

Durham E-Theses

Activity, ranging, and habitat use by rodents in county Durham

Potts, Stephen

How to cite:

Potts, Stephen (1991) Activity, ranging, and habitat use by rodents in county Durham, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/6060/

Use policy

The full-text may be used and/or reproduced, and given to third parties in any format or medium, without prior permission or charge, for personal research or study, educational, or not-for-profit purposes provided that:

- a full bibliographic reference is made to the original source
- a link is made to the metadata record in Durham E-Theses
- the full-text is not changed in any way

The full-text must not be sold in any format or medium without the formal permission of the copyright holders.

Please consult the full Durham E-Theses policy for further details.

ACTIVITY, RANGING, AND HABITAT USE BY RODENTS IN COUNTY DURHAM.

The copyright of this thesis rests with the author.

No quotation from it should be published without his prior written consent and information derived from it should be acknowledged.

Stephen Potts MSc. Ecology Thesis

Durham University, 1991



1.0. ABSTRACT.

The activity, home - ranging, and habitat use behaviour of two species of rodent, Apodemus sylvaticus (L.), the wood mouse, and Clethrionomys glareolus (Schreber), the bank vole, was investigated over a period of 14 weeks in two contrasting habitats.

In farmland, woodmice utilised the rough vegetation around a crop of winter - sown wheat as a nest site, and probably as a food source, while the field surface also formed part of the home range of many animals studied. Weather conditions had little effect on the capture success of woodmice in farmland. Bank voles were caught exclusively in the boundaries around the edge of the field.

Home range sizes and levels of activity of woodmice in woodland were lower than those of animals in farmland. Capture success of woodmice was not related to vegetative cover in woodland.

Bankvoles were caught preferentially in scrub vegetation in all weather conditions, though weather was an important factor in capture success under other catagories of vegetation.

The extent of intersexual range overlap of bankvoles in woodland fell significantly during the period of the study though no other changes were apparent for either species.

Home range sizes and levels of activity were consistantly lower than those reported in other studies.



ACKNOWLEDGEMENTS.

I would like to thank the following people who contributed their time and effort to the production of this paper;

Prof. P.R. Evans for supervision of the project and the provision of reference materials,

The lab. technicians, especially Jack and Paul, for help with transport and equipment,

Mr. H.W. Pepper of the Mammal Society, for the loan of extra traps,

Mr. Fernando Fernandez, for advice concerning trapping and small mammals in general,

Dr. Brian Huntley, for information and advice regarding statistical appraisal of data,

Mrs. Warner, for provision of weather data,

The management and staff of Houghall Farm, for permission to work on their land, for the storage of equipment, and for their advice regarding local wildlife and farming practices, and,

Miss Gillie M.T. Sargent, for assistance with literature, fieldwork, and vegetation analysis.

Ш

CONTENTS.

1.0. ABSTRACT.	I
ACKNOWLEDGEMENTS.	II
2.0. INTRODUCTION.	1
3.0. MATERIALS AND METHODS. 3.1. Study Period 3.2. Study Sites 3.3. Trap Proceedure 3.4. Statistical Methods 3.5. Weather Data	3 3 6 6 12
HOME RANGE RESULT DIAGRAMS.	13
 4.0. RESULTS. 4.1. Trapping Success and Measures of Activity i) Arable Land ii) Woodland iii) Arable Land and Woodland 	14 14 18 21
4.2. Vegetation, Weather and Trap Successi) Woodmiceii) Bankvoles	22 22 22
4.3. Range Overlapi) Arable Landii) Woodlandiii) Arable Land and Woodland	25 25 25 28
5.0. DISCUSSION . 5.1. Problems	29
5.2. Effect of Age, Sex and Habitat on Capture Success	29
5.3. Home Ranges and Mean Movement Indices	31
5.4. Capture Success Between Trapping Sessions in Woodland	33
5.5. Weather Conditions, Vegetation and Capture Success	33
5.6. Range Overlaps	35
APPENDIX.	37
BIBLIOGRAPHY AND REFERENCES.	39

2.0. INTRODUCTION.

There is a long and distinguished history of the study of rodents which is borne out by the vast amount of literature which concerns itself with every aspect of their ecology and biology. Such intensive investigation of rodent species is partly attributable to their abundance and partly to their relative ease of study. They have provided valuable information not merely related to their own ecology but have also been used in, for example, examinations of population - cycle dynamics (Krebs et al, 1973), dispersal characteristics (Gaines and McClenaghan, 1980), competition (Bowers and Brown, 1982), and in population genetics (Charnov and Finerty, 1980; Chitty, 1960).

Two species of rodent which have been studied extensively in the United Kingdom are the bank vole (*Clethrionomys glareolus*) (Schreber) and the wood mouse (*Apodemus sylvaticus*) (L.). Both are present throughout mainland Britain, with the exception of some offshore islands, and they occupy similar habitat types, although the vole prefers denser ground cover (Corbet and Harris, 1991). Both species occur in deciduous woodland where they are important agents of seed dispersal, as well as being implicated in the destruction of saplings, thereby reducing regeneration (Ashby, 1967). They also inhabit grasslands, coniferous woods, and hedgerows, though the wood mouse is more widespread, also being found in dry stone walls (Corbet and Harris, 1991).

Both species take a wide variety of food types including fruit, seeds, leaves, mosses, grasses and flowers, as well as insects and worms. Their main predators in Great Britain include the tawny owl (Strix aluco), stoat (Mustela erminea), fox (Vulpes vulpes), and the domestic cat (Felis domesticus).

Bankvoles are diurnal whilst woodmice are mainly nocturnal, though pregnant females have been known to be active during the day also (Wolton, 1983). For a full review of the ecology of these species see Corbet and Harris (1991).

Because considerable sympatry occurs within many populations of the two species, especially in deciduous woods, a large proportion of research effort has been concentrated on their comparative ecology in such areas. Past studies have, for example, considered rodent home ranges (Crawley, 1965,1969; Kikkawa, 1964), dispersal (Watts, 1970), nesting behaviour (Wolton, 1985), ecological energetics (Campbell, 1974; Smal and Fairley, 1980), and parasitisation (Healing and Nowell, 1985). However, more recent analyses have concerned themselves with the activities of small mammals in previously less - well studied habitats such as arable land (Green, 1979) and sand dunes (Attuquayefio and Gorman, 1986), which are occupied by the more adaptable wood mouse but not by the bank vole.

The primary aim of my study project was to investigate aspects of the home range, as defined by Burt (1943), of the wood mouse and the bank vole as they relate to the animal's

species, sex, and the habitat in which they live. The habitats studied comprise a cereal field of winter - sown wheat and an area of mixed deciduous woodland.

Home range analysis is important in that range size and possibly shape relate to habitat quality and the spatial distribution of resources such as food (Attuquayefio et al, 1986), therefore giving an indication of habitat utilisation by the study species. This information can then be related to the activity of predatory species, or to formulate habitat management programmes, for example.

Prior investigations have indicated that factors other than those studied here can influence estimated range sizes. These include population density, season, and individual animal behaviour (Crawley, 1969; Randolph, 1977; Wolton and Flowerdew, 1985). Extraneous factors such as variations in study methods and treatment of the data can also cause discrepancies in range estimates (Flowerdew et al, 1985; Kikkawa, 1964). Some of the problems caused by the artefacts of data gathering and analysis are considered, as are problems encountered during the course of work in the field.

Differences in utilisation of habitat by rodents is also considered below. The effect of vegetative cover on actual, as opposed to maximum range size and location has been commented on by Montgomery et al (1991). I examined the extent to which ranges are 'defined' in the two habitats in relation to vegetative cover and temporal usage.

The extent of range overlap both inter and intrasexually is analysed, as is overlap of species.

Trapping success is discussed in relation to weather conditions.

An alternative form of measure for use in the analysis of rodent activity was employed, its utilisation prompted by low numbers of captures caused by the truncated nature of the project.

3.0. MATERIALS AND METHODS.

3.1. Study Period.

Between 17th April and the 11th July 1991, a programme of trapping of small mammals was conducted at two sites in County Durham, about 1 mile south of the centre of Durham City. The trap - programme made use of grids and lines of Longworth small mammal live traps which operated for varying periods of time in the following habitat types:

3.2. Study Sites.

i) Great High Wood. (O.S.274405).

Two trap grids operated at this site (see fig. 3.1) which comprised an area of mixed deciduous woodland of predominantly Oak and Birch trees (figure 3.2 and Table 3.4).

- a) Grid A consisted of 42 traps, laid out in a rectangle of 6 x 7 with one trap at each point. The traps were spaced 10 metres apart. This grid was operational for two periods, between 16/4 and 10/5, and 19/6 to 11/7.
- b) Grid B lay 15 metres from Grid A. Thirty five traps were laid out in a 5 x 7 configuration, again with 10m between consecutive traps. This grid operated for the latter trap period only. The size of both grids was dictated by the size and shape of the woodland.

All traps were concealed under vegetation in order to prevent the possibility of removal by the public. This practice, coupled with the topography of the site meant that traps occaisionally had to be placed a short distance away from the exact location dictated by the grids.

ii) Houghall Farm; "Fattening Pasture". (O.S.284395).

This study site was located approx. 1 mile from the region of Great High Wood which was being trapped, and it consisted of a 10.1 ha field of improved winter - sown wheat of variety "Haven".

Two trap grids operated in the field (see figure 3.3). Each grid consisted of 42 traps in a rectangular 7 x 6 trap configuration and at 10m intervals. Grid A was used for a total of 5 weeks (23/4 to 6/6) while Grid B was in use for two weeks during the period 29/5 to 13/6. Additionally, 3 trap lines of 20 traps at 5m intervals were in operation during the study. Line A was set to catch for 6 weeks (14/5 to 12/6), Line B for 1 week (14/5 to 16/5), and Line C for 4 weeks from 21/5 to 12/6.

