small mammal captured only two, *Apodemus sylvaticus* and *Clethrionomys glareolus* were found inhabiting the sites in large numbers. This is partly a result of the paucity of small mammal species that are present in the British Isles but also underlines the ability of these two species to survive in these habitats (Southern 1964). Two other species, *Microtus agrestis* and *Apodemus flavicollis* are abundant in England but *A. flavicollis* has a distribution limited to areas of southern England and Wales (Corbet & Southern 1977, Flowerdew 1984) and would not be expected to be found this far north. The field vole, *Microtus agrestis*, has been previously captured in Hamsterley forest (Gibson 1989), but this year, even when trapping in the same grids, none were caught. Low numbers of individuals have been found in other parts of the forest (F. Fernandez pers. comm.) together with woodmice and bank voles. The contrast in numbers between these two years suggests that the species is at a low level the low phase in it's cycle of abundance. It is well known that field vole populations in Britain fluctuate with a periodicity of three to four years (Chitty 1952, 1960).

A single individual of *M. agrestis* was captured in a young plantation which could be interpreted to indicate a low abundance of the species. Alternatively it is more likely the individual arrived into the grid from an area nearby. This may also explain the similar occurrence of a bank vole in clear felled area C3. This animal may have wandered into the grid from the young plantations (C2) or farmland that border this area. The near absence of bank voles from the clear felled habitats supports the view proposed in many studies that this species prefers sheltered areas with ground cover (Ashby 1967, Gurnell 1985b). However, the capture of bank voles in other recently clear felled areas (by F. Fernandez) suggests there may be other factors influencing the distribution of bank voles.

Why were bank voles found in mature plantations? Despite little or no vegetation cover the density of bank voles was not too different from that of woodmice. The most important factor here may be that the high density of Sitka spruce produced lateral branches, almost to ground level, which afforded protection from predators. The captures of bank voles within mature plantations was observed to occur in areas where fallen trees, rides and open glades were present. The voles may prefer these areas as they support more ground vegetation and provide nesting places such as tree roots and trunks. These observations suggest the presence of bank voles in patches of mature forest plantations which appear to be open and contain more vegetation. Woodmice were common in all types of habitat a feature documented in previous studies (Flowerdew 1984, Gurnell 1985, Dickman & Doncaster 1989) in which the woodmice is regarded as a habitat generalist. It was the only species captured in large numbers in the felled habitats. The large piles of brash in the felled habitats may well have been a feature attractive to woodmice by providing places where they could hide and build nests. Work is currently being carried out in Hamsterley Forest to test this view (F. Fernandez pers. comm).

Population sizes and Densities of small mammals.

Population sizes of mice and voles were only found to differ between the mature plantations and the young plantations. The numbers of woodmice in felled habitats were not statistically different from the numbers in young habitats, indicating that woodmice are more widespread. Thomson (1986) found low densities of woodmice in standing Sitka spruce and clear felled habitats, but in contrast to this study, he captured bank voles at densities nearly 2.5 times greater than woodmice. However, populations of woodmice and bank voles in broadleaved woodland show considerable (and independent) yearly variations in population levels (Ashby 1967). Therefore, should similar variations occur in Sitka spruce then the discrepencies between Thomson's and our results may be explained. The distribution of woodmice, bank voles and other small mammals in coniferous forest, especially second rotation Sitka spruce, is not well understood. The general view is that woodmice densities are high in comparison to bank voles in the two habitats, mature and clear felled, but young plantations appear to support a higher abundance and diversity of small mammals (Staines 1985, Gibson 1989). It is important to note that due to the "edge effect" estimates of densities of woodmice would be positively biased in relation to the estimates of bank vole density because woodmice moved further. However the pattern of trapping involving several grids has had the effect of reducing this bias by distributing the captures, and therefore the "edge effect" among the grids. Estimates of home range size are also more reliable because captures could be mapped over a larger area than the one available in a single grid study.

Movements

The mean distances moved by males and females of the two species *A. sylvaticus* and *C. glareolus* support the general view on the movements by small mammals (Kikkawa 1964, Brown 1966, Gurnell and Gipps 1989). The movements of woodmice were greater than for bank voles and only in woodmice were males found to move further than females. These results may also explain the sex ratios, which differ from 1:1 in woodmice but not in bank voles. The probability of capture increases for individuals that move further because of the greater chance of encountering a trap. On average in *Apodemus sylvaticus*, males moved twice as far as females and therefore the chances of capturing a male woodmouse are nearly twice that for females. This would tend to give a ratio of 2:1, males to females, which is the result obtained in this study. In bank voles there was no difference in the mean distance moved by males and females and the ratio of the sexes did not differ from 1:1.