Dates and details of chemical treatment of the wheat crop are shown in Table 3.5.i. The crop field was bounded on its northern edge by a predominately hawthorn hedgerow and a strip of grass, and beyond that a field of spring wheat and potatoes. The eastern side of the crop comprised an uncultivated headland, beyond which lies the River Wear, and the southern end of

N

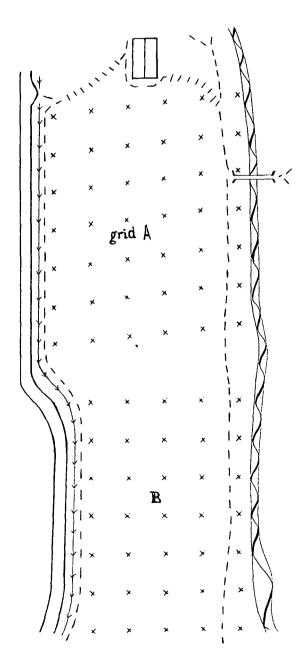


Figure 3.1. Great High Wood: Trap Layout

:Track
----: :Path
----: :Stream
:Bridge
:Field Station
:Steps

x :Trap Point

10 metres



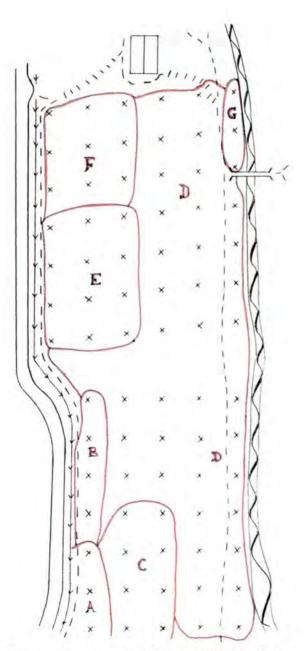


Figure 3.2. Great High Wood: Habitat Types

:Track
----: Path
----: Stream
:Bridge
:Field Station
:Steps

× :Trap Point

10 metres

the crop was contiguous with an area of pasture which was cut for silage. Another headland consisting of mixed grasses and weeds on a steeply - sloping bank ran along the western edge of the crop field (see Table 3.6).

3.3. Trap Proceedure.

Operational traps were provisioned with hay for insulation. This was replaced if it became wet. Each trap was baited with wheat which was replenished as necessary. Due to the limited time available for the study, no prebaiting was carried out. All traps were checked twice a day, in the morning at 8.00am and in the afternoon at 4.00pm. One "trap week" consisted of 3 nights (and so 2 days) of consecutive trapping. Reference made below to "Trap Opportunities" therefore relates to the total number of times that the traps were set to catch, both during the day and night. This is in contrast to "Trap Nights", which refers only to traps set to catch animals overnight in readiness for processing the following morning.

Captured animals were transferred from the trap into a clear polythene bag for easy inspection. Each animal was individually marked using fur - clipping, with a maximum of 3 clips being made. Juveniles (of 14g and under) were marked with a maximum of two clips. The fore - limb area of juveniles was avoided due to the sparsity of fur in this region. Fur clipping was used as a means of identification because it is relatively easily carried out by one person and it does not rely upon tags which may be lost or removed by the animal. It does not endanger the welfare of the animal and the fur regrows after a relatively short period of time if the clip is not renewed by the researcher.

All animals were weighed to the nearest gramme and a record made of their sex and sexual condition, before they were released at the point of capture.

3.4. Statistical Methods.

i) Home Ranges.

Animals trapped three or more times were used in estimation of home ranges. Ideally, this minimum number of recaptures would have been decided by the asymptote of a plot of number of captures against observed range size (Voigt and Tinline, 1980), but this was not possible due to the small sample sizes involved. Ranges were calculated by means of the Minimum Convex Polygon technique (Dalke, 1942; Macdonald et al, 1980), and are shown below. "Ranges" produced by animals moving in a straight line along a line of traps in a grid are not included in these figures, although their data are used in calculations of the "Mean Movement Indices". A Mean Movement Index was produced by calculating the sum of the distances between the traps where an animal was consecutively caught, and dividing by the

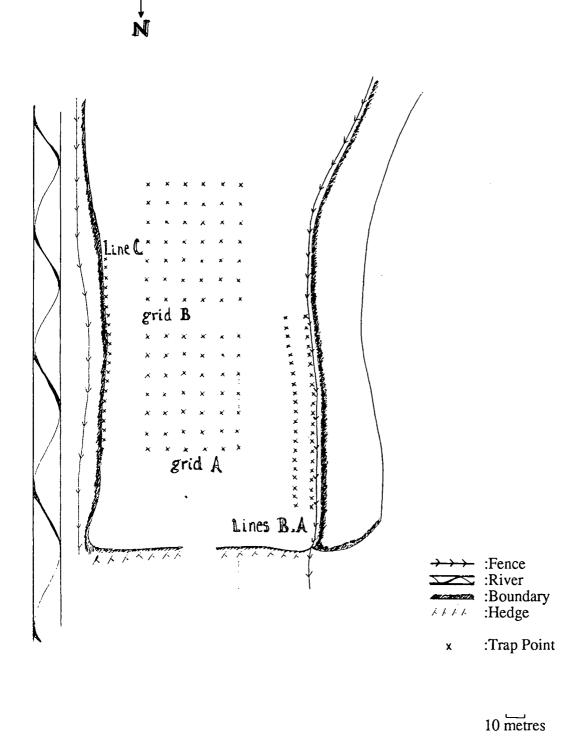


Figure 3.3. Fattening Pasture: Trap Layout

number of traps occupied by the individual, minus one. Similar types of measure have been employed by other authors (eg. Crawley, 1969; Green, 1979) to give an indication of activity levels where sample sizes are small.

- ii) Vegetation Survey and Cover Index.
- a) Houghall Farm: Fattening Pasture. (see Table 3.6).

A 10 - minute survey was carried out within Grid A in order to ascertain which plant species other than the wheat crop were present, though no quantitative measure was made. This time period was chosen arbitrarily, all the species noted were recorded during the first five minutes of the search. At each of Trap Lines A and C, five sites were surveyed to ascertain their vegetative composition. The sites chosen corresponded to the location of traps 1, 5, 10, 15, and 20. In addition, the mean heights of 42 randomly - chosen wheat plants were monitored during the study, the results being shown in Table 3.5.ii.

b) Great High Wood (see fig. 3.2 and Table 3.4).

At this location, the area covered by Trap Grids A and B was divided into "habitat types" on the basis of a vegetational survey. A five minute search was carried out in order to establish the main species present in each habitat type.

At all locations except Fattening Pasture Grid A, the plant species present were given a cover - abundance rating on the DAFOR scale (Tansley, 1939):

```
Dominant; Abundant; Frequent; Occasional; Rare.

CD = CoDominant.

t = tree; s = sapling; b = bush.
```

Additionally, tree species present were noted.

Each trap at Great High Wood was allocated a cover index score between 0 and 14 based on the amount of concealment perceived to be afforded a small mammal from above (from an aerial predator for example) by the attendant vegetation. No account was taken of the effect of vegetation on the hunting ability of terrestrial predators. This index was composed of 'marks' awarded in each of the following catagories:

```
SOIL = 0; LEAF LITTER = 1; GRASS(Short) = 2

SCRUB(Eg. Rubus, Lonicera, fallen branches) = 4

SHRUBS(Eg. Lonicera, Ilex) = 3

LOW CANOPY(Eg. Betula, Sambucus) = 2

CANOPY(>5m)(Eg. Quercus, Larix, Betula) = 2
```

At all locations a sample of any plant species which could not readily be identified in the field was taken back to the laboratory for identification. All plant surveys were undertaken on the 21st of June.

Table 3.4. Great High Wood: Habitat Vegetation Types.

НАВІТАТ ТҮРЕ	SPECIES AND COVER SCORE (see "Methods" sec. 3.4.ii).b. for an explanation of symbols)
Α	Urtica dioica(CD), Rubus fruticosus(CD), Chamaenerion angustifolium(CD), Gramineae (D.flexuosa & H.lanatus)(A), Cirsium spp.(F), Galium aparine(O), Anenome ranunculoides(O), Heracleum sphondylium(R), Sambucus nigra(t)(O)
В	Rubus fruticosus(D), Gramineae(F), Endymion nonscriptus(O), Galium aparine(R),(Leaf Litter(A), Quercus petraea(t & s)(D), Betula pendula(t)(O), Ilex aquifolium(t)(R)
C	Endymion nonscriptus(O), Moss spp.(O), Gramineae(O), (Leaf Litter(D), Fagus sylvatica(t)(D), Ilex aquifolium(b)(R), Sorbus aucuparia(s)(R)
D ,	Gramineae (D. flexuosa & H. lanatus)(D), Rubus fruticosus(F), Trifolium spp.(F), Pteridium spp.(O), (Leaf Litter & Dead Wood(O), Lonicera pericymenum(F), Quercus petraea(t)(D), Sorbus aucuparia(s)(F), Ilex aquifolium(b)(O), Fagus sylvatica(t) (O), Betula pendula(t=R)/(s=F)
Е	Gramineae(esp. D.flexuosa)(D), Rubus fruticosus(A), Pteridium spp.(O), (Leaf litter(O), Lonicera periclymenum(b)(F), Ilex aquifolium(b)(F), Quercus petraea (s=F)/(t=D), Sorbus aucuparia(t)(O), Betula pendula(t)(A), Larix decidua(t)(O)
F	Rubus fruticosus(D), Gramineae(esp. H.lanatus)(F), Stellaria holostea(O), Galium palustre(O), Silene dioica(R), (Leaf Litter(F), Ilex aquifolium(b=F)/(t=O), Sorbus aucuparia(s)(O), Betula pendula(s=F)/(t=CD), Quercus petraea (s=O)/(t=CD), Larix decidua(t)(R), Sambucus nigra(t)(R)
G	Gramineae(esp. D.flexuosa)(D), Equisetum spp.(O), Stellaria holostea(O), Pteridium spp.(R), (Leaf Litter(O), Quercus petraea (s=O)/(t=O), Betula pendula(s=R)/(t=O), Fagus sylvatica(t)(O), Larix decidua (t)(R).

Table 3.5.i. Fattening Pasture: Chemical Treatments.

PRESENT CROP VARIETY	Winter Wheat Haven	
PREVIOUS CROP	Winter Wheat	
USE	Feed Wheat	
DRILLING DATE SEED RATE SEED DRESSING	10th October 1990 196kg per Hectare Duel Purpose Dressed (inc. Mercury)	I
FERTILISER November 4/3/91 16/4/91 30/4/91	N P K 0 24 24 33.5 33.5 33.5	of 250kg of 127kg of 230kg of 125kg
CHEMICALS November	Cypemethrium Fanfare Intake	250ml/ha 1lb/ha 2lb/ha
22/4/91	Hispar Chlorinequat Starane	11b/ha 1.751b/ha 0.51b/ha

Table 3.5.ii. Fattening Pasture: Mean Crop Heights.

DATE	MEAN CROP HT.	S.E.	n
	F R		
08/5	221.83 cm	5.96	42
21/5	361.05 <u>¢</u> m	7.45	42
04/6	545.07 ¢m	8.54	42

Table 3.6. Fattening Pasture: Vegetation Types.

HABITAT

SPECIES AND COVER SCORE

Crop Field**

Galium aparine, Impatiens glandulifera, Matricaria matricariodes, Viola tricolor, Cirsium spp., Gramineae spp.

Trap Line A

Gramineae spp.(D), Galium aparine(A), Urtica dioica(A), Impatiens glandulifera (F), Cirsium spp.(O), Heracleum sphondylim(R), Rubus fruticosus(R), Quercus robur(t)(D), Fraxinus excelsior (t)(O), Sambucus nigra(t)(O), Fagus sylvatica(t)(R)

Trap Line C

Gramineae spp.(D), Cirsium spp.(A),
Galium aparine(A), Heracleum sphondylim
(A), Lamium album(A), Cruciata laevipes
(F), Papaver rhoeas(F), Urtica dioica(F),
Anthriscus sylvestris(O), Capsella bursapastoris(O), Cerastium arvense(O),
Lysimachia nummularia(O), Petasites
hybridus(O), Siline alba(O), Siline
dioica(O), Sinapis arvensis(O), Vicia
sepium(O), Chamaenerion angustifolium(R),
Rumex spp.(R), Senecio jacobaea(R).

** Crop = Winter sown wheat; variety "Haven".

See "Methods" section 3.4.ii)b). for explanation of symbols.

iii) Range Overlap.

Movements of animals which enclosed an area of ground (as opposed to those between traps of animals recaptured along a straight line), were used in the calculation of range overlaps. The extent of range overlap between pairs of animals based on their species and sex was calculated in the following manner:

The home range size of each individual rodent was determined by drawing the range on a sheet of graph paper on a scale of 1mm equal to 1 metre;

The range of the animal with which all other ranges were being compared was drawn on a clear acetate sheet and placed over the other ranges in turn. The number of squares enclosed by both ranges (the sympatric range or overlap) was counted and the following formula was applied:

 $P = 2 SA/T \times 100$ where,

P is the proportion of total range area of both animals which is shared, SA is the actual area shared, the sympatric range (measured in sq. metres), and T is the total area covered by the two ranges combined.

The proportions of total range areas which were shared were then subjected to statistical analyses (see below). The "mean overlap" values were obtained by summing the proportions ("P" above) and dividing by n, the number of pairs of ranges.

3.5. Weather Data.

Information regarding weather conditions during the study was obtained from the Durham University Observatory. Wind speed was measured at 0900hrs while cloud cover and rainfall figures refer to the recordings of the previous 24 hours. Dry - bulb daytime maximum temperatures are those of the afternoon during which "PM" captures (mainly of bank voles) took place, while dry - bulb minimum temperatures are taken to be the temperature of the previous night, during which animals were being caught in readiness for inspection the following morning. The observatory is located just over half a mile north of the Great High Wood site and as such is assumed to give a good indication of weather conditions experienced at both study sites.

HOME RANGE RESULTS: WOOD MICE AND BANK VOLES

FIGURE

4.1.a. to 4.1.g. incl. Houghall Farm: Fattening Pasture -

Male Woodmice.

4.1.h. to 4.1.l. incl. Houghall Farm : Fattening Pasture -

Female Woodmice.

4.2.a. and 4.2.b. Great High Wood: Male Woodmice.

4.2.c. Great High Wood: Female Woodmouse.

4.3.a. to 4.3.e. incl. Great High Wood: Male Bankvoles -

Session 1.

4.3.f. and 4.3.g. Great High Wood: Female Bankvoles -

Session 1.

4.3.h. to 4.3.m. incl. Great High Wood: Male Bankvoles -

Session 2.

4.3.n. to 4.3.r. incl. Great High Wood: Female Bankvoles -

Session 2.

All ranges determined using the minimum convex polygon technique based on three or more captures.

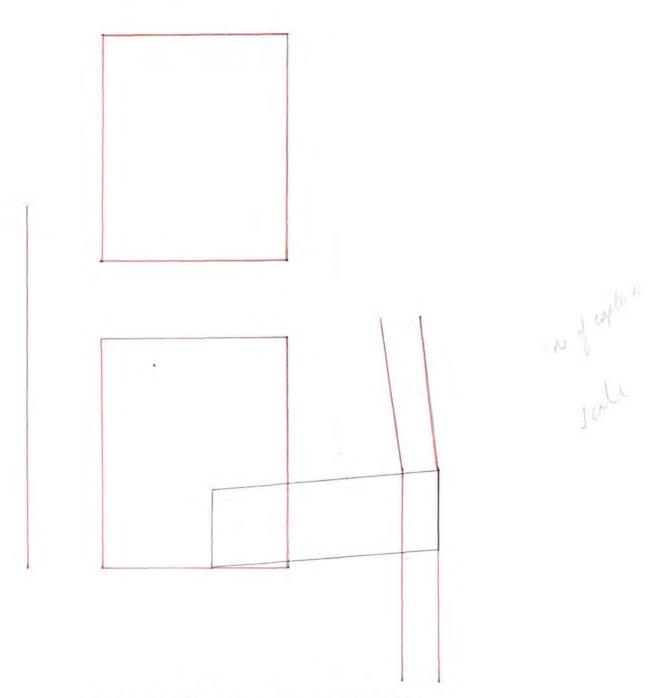


Figure 4.1.a. Home Range: Houghall W.M. Male a.

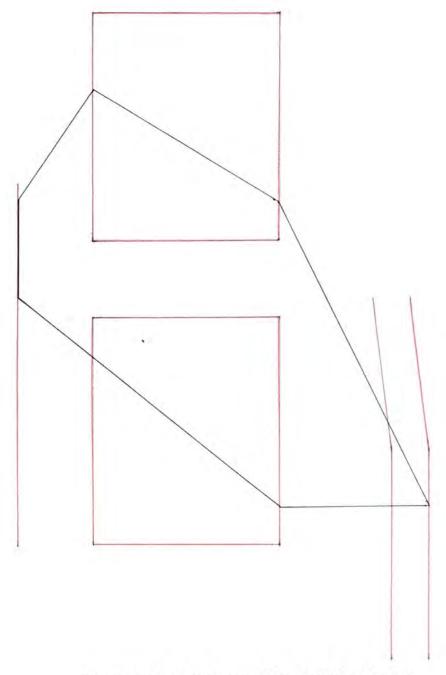


Figure 4.1.b. Home Range: Houghall W.M. Male b.

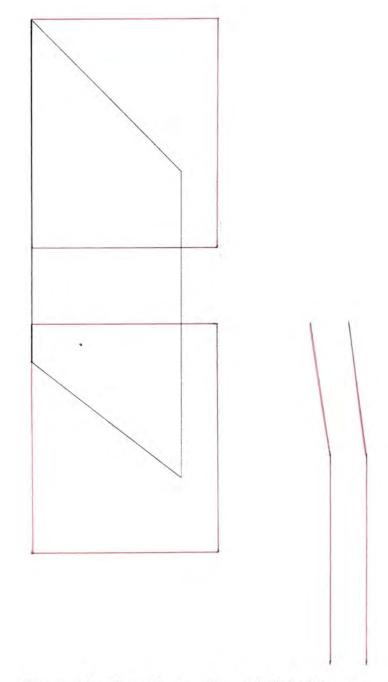


Figure 4.1.c. Home Range: Houghall W.M. Male c.

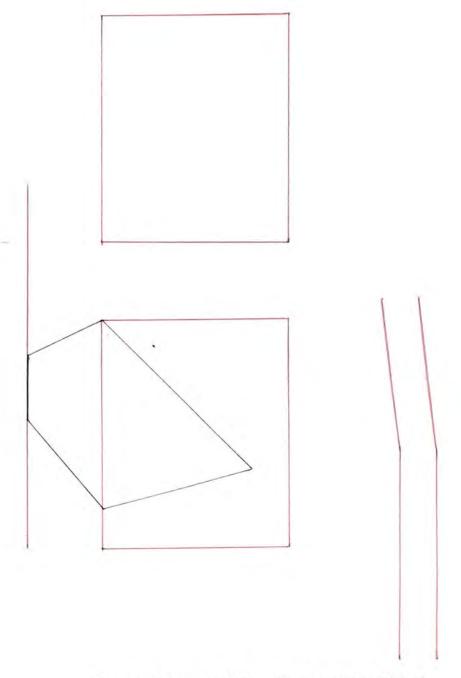


Figure 4.1.d. Home Range: Houghall W.M. Male d.

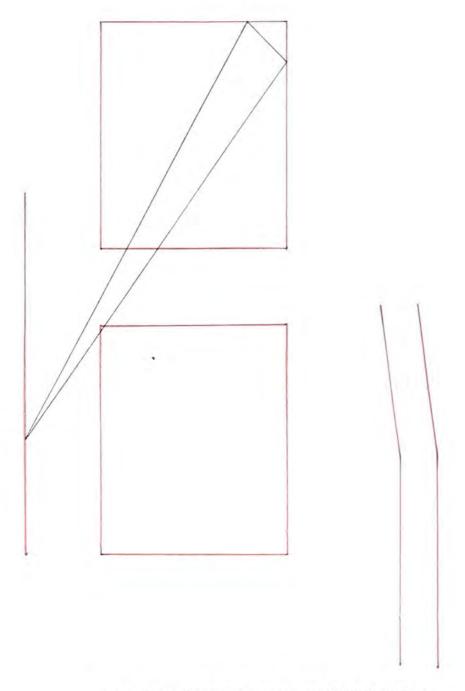


Figure 4.1.e. Home Range: Houghall W.M. Male e.

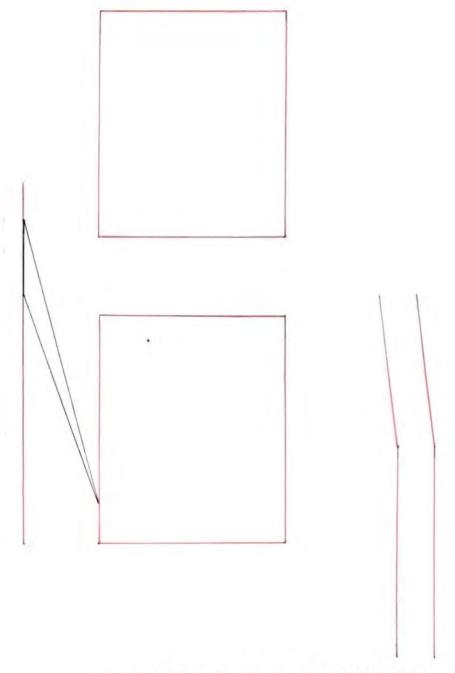


Figure 4.1 f. Home Range: Houghall W.M. Male f.