Intergrid movements were detected in *A. sylvaticus*, and similar types of movement have been found to occur in male woodmice (Montgomery 1989b). There appear to be two types of movement according to the distances travelled (Figure 10). Common excursions within the home range dominate but sallies by individuals over greater distances are also present. Such movemnts may be be explained by one or more of the following factors;

Exploratory behaviour.

Dispersal.

Social interactions.

Population densities may also influence movement, evidence to support this is documented by Wolton and Flowerdew (1985) and in studies by Brown (1966) and Kikkawa (1964). The relationship both for woodmice and bank voles, suggests that at low densities individuals move further on average than at high densities. Brown (1966) showed that movements of dominant male woodmice were greater than for subordinate individuals. This suggests that the dominant (usually older) woodmice can restrict the movements of the subordinate, younger woodmice in an area. Age, sex and season affect movements, Montgomery (1989b) found that movements between trapping grids in mixed woodland indicated that dispersal occurred throughout the year reaching a peak in Autumn.

The movements by bank voles may also be the result of the factors mentioned above but their movements are rarely recorded in studies. Evidence of dispersal of young voles from optimal to suboptimal habitats is given in a study by Gliwicz (1989) and indicates the importance of social factors in movements. In this study I believe the lack of records of such movements is a consequence of the coniferous forest habitat. Mature plantations have low populations due to the patchiness of resources and therefore mammal dispersal is low. In young plantations, where densities are higher, movements and dispersal are low possibly because the benefits of more abundant resources outweigh the social factors that cause these movements. These ideas require more studies on vole migration and habitat preferences to support them or to suggest alternative explainations.

Home ranges

Home range is defined by Burt (1943) as the area traversed by an individual during its normal activities of food gathering, mating and caring for young. The minimum convex polygon method (MCP Mohr 1947, Southwood 1966), is the standard method used in the study of many different species. It is therefore at an advantage being the only method strictly comparable between studies and so should be considered where more than one method can be applied to range estimation. The advantages and disadvantages in the MCP method are described below; (Harris *et al* 1990).

Advantages.

a) Robust method useful when the number of fixes are low.

b) Simple widely used and so comparisons between studies are possible.

Disadvantages.

a) Range boundary includes all fixes including those beyond the main area of activity and so a strong influence by peripheral fixes may occur.

b) Intensity of range use cannot be indicated.

The estimates for home range size of woodmice and bank voles correspond closely to estimates from other studies (see Wolton and Flowerdew 1985) bearing in mind that separate home range area estimates for males and females could not be made. The same factors that are found to influence movement may be expected to affect home range size but additionally, the effects of habitat quality may be better understood in the context of home range size and position in the habitat. There is evidence, by Smal and Fairly (1982) for woodmice, and by Alibhai and Gipps (1985) for bank voles, that ranges are larger when the population density is low. A recent article by Montgomery (1989b) associates habitat heterogeneity with variation in density of woodmice in mixed coniferous and deciduous forest. The influence of habitat on home range size needs further study and problems in differentiating between particular aspects of the habitat will have to be approached.

Small mammals and the forest habitat.

In relating the observations on density, movement and home range of *Apodemus sylvaticus* and *Clethrionomys glareolus* to the habitats one of the major factors to consider is the influence of the managed conifer plantation. Woodmice are certainly more ubiquitous than bank voles but both species show preferences for particular types of habitat. To understand why such preferences are found it is worthwhile considering the type of foods these two rodents eats and the characteristics of the habitats in which they are most commonly found.

Studies into the diets of small mammals are limited because of the difficulty in identification of the finely masticated food particles (Hansson 1970). Watts (1968) documented the foods eaten by woodmice and bank voles in deciduous woodland. Analysis of food fragments in the stomach demonstrated the similarities in the types of plant and animals eaten by these species. Several studies have shown that bank voles take a larger variety of plant species including those also eaten by woodmice (Hansson 1985). In mature coniferous forest seeds were found to be the major food group for both mice and voles (Thomson 1986), with arthropods and fungi showing Spring and Autumn peaks respectively. Individuals from clear felled areas had a higher content of leaves and herbaceous plant material (forbs) in their stomachs than individuals in mature plantations. The seasonal differences in diet also appear to be widespread among small rodent mammals. Evidence from Thomson (1986), Smal and Fairley (1980) and Watts (1968) point to the importance of changing food availability at different times of the year. In an overview,the two species of rodent in this study have food requirements which overlap but are broad enough, and distinct enough not only to make competition for food resources unlikely (Gurnell 1985), but to produce differences in what habitat is the optimal one for each species.