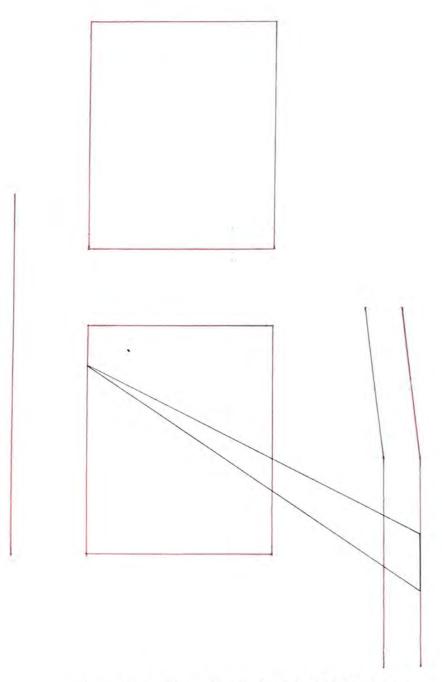


Figure 4.1.g. Home Range: Houghall W.M. Male g.

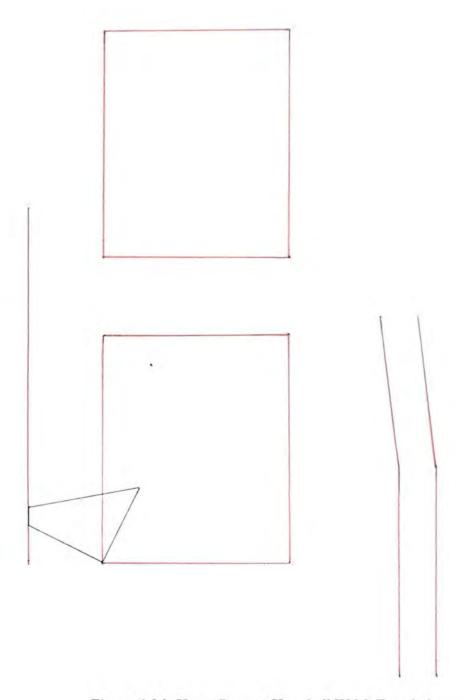


Figure 4.1.h. Home Range: Houghall W.M. Female h.

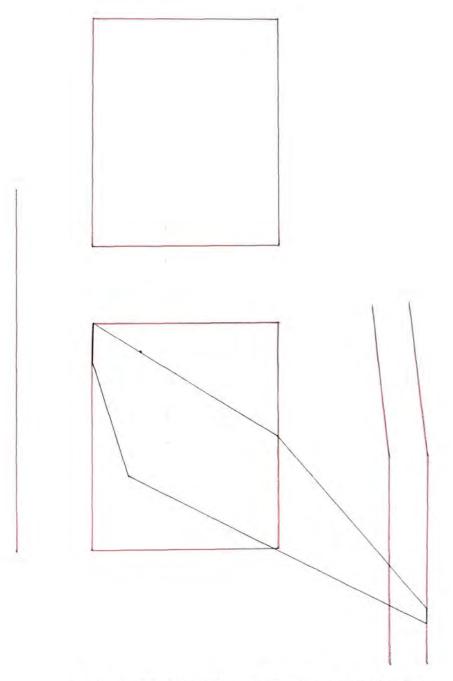


Figure 4.1.i. Home Range: Houghall W.M. Female i.

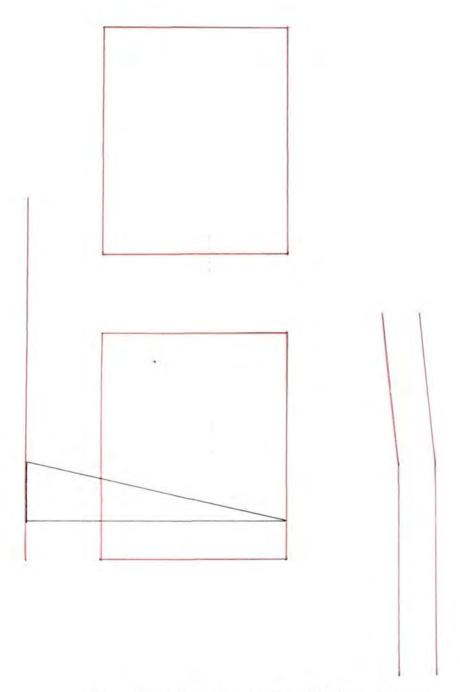


Figure 4.1.j. Home Range: Houghall W.M. Female j.

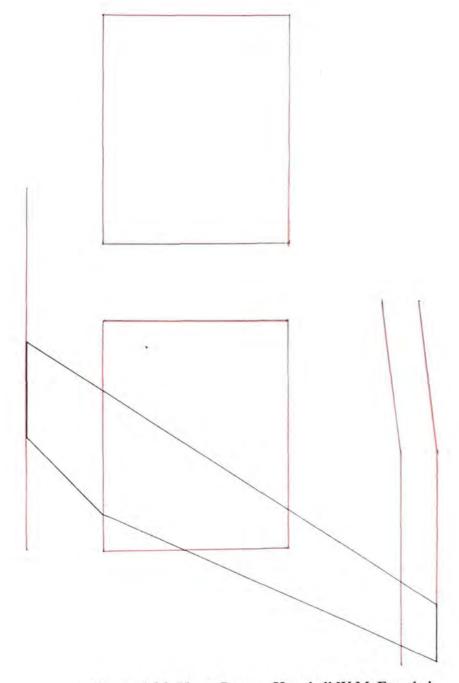


Figure 4.1.k. Home Range: Houghall W.M. Female k.

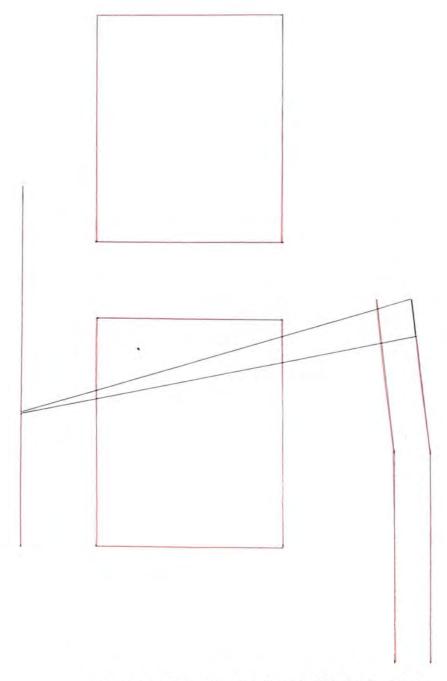


Figure 4.1.1. Home Range: Houghall W.M. Female 1.

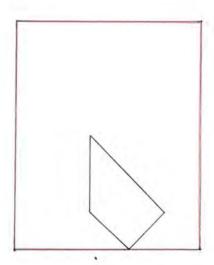


Figure 4.2.a. Home Range: Great High Wood W.M. Male a.

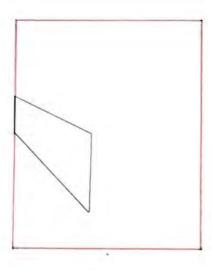


Figure 4.2.b. Home Range: Great High Wood W.M. Male b.

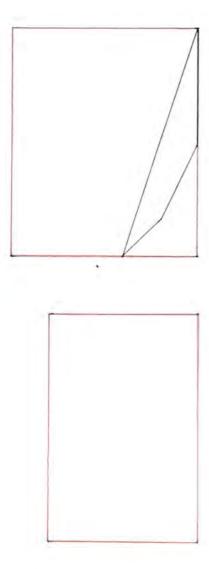


Figure 4.2.c. Home Range: Great High Wood W.M. Female c

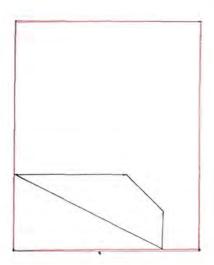


Figure 4.3.a. Home Range: Great High Wood B.V. Male a.

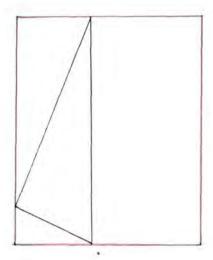


Figure 4.3.b. Home Range: Great High Wood B.V. Male b.

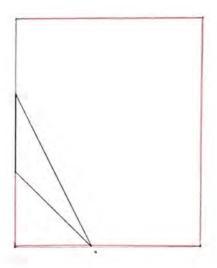


Figure 4.3.c. Home Range: Great High Wood B.V. Male c.

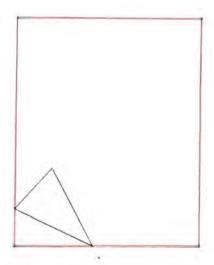


Figure 4.3.d. Home Range: Great High Wood B.V. Male d.

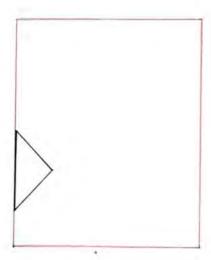


Figure 4.3.e. Home Range: Great High Wood B.V. Male e.

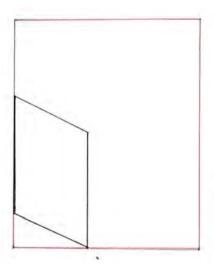


Figure 4.3.f. Home Range: Great High Wood B.V. Female f

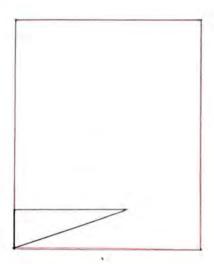


Figure 4.3.g. Home Range: Great High Wood B.V. Female g

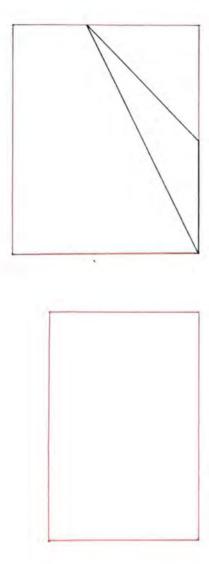
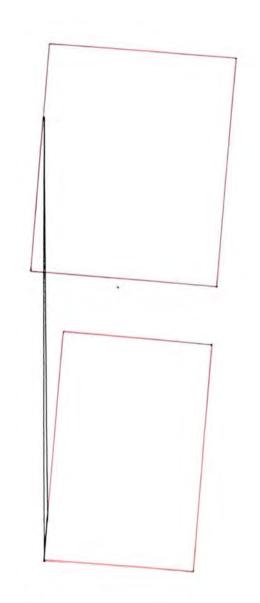


Figure 4.3.h. Home Range: Great High Wood B.V. Male h.



manufactured and I

Figure 4.3.i. Home Range: Great High Wood B.V. Male i.

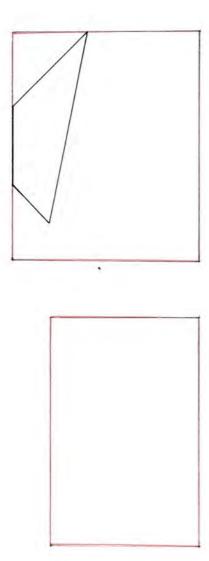


Figure 4.3.j. Home Range: Great High Wood B.V. Male j.

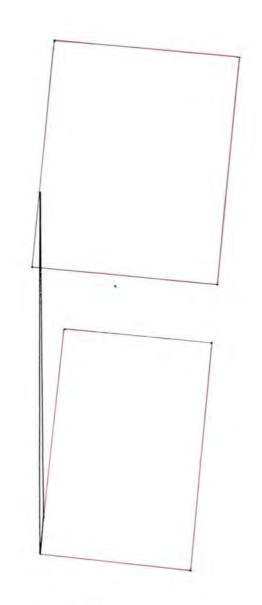


Figure 4.3.k. Home Range: Great High Wood B.V. Male k.

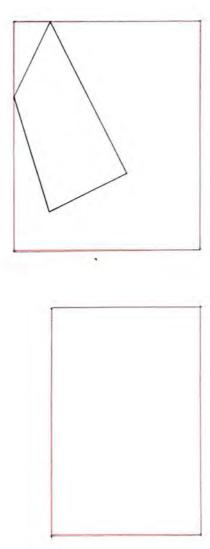


Figure 4.3.1. Home Range: Great High Wood B.V. Male 1.

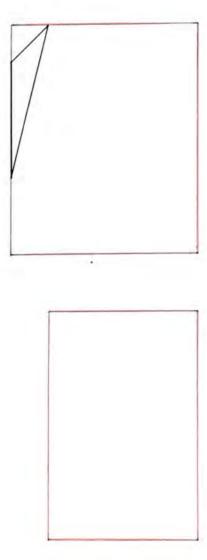


Figure 4.3.m. Home Range: Great High Wood B.V. Male m.

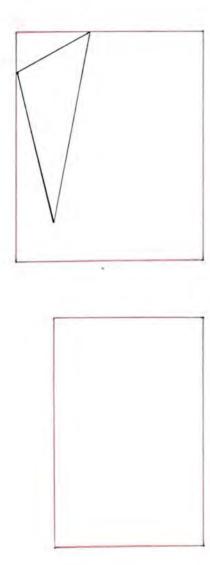


Figure 4.3.n. Home Range: Great High Wood B.V. Female n

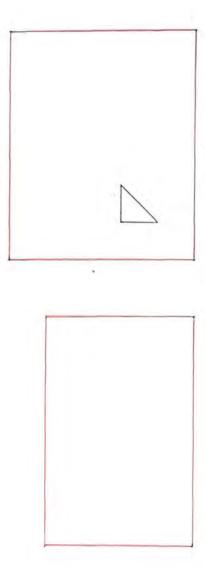


Figure 4.3.o. Home Range: Great High Wood B.V. Female o

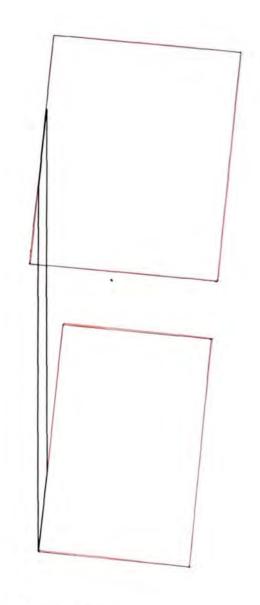


Figure 4.3.p. Home Range: Great High Wood B.V. Female p

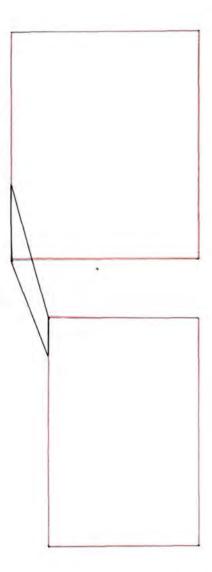


Figure 4.3.q. Home Range: Great High Wood B.V. Female q

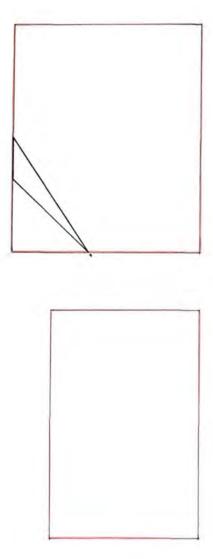


Figure 4.3.r. Home Range: Great High Wood B.V. Female r

4.0. RESULTS.

- 4.1. Trapping Success and Measures of Activity.
 - i) Arable Land.

In a total of 2570 trap opportunities at Houghall Farm Fattening Pasture, 32 individual woodmice were captured, of which 18 were males and 14 females. Total recaptures numbered 114 animals, comprised of 63 males and 51 females, making an average overall trap success of 4.4%.

There was considerable variation in trap success between areas of the study site. Excluding the 5 daytime captures, 109 woodmice were (re)caught at night out of a total of 1523 trap nights. Of these, 942 trap nights were located in the crop, and 47 animals were caught there, making a crop - trap success of 5%. Line A was trapped for 360 trap nights, resulting in the (re)capture of 33 animals (9.2%), while Line C, trapped for 221 trap nights, had a success of 13.1% (n=29 (re)captures). This made an average trap success of 10.7% for traps situated in the field boundaries.

The difference in the numbers of recaptured animals in the boundaries and in the the crop was found to be not significant (t=-1.004, df=4, N.S.). Similarly, there was no significant difference between the (re)capture success of adults and juveniles caught in the crop (chi-sq.=1.137, df=1, N.S.), nor between the total recapture success of adults and juveniles caught in the field edge (chi-sq.=0.012, df=1, N.S.) (see Table 4.5).

Trap success (captures plus recaptures) for adult males was lower in the field than in the field boundary (1.7% vs 2.7%), this pattern being repeated for adult females (1.1% vs 3.1%). There was an insignificant difference between the numbers of all combined male and female (re)captures in the boundary when compared with the numbers of males and females captured in the crop however (chi-sq.=4.632, df=3, N.S.). Likewise, there was no significant difference between the numbers of all juveniles trapped and retrapped in the edge and in the crop (chi-sq.=4.712, df=3, N.S.) at the 5% level. Juvenile females had a higher capture rate in the boundary than in the field (0.2% vs 0.1%, n=3), while trap success of juvenile males was highest in the crop (0.5% vs 0.3%, n=10) (see Table 4.5).

No significant difference was apparent between the home range sizes of male and female wood mice (t=0.692, df=10, N.S.) and the mean movement indices of males and females also differed insignificantly (t=0.869, df=12, N.S.) when both age groups were combined (see Table 4.4).

During the period of the study, no bank voles were captured in the crop; all 145 captures were made in the field boundaries (see Table 4.6). Of the 145 captures, 142 occured in Line A and 3 in Line C. This difference was found to be not significant (MW-U=0.245, df=10, N.S. at 0.05), probably due to the low sample sizes involved. Overall trap success (captures plus

Table 4.4. Summary of Statistical Tests Performed on Rodent Home Range and Mean Movement Index Data in Both Habitats.

HABITAT & SPECIES/TEST	n	MEAN & (S.E).	RESULT	TABLES VALUE	SIGNIFICANCE LEVEL
Arable Crop: Woodmouse					
Male vs Fem. Range Size (sq.m).	7/5	1934/1230 (778)(488)	t=0.692 F=3.557	2.23 df=10	N.S.
Male vs Fem. MMI (m).	8/6	43.9/35.7 (4.4)(9.2)	t=0.869 F=3.264	2.18 df=12	N.S.
Trap Success Edge vs Crop	4/4	1.2%/2.7% (0.5)(1.3)	t=-1.004 F=6.303	2.78 df=4	N.S.
Woodland: Woodmouse		!			
Trap Success per Line of Grid A Sess.1 vs 2	6/6	8.7%/2.2%	t=3.708 F=5.200	2.37 df=7	P < 0.05
Woodland: Bankvole					
Trap Success per Line of Grid A Sess.1 vs 2	6/6	19.3%/16.8% (6.3)(6.3)	t=0.282 F=1.006	2:23 df=10	N.S.
Male vs Fem. Range Size: Sess.1	5/2	280 / 375	t=-0.494	2.57	N.S.
Sess.2	6/5	(90.3)(225) 322 / 181 (118) (67)	F=2.481 t=0.988 F=3.740	df=5 2.26 df=9	N.S.
Male Range Size Sess.1 vs 2	5/6	280 / 322 (90)(117)	t=-0.275 F=2.029	2.26 df=9	N.S.
Fem. Range Size Sess.1 vs 2	2/5	375 / 181 (225)(67)	t=1.191 F=4.575	2.57 df=5	N.S.
Male Sess.1+2 vs Fem. Sess. 1+2 Range Size	11/7	303 / 236 (73) (76)	t=0.607 F=1.433	2.12 df=16	N.S.

continued over...

Woodland: Bankvole (cont)					
Mean Movement Indices (m)					
Male vs Fem. Session 1	9/4	11.9/13.5 (3.6)(5.1)	t=-0.249 F=1.126	2.20 df=11	N.S.
Male vs Fem. Session 2	9/6	26.9/13.5 (8.9)(3.8)	t=1.405 F=8.318	2.20 df=11	N.S.
Male Sess.1 vs 2	9/7	11.9/14.7 (3.6)(4.4)	t=-0.496 F=1.149	2.15 df=14	N.S.
Female Sess.1 vs 2	4/6	13.5/11.9 (5.1)(5.6)	t=0.210 F=1.212	2.45 df=6	N.S.
Male Sess.1+2 vs Female Sess.1+2	18/10	19.4/13.5 (4.9)(2.9)	t=1.038 F=5.459	2.06 df=25	N.S.
Woodland: Woodmouse vs Bankvole				<i>;</i>	
Range Size: Mouse vs Vole Sess.1	3/7	316/307 (16)(81)	t=0.107 F=60.189	2.45 df=6	N.S.
MMI: Mouse vs Vole	7/24	12.8/12.9 (4.4)(2.1)	t=-0.049 F=1.260	2.05 df=29	N.S.
Arable Crop vs Woodland: Woodmouse					
Range Size: Crop vs Wood	12/3	1641/316 (489)(16)	t=2.703 F=3749.44 MWU=0.051	2.20 df=11	P < 0.05 N.S. at 0.05
MMI: Crop vs Wood	14/7	40.4/12.8 (4.6)(4.4)	t=3.796 F=2.173	2.86 df=19	P < 0.01

Table 4.5. Summary of Statistical Tests Performed on Woodmouse Capture Success Data for Traps Positioned in Boundaries and in the Crop at Fattening Pasture.