The vegetation of forests play an important part in the abundance of rodent populations. Woodmice thrive in many habitats but have their highest densities in broadleaved woods and hedgerows. In coniferous plantations Flowerdew (1984) suggests the lower densities are caused by poor availability of seeds to assist survival through the winter. Bank voles also prefer broadleaved woodland and coniferous plantations, but they occur in high numbers only where ground cover is abundant (Gurnell 1985) However, the young stages of conifer plantations seem to be the most diverse, are richer in small mammals and may be regarded as a productive phase for most wildlife (Ratcliffe 1986). In studies by Wolk and Wolk (1982) and Venables and Venables (1971) a particular stage was identified, when population changes in woodmice and voles occur. The time around six to ten years of growth of the plantation was found to relate to changes in the populations. This is more precisely related to canopy closure and subsequent decrease in the ground flora affecting the abundance of food plants.

Over the coming years one of the major changes to occur in coniferous plantations will be an increase in area of young forest as plantations are logged and replanted. This second rotation will be structurally more variable, and in Sitka spruce plantations, where the rotation cycle is shorter, proportionately more extensive in area. Initially with the increase in felled areas forests may experience a decrease in the diversity of small mammal species but this may be short lived. Generally the second rotations of Sitka spruce plantations should provide good habitats for many species of vertebrates and on the basis of results found in this study promote increased population levels of small mammals.

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Appendix 1

A plant species list for the areas studied in Hamsterley Forest.

Flowering plants.	Common name.
Bellis perennis	Daisy
Calluna vulgaris	Ling heather
Cardamine impatiens	Narrow leaved bittercress
Cerastium fontanum	Common mouse ear
Circaea lutetiana	Enchanters nightshade
Cirsium spp.	Thistle
Digitalis purpurea	Foxglove
Empetrum Nigrum	Crowberry
Epilobium angustifolium	Rosebay willowherb
Erica tetralix	Cross leaved ?
Gallium saxatile	Heath bedstraw
Gallium odoratum	Woodruff
Moenchia erecta	Upright chickweed
Myosotis arvensis	Field forgetmenot
Potentilla erecta	Tormentil
Prunella vulgaris	Self-heal
Ranunculus acris	Meadow buttercup
Ranunculus repens	Creeping buttercup
Rubus fruticosa	Bramble/Blackberry
Rumex acetosa	common sorrel
Rumex acetosella	Sheep's sorrel
Urtica dioica	Nettle
Vaccinium myrtillus	Bilberry
Trees and shrubs.	
Betula pendula	Silver birch
Betula pubescens	Hairy birch
Picea sitchensis	Sitka spruce
Sorbus acuparia	Mountain ash
Grasses.	
Agrostis canina	Velvet bent
Agrostis capillaris(tenu.)	Common bent
Agrostis curtisii	Bristle bent
Deschampsia flexuosa	Wavy hair grass
Festua ovina	Sheeps'fescue
Holcus lanatus	Yorkshire fog
Molinia caerulea	Purple moor grass
Nardus stricta	Matt grass
Sedges.	
Carex echinata	Star sedge
Carex laevigata	Smooth stalked sedge
Carex panicea	Carnation sedge
Eriophorum vaginatum	Harestail cotton grass

Appendix 1. continued

Rushes.	
Juncus effusus	Soft rush
Juncus squarrosus	Heath rush
Luzula campestris	Field woodrush
Ferns.	
Blechnum spicant	Hard fern
Dryopteris dilatata	Broad buckler fern
Pteridium aquilinum	Bracken

Mosses.
(Identified to Genus in most cases)
Bryum spp.
Hypnum cupressiforme
Pleurosium schreberi
Pohlia nutans
Polytricum spp.(several)
Sphagnum fimbriatum
Sphagnum papillosum

Appendix 2 : Vegetation data set of quadrats from study grids in Hamsterly forest values are on the Domin cover / abundance scale.

(+ species present in area near quadrat)

QUADRAT NUMBER.