AGE / SEX	CAPTURE	RECAPTURES/	% RECAPTURE			
CATAGORY	LOCATION	OPPORTUNITIES	SUCCESS*			
Male / Adult	Boundary	27/1000	2.70%			
Female / Adult		31/1000	3.10%			
Male / Juvenile	Boundary	3/1000	0.30%			
Female / Juvenile		2/1000	0.20%			
Chi-sq. = 0.012, df=1, Tab	Chi-sq. = 0.012, df=1, Tables value = 3.84 at 0.05, N.S.					
Male / Adult	Crop	26/1570	1.66%			
Female / Adult		17/1570	1.08%			
Male / Juvenile	Crop	7/1570	0.45%			
Female / Juvenile		1/1570	0.07%			
Chi-sq. = 1.137, df = 1, Tables value = 3.84 at 0.05, N.S.						
Male / Female (Adult + Juvs.)	Boundary vs	63/1000	1.58%			
	Crop	51/1570	0.82%			
Chi-sq. = 4.632, df = 3, Tables value = 7.81 at 0.05, N.S.						
Juvenile	Boundary vs	5/1000	0.25%			
	Crop	8/1570	0.58%			

Chi-sq = 4.712, df = 3, Tables value = 7.81 at 0.05, N.S.

Yate's correction used where sample sizes less than 5.

^{*} Recapture Success figures are taken as a percentage of all trap opportunities, day and night.

recaptures) of bank voles in Line A was 23.7%, comprised of 13.2% male capture success (n=79 recaptures), and 10.3% female success (n=62 recaptures).

The numbers of woodmice of both sexes caught in Line A traps were significantly lower than the numbers of bankvoles caught in Line A traps over the same period (chi-sq.=5.516, df=1, P<0.025) (Table 4.6). Eleven male and 22 female *Apodemus* were (re)captured in Line A out of a total of 600 opportunities (trap days and nights), making a capture success of 1.8% for males and 3.7% for females (5.5% overall). (However, see Table 4.6 for night - time capture success).

Of the 3 bank voles caught in Line C traps out of 400 opportunities, 2 were males (0.5% success) and 1 female (0.25% success). Woodmouse captures in Line C numbered 30 over the same period (7.5% success), composed of 19 males (4.75% success) and 11 females (2.75%). The difference between trapping success of mice and voles in Line C was not significant (chi-sq.= 0.265, df=1, N.S. using Yate's correction for low sample sizes) at the 5% level. Similarly, the numbers of woodmice caught in Lines A and C were also not significantly different (Table 4.6).

- ii) Woodland.
- a) Woodmice. The total numbers of woodmice caught in Grid A differed between the two trapping sessions at Great High Wood, with session 2 (19/6 to 11/7) providing significantly fewer recaptures than session 1 (17/4 to 10/5) (t=3.708, df=7, p<0.05) (Table 4.4).

There were no significant differences in capture success of traps placed under scrub cover as opposed to under non - scrub vegetation (t=0.810, df=40, N.S.), nor between traps placed under shrub or canopy cover, as opposed to under no shrubs or in the open (t=0.286, df=40 and t=0.165, df=40 respectively, both N.S.) (see Table 4.7).

b) Bankvoles. Totals of bank voles captured and recaptured at Great High Wood did not differ significantly between the two trapping sessions for Grid A (t=0.282, df=10, N.S.) (Table 4.4). Only one vole marked in session 1 was identified in session 2 also.

Female bank voles had larger mean home ranges than males in session 1 but male mean home range sizes were larger in session 2, although neither of these differences were significant (t=-0.494, df=5 and t=0.988, df=9, both N.S.). Male home ranges did not vary significantly in size between sessions 1 and 2 (t=-0.275, df=9, N.S.), this pattern being repeated for female bank voles (t=1.191, df=5, N.S.).

Analysis of mean movement indices (MMIs) for sessions 1 and 2 revealed no significant difference between the distances travelled by males and females. However, the t-value for session 2 was of a much closer proximity to significance than for session 1, with males moving greater distances on average during this session (t=-0.249, df=11 and t=1.405, df=11, both N.S.).

Table 4.6. Summary of Statistical Tests Performed on Capture Success of Rodents in the Field Boundaries at Fattening Pasture.

SPECIES & TRAP LOC'N	n CAUGHT	% SUCCESS S.E.	RESULT	TABLES VALUE	SIGNIFICANCE LEVEL
Bankvole :					
Line A					
All	142/600	23.7%			
Male	79/600	13.2% 8.5	0.404		
Female	62/600	10.3%	t=8.104 F=289.00	12.71 df=1	N.S.
Line C					
All	3/400	0.75%	MWU=0.245		N.S. at 0.05
Male	2/400	0.50% 0.5			
Female	1/400	0.25%			
Woodmouse :					
Line A	; ;				
All	33/600	5.5%			
Male	11/600	1.8% 5.5			
Female	22/600	3.7%			
	, ~~~	211.10	t=0.221	4.30	N.S.
Line C			F=1.891	df=2	
All	30/400	7.5%	1 110/1	G. 2	
	19/400	4.8% 4.0			•
Female	11/400	2.8%			
Woodmouse:					
(Night Only)	·				
Tina A					
Line A	22.000	0.00			
All	33/360	9.2%			
Male	11/360	3.1%			•
Female	22/360	6.1%		,	
Line C				<i>,</i> ,	
All	29/221	13.1%		. S	
Male	18/221	8.1%			
Female	11/221	5.0%			
Woodmouse vs Bankvole :					
Line A	WM 33/600 BV 142/600		Chi-sq. 5.516	5.02 df=1	P < 0.025
Line C	WM 30/400 BV 3/400		Chi-sq. 0.265	3.84 df=1	N.S.

Table 4.7. Summary of Statistical Tests Performed to Investigate the Relationship Between Capture Success and Vegetative Cover in Great High Wood; Trap Grid A / Sessions 1 and 2.

VEGETATIVE COVER AND SPECIES	NOS. CAUGHT	MEAN WITH ST.D ERROR (BELOW)	T-VALUE	TABLES VALUE	SIG. LEVEL
Scrub vs No Scrub Woodmouse:	48/17	1.8 / 1.1 (0.5)(0.6)	t=0.810 F=1.246	2.02 df=40	N.S.
Bankvole:	202/15	7.5 / 1.0 (1.4)(0.7)	t=4.218 F=5.982	2.02 df=38	P < 0.001
Shrub vs No Shrub Woodmouse:	21/44	1.4 / 1.6 (0.6)(0.5)	t=0.286 F=1.182	2.02 df=40	N.S.
Bankvole:	69/148	4.6 / 5.5 (1.4)(1.4)	t=-0.424 F=1.971	2.02 df=40	N.S.
Canopy Cover vs Open Canopy Woodmouse:	40/25	1.6 / 1.5 (0.5)(0.5)	t=0.165 F=1.449	2.02 df=40	N.S.
Bankvole:	104/113	4.2 / 6.6 (1.2)(1.8)	t=-1.176 F=1.430	2.02 df=40	N.S.

Table 4.8. Summary of Mean Home Range Sizes and Mean Movement Indices of Rodents in Both Habitats.

	HOUGHA All Woods male	LL FARM nice female	GREAT HIGH Woodmice total	WOO! Bankvo male f	oles
Mean Home Range	1934.1	1230	316	303 2	36.3
(sq.metres) S.E. n	778.6 7	488.4 5	16 3	72.7 7 11	6.2 7
Mean Movement	43.9	35.7	12.8	19.4 1	3.5
Index (metres) S.E. n	4.4	9.2 6	7	5 18	2.9 10

Though male MMI increased from session 1 to session 2, and female MMI fell during this period, comparison of male indices between sessions, and female indices between sessions showed no significant rise or fall respectively (t=-0.496, df=14 and t=0.210, df=6, both N.S.). Overall, a comparison of male movements in sessions 1 and 2 combined, compared with female combined session scores showed that males tended to have a higher level of movement than females (mean = 19.4m as opposed to 13.5m), although this difference was not significant (t=1.038, df=25, N.S.) (see Table 4.4). (See also Table 4.8 for a summary of home range and MMI data).

There were no significant differences in the capture success of bank voles in traps located under shrub as opposed to under non - shrub vegetation (t=-0.424, df=40, N.S.), nor under canopy cover as opposed to in the open (t=-1.176, df=40, N.S.). Comparison of capture success between traps placed under scrub and no scrub vegetation supported the hypothesis that voles are caught preferentially under scrub cover with 88.2% of captures occuring here, as opposed to 11.8% under no scrub. This difference proved to be highly significant (t=4.218, df=38, p<0.001) (see Table 4.7).

c) Woodmice and Bankvoles. Out of a total of 420 trap nights at Great High Wood in Grid B, a single (male) wood mouse was captured. Over the same period, 26 bank voles were recaptured at night (6.2% success), and 14 during the day (5%). Of the 40 voles caught, 37 (92.5%) were detained in traps in Line 1 of the grid. All of these traps were situated under scrub vegetation and the location of the other 3 captures (trap 3G), was also under scrub. Thus, 100% of bank vole captures in Grid B occurred in the traps placed under scrub vegetation.

Comparison of the home range sizes of wood mice and bank voles inhabiting Great High Wood gave no significant difference (t=0.107, df=6, N.S.), nor was there any difference in the mean movement indices of the two species (t=-0.049, df=29, N.S.) (Table 4.4).

iii) Arable Land and Woodland.

A comparison of the home range sizes of wood mice inhabiting Fattening Pasture and Great High Wood sites showed that ranges of animals inhabiting the farmland were significantly larger than those of the woodland animals (t=2.703, df=11, P<0.05) though the variances of the two data sets were not comparable (F=3749.44). Performance of a non-parametric Mann Whitney - U test upon the same data revealed a difference which approximated significance but which was not significant at the 5% level (MW-U=0.0513, N.S.). The mean movement indices of mice at Fattening Pasture were significantly greater than those of woodland mice (t=3.796, df=19, P<0.01, F=2.173) with a stable F - value (see Table 4.4).

4.2. Vegetation, Weather and Trap Success.

i) Woodmice.

Higher average capture success of mice in both the crop field and the field boundary at Fattening Pasture occured after rainfall although in neither case was the rainy - night success significantly greater (t=0.724, df=9 and t=0.181, df=9 respectively, both N.S.). Similarly there was no significant difference between the success of traps situated in the crop when comparing captures on cloudy and clear nights (t=0.392, df=10, N.S.).

Rainfall did not influence the capture success of traps placed in the crop or the edge, with no significant difference in success at these locations on rainy nights (t=-0.711, df=10, N.S.). A similar result was obtained when cloud cover was considered (see Table 4.9.).

At Great High Wood, trapping success of woodmice was not found to be related significantly to vegetative cover or to the weather conditions studied (see Table 4.9. for full results).

ii) Bankvoles.

Capture success in traps under scrub vegetation was significantly higher than in traps not located in scrub during rainy nights (t=8.906, df=19, P<0.001) and on nights during which cloud cover was 50% or more (t=8.874, df=20, P<0.05). This result indicates the importance of scrub vegetation noted previously, in that captures in such habitat form the majority of total captures at all times, regardless of weather conditions studied (see section 4.1.ii.b. above).

Significantly more bank voles were caught in non - shrub traps on rainy nights (t=-2.142, df=28, P<0.05) than in traps situated under shrub vegetation. There was no such significant relationship between capture success of voles in shrub and non shrub traps on cloudy (50% or more sky cover) nights (t=-1.315, df=30, N.S.). Comparison of success of traps positioned under canopy cover with those set in the open showed that significantly more animals were caught in the open on wet nights (t=-2.882, df=28, P<0.05) and on cloudy nights (t=-2.159, df=30, P<0.05) (Table 4.9). When weather was not accounted for, there proved to be no difference in the success of canopy - shaded and non canopy - shaded traps (see 4.1.ii.b. above).

Capture success of bank voles active during rainy days was significantly higher in traps situated under scrub - type vegetation as opposed to under vegetation not classified as scrub (t=5.145, df=20, P<0.001) though the F value was unsteady (F=7.461). The result of a Mann Whitney - U test performed on the same data proved to be significant at the 0.1% level (P<0.001). There was no such difference in success between shrub - covered and non - shrub traps (t=-0.562, df=20, N.S.).

Table 4.9. Summary of Statistical Tests Performed to Establish the Relationship Between Capture Success, Vegetative Cover, and Selected Weather Conditions.

SPECIES/SITE/ TEST	n	MEAN TRAP SUCCESS AND S.E.(BELOW)	T-TEST	TABLES VALUE	SIG.LEVEL
Woodmouse: Houghall Fm.: rain nights					
vs no rain: i)Crop	6/5	9.93% vs 7.14%% (3.0) / (2.1)	t=0.724 F=2.441	2.26 df=9	N.S.
ii)Boundary	6/5	12.50% vs 11.76% (1.9) /(3.8)	t=0.181 F=3.178	2.26 df=9	N.S.
cloud score* 0-4 vs 5-8:					
In Crop	4/8	9.53% vs 8.04% (1.7) / (2.5)	t=0.392 F=4.459	2.23 df=10	N.S.
Traps in crop vs traps in edge on rain nights	6/6	9.93% vs 12.50% (3.0) /(1.9)	t=-0.711 F=2.382	2.23 df=10	N.S.
Traps in crop vs traps in edge on cloud 5-8 nights	8/7	8.17% vs 11.69% (2.5) / (2.7)	t=-0.991 F=1.029	2.16 df=13	N.S.
Gt. High Wood**: Traps under canopy vs traps in open on rain nights	15/15	6.40% vs 5.89% (1.3) /(1.9)	t=0.224 F=2.199	2.05 df=28	N.S.
Traps under scrub vs traps in no scrub on rain nights	15/15	6.91% vs 4.90% (1.6) /(1.5)	t=0.894 F=1.175	2.05 df=28	N.S.
Traps under canopy vs trap in open on cloud 5-8 nights	16/16	6.50% vs 6.62% (1.3) / (1.9)	t=-0.051 F=2.157	2.04 df=30	N.S.
Traps under scrub vs traps in no scrub on cloud 5-8	16/16	7.40% vs 5.01% (1.8) / (1.4)	t=1.055 F=1.511	2.04 df=30	N.S.
nights			continued ov	er	

Bar	ikvole	:	
Gt.	High	Wood	:

· ·							
Traps under canopy vs trap in open on rain nights	15/15	13.07% vs 21.17% (1.7) /(2.2)	t=-2.882 F=1.649	2.05 df=28	P < 0.05		
Traps under shrub vs traps in no shrub on rain nights	15/15	12.44% vs 17.55% (1.4) /(1.9)	t=-2.142 F=1.775	2.05 df=28	P < 0.05		
Traps under scrub vs traps in no scrub on rain nights	15/15	23.51% vs 3.57% (2.1) / (0.9)	t=8.906 F=5.278	2.86 df=19	P < 0.001		
Traps under canopy vs traps in open on cloud 5-8 nights	16/16	13.50% vs 19.48% (1.7) /(2.2)	t=-2.159 F=1.734	2.04 df=30	P < 0.05		
Traps under shrub vs traps in no shrub on cloud 5-8 nights	16/16	13.33% vs 16.46% (1.4) /(1.9)	t=-1.315 F=2.068	2.04 df=30	N.S.		
Traps under scrub vs traps in no scrub on cloud 5-8 nights	16/16	23.22% vs 3.35% (2.1) / (0.9)	t=8.874 F=6.096	2.09 df=20	P < 0.05		
Bankvole : Day Captures :			*Cloud cover=0 (nil) to 8 (total). **All Grid A captures/both sessions.				
Traps under canopy vs traps in open on rain days	11/11	11.27% vs 18.16% (1.9) / (2.4)	t=-2.218 F=1.590	2.09 df=20	P < 0.05		
Traps under shrub vs traps in no shrub on rain days	11/11	15.16% vs 16.80% (2.4) / (1.7)	t=-0.562 F=2.071	2.09 df=20	N.S.		
Traps under scrub vs traps in no scrub	11/11	19.52% vs 4.26% (2.8) / (1.0)	t=5.145 F=7.461	2.09 df=20	P < 0.001		
on rain days			MWU=		P < 0.001		

Traps placed away from tree canopy cover were found to be significantly more likely to catch bank voles than those located under the canopy on rainy days (t=2.218, df=20, P<0.05).

4.3. Range Overlap.

i) Arable Land.

At Houghall Farm Fattening Pasture, pairs of male woodmice were found to share an average of 9.5% of their combined ranges, while the maximum area shared by two males was 64.7% of their combined ranges. Females were found to have a higher mean range overlap (or sympatric range) of 11.6%, with a maximum of 47.0%. The resulting difference between mean range overlaps of males and females was, however, insignificant (t=-0.353, df=29, N.S.) (Table 4.10).

The extent of sympatry between male and female overlapping ranges was 7.7% on average (maximum 49.3%). Neither the amount of intrasexual range overlap for males or females differed significantly from the extent of intersexual overlap (t=0.483, df=54 and t=0.822, df=43, both N.S.) for the mice studied.

ii) Woodland.

a) Bankvoles. Male bankvoles had a mean range overlap of 21.4% in session 1 and 11.1% in session 2 of trapping at Great High Wood. This difference was not significant (t=1.270, df=23, N.S.). Over the same period, female mean range overlap fell from 18.7% (n=1) to 3.1%. This difference could not be tested due to the single value for session 1, the same being true for a comparison of male and female sympatry in session 1. During session 2, male mean range overlap (11.1%) was found not to be significantly greater than female mean range overlap (3.1%) (t=1.294, df=19, N.S.).

Intersexual mean range overlap was significantly greater in session 1 (28.7%) than in session 2 (10.7%) at the 5% level (t=2.553, df=38, P<0.05).

Males shared no more of their range with females than with other males (t=-0.834, df=18 and t=0.061, df=43, both N.S. for sessions 1 and 2). Similarly, females in session 2 shared more of their ranges with males than with other females, but not significantly so (t=-1.762, df=35, N.S.) (see Table 4.10).

b) Woodmice and Bankvoles. Intersexual mean range overlap was significantly lower in woodmice (4.6% for both sessions combined) than in bankvoles (28.7%) during session 1 (t=-2.904, df=10, P<0.05). The difference in intersexual range sympatry between woodmice for both sessions (4.6%) and bankvoles (10.7%) during session 2 of trapping also proved insignificant (t=-1.052, df=5, N.S.).

Table 4.10. Summary of Statistical Tests Performed on Rodent Home Range Overlap Data.

HABITAT & SPECIES/TEST	n	MEAN OVERLAND (S.E.)	PRESULT	TABLES VALUE	SIGNIFICANCE LEVEL
Arable Crop: Woodmouse.					
Male & Female	21/10	9.5% /11.6% (3.4)(5.2)	t=-0.353 F=1.108	2.05 df=29	N.S.
Male & Male/Female	21/35	9.5% /7.7% (3.4)(2.1)	t=0.483 F=1.513	2.01 df=54	N.S.
Female & Male/Female	10/35	11.6%/7.7% (5.2)(2.1)	t=0.822 F=1.677	2.02 df=43	N.S.
Woodland: Bankvole.					
Male & Female Session 1 Session 2	15/10	11.1%/3.1% (5.5)(2.6)	N/A t=1.294 F=6.873	2.09 df=19	N.S.
Male Sess.1 vs Sess.2	10/15	21.4%/11.1% (5.4)(5.5)	t=1.270 F=1.570	2.07 df=23	N.S.
Female Sess.1 vs Sess.2			N/A		
Male/Fem. Sess.1 vs 2	10/30	28.7%/10.7% (6.9)(3.4)	t=2.553 F=1.347	2.02 df=38	P < 0.05
Sess.1 Male vs Male/Fem.	10/10	21.4%/28.7% (5.4)(6.9)	t=-0.834 F=1.601	2.10 df=18	N.S.
Sess 1 Fem. vs Male/Fem.			N/A		
Sess.2 Male vs Male/Fem.	15/30	11.1%/10.7 (5.5)(3.4)	t=0.061 F=1.321	2.02 df=43	N.S.
Sess.2 Fem. vs Male/Fem.	10/30	3.1%/10.7% (2.6)(3.4)	t=-1.762 F=5.203	2.03 df=35	N.S.

continued over...

Woodland: Woodmouse and Bankvole.					
Male/Fem. Mouse vs Vole Sess.1	3/10	4.6%/28.7% (4.6)(6.9)	t=-2.904 F=7.323	2.23 df=10	P < 0.05
Sess.2	3/30	4.6%/10.7% (4.6)(3.4)	t=-1.052 F=5.436	2.57 df=5	N.S.
Arable Crop vs Woodland: Woodmouse	35/3	7.7%/4.6% (2.1)(4.6)	t=0.406 F=2.483	2.03 df=36	N.S.

N/A = There was only one overlap by female ranges in session 1. Thus, no tests can be performed on this data set. iii) Arable Land and Woodland.

There was no significant difference in the amount of intersexual mean range overlap by woodmice at Fattening Pasture and Great High Wood (t=0.406, df=36, N.S.).

5.0. DISCUSSION.

5.1. Problems.

Kikkawa (1964) has stated that biological characteristics prevent random sampling of populations. Thus, for example, the age or sex of an individual of any given species might be expected to influence the location and frequency of its capture, amongst other things. However, natural biological factors are not the only parameters governing the outcome of sampling investigations into, for example, small mammal populations.