	Plant species.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
1	*Calluna vulgaris*					7		6	9	5						6				4	4		8	5									6	8	6	6			2		4
2	*Picea sitchensis*					4		1	5	1			+			5	4			5		4	4									4		7	5	7				+	
3	*Epilobium angustifolium*						4			4										3		5	4			1						1	4								2
4	*Vaccinium myrtillus*											+									5																				
5	*Gallium saxatille*													+																	5	5						2			
6	*Rumex acetosella*					2	4	5		1	+																														
7	*Betula pubescens*					+																	+																		
8	*Empetrum nigrum*																				8																				
9	*Juncus effusus*																			4				6									6					4			2
10	*Nardus stricta*					5	4				1	7	4																		+						+	7			
11	*Juncus squarrosus*													+																			6								
12	*Dryopteris dialata*			+								4	2					2											2		1							5			
13	*Agrostis capillaris*					4														7		3	4																		
14	*Eriophorum vaginatum*																						1																		
15	*Deschampsia flexuosa*							1												6	4					2				4	9										
16	*Cerastium fontanum*																									4															
17	*Sphagnum spp.*			+	+													+				5																			
18	*Mosses*			8	7	1										6	3	7				3		3					5	7		4				3					3
19	*Calamagrostis pseudophragmites*																										6														
20	*Pteridium aquilinum*																							2																	
21	*Blechnum spicant*																																					4			
22	*Betula pendula*																																		5						2
23	*Potentilla errecta*																																								
24	*Rubus fruticosus*																							+								1									
25	*Sorbus ocuparia*										+																														
26	*Digitalis purpurea*																					4																			
27	*Cirsium spp.*																										+														
28	*Rumex acetosa*																															+									
29	Litter/bare soil.	10	10	7	5	5	8	7		8	9	5	8	10	10		9	6	10		8	8	6	7	10	8	8	10	8	6							10		10	10	9
		A1				A2					A3				B1					B2					B3			C1				C2					C3				

1 = MATURE SITES 2 = YOUNG SITES 3 = CLEAR FELLED SITES

Appendix 3. Estimates of population size for *A. sylvaticus* (A. s.) and *C. glareolus* (C. g.)in three habitat types using three methods associated with capture-mark-recapture of individuals.

MNKA	Minimum number known alive, after Krebs 1966.
L/P	Lincoln / Petersen (1896) estimate, using Bailey's modification (1951) for low sample numbers.
M h	Model for Heterogeneity, Burham and Overton estimate for individuals with differing capture probabilities (1979).

SITES		MNKA		L / P		M h	
		A.s.	C.g.	A.s.	C.g.	A.s.	C.g.
A1	1	11.00	1.00	11.25	1.00*	14.60	0.83[1]
	2	9.00	5.00	9.00	5.33	9.83	6.67
	3	0	0	0	0	0	0
A2	1	9.00	2.00	10.67	2.00*	14.67	4.00[1]
	2	7.00	20.00	7.50	21.25	8.33	28.17
	3	7.00	7.00	7.20	7.00	8.67	9.00
A3	1	3.00	0	3.00	0	2.83	0
	2	7.00	0	7.00	0	9.83	0
	3	4.00	0	4.00	0	3.67	0
B1	1	9.00	2.00	9.00	1.50	10.33	2.83
	2	8.00	2.00	7.20	2.00	9.50	2.00
	3	12.00	5.00	12.50	5.00	14.33	5.67
B2	1	29.00	5.00	30.26	4.00	34.17	5.33
	2	27.00	7.00	32.45	7.50	37.50	10.67
	3	19.00	7.00	19.42	7.00	21.17	8.50
B3	1	8.00	0	7.88	0	8.33	0
	2	9.00	0	10.50	0	13.83	0
	3	8.00	0	8.00	0	9.33	0
C1	1	4.00	2.00	4.00	2.00	3.33	1.33
	2	6.00	5.00	6.25	5.00	9.00	6.67
	3	1.00	6.00	1.00	6.00	1.00	6.83
C2	1	5.00	21.00	6.00	23.18	8.83	29.50
	2	14.00	21.00	16.67	23.17	20.17	30.17
	3	9.00	20.00	9.80	21.64	11.50	33.17
C3	1	11.00	0	12.50	0	16.33	0
	2	11.00	0	11.25	0	13.33	0
	3	10.00	0	9.63	0	12.67	0

* = Incidence where low numbers were captured with no tagged recaptures
1 = Data not applicable when there are no recaptures.