Longworth small mammal live traps, such as those used in my study, have been in use for many years as the basic tool for those seeking to understand the way in which small mammals interact with each other and with their environment. Until recently, trapping was the sole method available for the study of range size, and only with the introduction of miniaturised radio - tracking techniques have researchers been able to gain a more accurate insight into the activity of small mammals.

Because this study relied on live - trapping data, it is important that the limitations of this method (some of which are outlined in the Appendix) are borne in mind when drawing conclusions from the results obtained.

5.2. Effect of Age, Sex and Habitat on Capture Success.

There existed considerable variation in both the total numbers of recaptures, and the trapping success of woodmice at different sites within Houghall Farm Fattening Pasture, dependent on the habitat in which the traps were placed. There were, however, no significant differences between the numbers of recaptures or the capture success values of animals of each sex or age group captured in the rough vegetation of the boundary areas, or in the wheat crop itself (Tables 4.4 and 4.5). This result is in contradiction of Jefferies et al (1973) who found that the ratio of male to female *Apodemus* captured increased with distance further into a field of winter - sown wheat. The same study also found that heavy males (unlikely to be juveniles) were more likely to be captured farther onto the field surface in late autumn / winter. No such correlation was apparent at Houghall Farm during the period April to July.

The indication by Jefferies et al (1973) that animals tended to live in field edges is supported by this study which found that all but one mouse caught on the field surface was also caught at least once in the field boundary (figure 4.1). Capture success was higher in the boundary areas than in the field for all categories of woodmouse except juvenile males, though not significantly so (Table 4.5). In contrast to this result, Green (1979) found that mice caught in fields of winter wheat also nested there, while Kikkawa (1964) concluded that mice moved into crop fields during the summer where they bred before returning to the woods after the harvest.

Long term habitation of, and nesting in the field surface necessitates the presence of food therein. Roebuck et al (1944) stated that woodmice consumed the growing shoots of the crop itself although more recent studies suggest otherwise. Tertil (1977) found that *Microtus arvalis* damaged winter wheat crops, but these animals were kept in enclosures with no alternative food source. Under natural conditions, Jefferies et al (1973) concluded that *Apodemus* moved into a field to forage, and Green (1979) has stated that seeding weeds such as *Poa annua* and *Stellaria media*, in addition to arthropods, provide food for mice living solely in the crop. Sargent (pers. comm.) has reported greater numbers of woodmice near clumps of weed in cereal crops during a radio - tracking study.

The results of my study indicate that mice at Fattening Pasture made extensive use of the rough vegetation around the edges of the cereal field. Since no nests were discovered in the field itself it is inferred that the animals also nested in the boundaries. Forays onto the field by sexually active males may have been made in order to increase contact with oestrous females as has been demonstrated for *Microtus pennsylvanicus* (Madison, 1980), and by juveniles possibly in the course of dispersal. Utilisation of both the field boundary and of the field itself would have been facilitated by the narrowness of the field at the location trapped, and is illustrated by the home - range diagrams presented in figure 4.1.

In common with other studies (Jefferies et al, 1973; Pollard and Relton, 1970) and Flowerdew (pers. comm.), captures of bank voles were restricted to the field boundaries. No Clethrionomys were trapped in the field, even once the crop became dense later in the year (Table 4.6). Voles did however appear to indicate a preference for the western side of the crop field with many more Clethrionomys of both sexes being trapped in Line A than Line C. This difference was not significant, possibly due to the low numbers of voles caught at Line C. Though the vegetative composition of these two areas of headland was similar, Line A was endowed with taller vegetation and trees were present. Significantly more bank voles than woodmice were captured at Line A though it is doubtful that this resulted in the exclusion of woodmice from traps by voles as only about 25% of traps were occupied at any one time on average at Line A.

Capture success of mice was higher than for voles at Line C, though again this difference was insignificant, possibly due to the low numbers of voles detained. The capture success of mice at Line C was not significantly different to that of Line A (Table 4.6). These results give an indication of the mouse's capacity to inhabit areas with a wider variety of ground cover. For example, *Apodemus* is found on sand dunes (Attuquayefio et al, 1986) where ground cover is sparse, while *Clethrionomys* is absent from such areas (see below also).

5.3. Home Ranges and Mean Movement Indices.

i) Arable Land.

There were found to be no significant differences between the home range sizes and mean movement indices (MMIs) of male and female woodmice at Fattening Pasture (Table 4.4). Other studies have found that male mouse ranges tend to be larger than those of females, especially during the breeding season (Randolph, 1977). Attuquayefio et al (1986), Crawley (1969), and Wolton (1985) all report male home ranges to be significantly greater in size than the corresponding values for female mice. Additionally, Randolph (1977) found no significant increase on female home range size during the breeding season, while Brant (1962) suggests that female mouse ranges may decrease in size during lactation and pregnancy.

My, sample sizes at Fattening Pasture were low however, and there was considerable variation between individuals in their home ranging and movement behaviour (see Table 4.8). One explaination of such variation may be the level of dominance or subordinance of a particular animal. Brown (1969), working in coniferous / deciduous woodland found a mean range size for dominant male woodmice of 13,063 sq.metres while the corresponding figure for subordinate males was 1284 sq.m. At Fattening Pasture, "Arnie", a mouse identified as the dominant male, had a range size of 6234 sq.m. In comparison, the calculated ranges of other males varied between 2700 sq.m. and 170 sq.m. Even so, the figures obtained by this study indicate smaller ranges for wood mice at Fattening Pasture than have been observed elsewhere. Green (1979) recorded mean home range sizes of 12,151 sq.m. for males, and 6337 sq.m. for female Apodemus in arable land during summer whereas I recorded 1934 sq.m. and 1230 sq.m. respectively at Houghall Farm. This discrepancy may be attributed to the observation that mice of both sexes at Fattening Pasture utilised the boundary areas, which may be a better source of food than the insects and patchy weed plants found amongst the crops. Since granivorous rodents tend to compete directly for food (Grant, 1978), one may expect higher densities of animals to occur where food is more abundant. Similarly, since both male and female mice occupy the field edges equally, male woodmice may not find it necessary to extend their ranges over such large areas as have been found elsewhere in order to encounter females. This conclusion is in contrast to that of Green (1979) who suggested that hedges were not visited by the animals which he studied.

ii) Arable Land and Woodland.

Though small in comparison with other studies, MMIs of woodmice based at Fattening Pasture were found to be significantly greater than those of mice at Great High Wood (see Tables 4.4 and 4.8). Attuquayefio et al (1986) stated that home range size and shape relate to habitat quality and the distribution of food. Superficially therefore, this significant difference in activity (and difference approximating significance in home range sizes) between the two

study sites could be attributed to the perceived 'higher quality' of the woodland habitat. However, both Green (1979) and Wolton (1985) have reported that ranges of woodmice in arable land and woodland appear to be of a similar magnitude.

An alternative suggestion may be that population density is influencing home range size and MMI. The effect of population density is difficult to separate from that of habitat quality (Wolton and Flowerdew, 1985). It is usually thought that a high population density causes range size to contract (Mazurkiewicz, 1981), and that 'higher quality' habitats with more abundant food are able to support higher population densities (Smal and Fairley, 1982). However, Pollard and Relton (1970) concluded that more mice inhabit arable land than woodland. During this study, the population density of all animals caught at Fattening Pasture was 0.016/sq.m. composed of 177 animals (32 woodmice) in 11,000 sq.m. At Great High Wood the corresponding figure was 0.015/sq.m. during session 1 (45 animals (17 woodmice) in 3000 sq.m.), and 0.006/sq.m. in session 2 (37 animals (3) in 6075 sq.m.). Thus, the density of animals in woodland was similar to or lower than that in arable land and so density does not seem to account for the smaller home range sizes therein.

It is possible therefore that woodmice at Fattening Pasture moved shorter distances than those in other studies who lived solely in a crop, in part because they utilised the field boundary. However, movements to and from the field edges led to greater levels of activity than those of mice inhabiting the woodland. Analysis of the gut contents of both populations of mice, along with a calorific assay of the foods could in future be carried out in order to validate this hypothesis.

iii) Woodland.

There was found to be no significant difference between the mean home range sizes or MMIs of male and female bankvoles at Great High Wood in either session of trapping (Table 4.4). This is in contrast to other studies (eg. Cody, 1982; Kikkawa, 1964; Wolton and Flowerdew, 1985) which have shown that male mean home range sizes exceed those of females. Such a discrepancy is most readily explained by the low sample sizes obtained in this study. As with the woodmouse data outlined above, mean home range sizes and MMIs of bankvoles at Great High Wood were lower than those quoted by other authors. For example, Crawley (1969) gives "average range lengths" for male *Clethrionomys* in woodland of 67m as opposed to 19.4m in this study, while female average range lengths were 49m compared with 13.5m here. The same 'underestimation' of range and activity was recorded for woodmice at Great High Wood (Table 4.8), and is possibly an artifact of the survey methods and trapping problems outlined below (see Appendix).

Female mean home range sizes and MMIs slightly exceeded those of males during session 1, but this trend was reversed in session 2 of trapping as males increased their activity

and range sizes while those of females fell. Though none of these changes were significant, they may give an indication that females reduced their activity during pregnancy and lactation, as has been suggested by Brant (1962) for woodmice. Consequently, males may be forced to increase their activity as the breeding season progresses in order to encounter the remaining oestrous females.

The fact that mean home range size and MMI of *Apodemus* were found not to be significantly greater than those of *Clethrionomys* at Great High Wood is most probably a result of the low sample sizes obtained at that location, especially for woodmice.

5.4. Capture Success Between Trapping Sessions in Woodland.

It is a well documented, though not so well - understood fact that many rodent populations tend to fluctuate cyclically, these fluctuations often being based around female territoriality (Ostfeld, 1990; Stenseth, 1985). In an extensive study of Houghall Woods, Durham, which are contiguous with Great High Wood, Ashby (1967) found fluctuations in both *Apodemus* and *Clethrionomys* populations. However, whereas Clethrionomys numbers tended to vary in a 3 to 4 - yearly cycle, Apodemus fluctuated during each year with population peaks in late autumn / winter and troughs in summer. The results of my investigation indicate similar effects to those found by Ashby (1967) over the summer months. The numbers of voles caught did not fall significantly between sessions 1 and 2 of trapping while the capture success of mice fell drastically over the same period with significantly fewer captures in session 2 (Table 4.4), suggesting a fall in the population and / or a drop in activity.

5.5. Weather Conditions, Vegetation, and Capture Success.

i) Woodmice.

The occurance of rainfall seemed to have no significant impact on trapping success at Fattening Pasture in either the crop or the field boundaries (Table 4.9). Similarly, capture success of traps placed in the wheat crop was not found to be related to cloud levels. Neither rainfall nor large quantities (>50%) of cloud cover seemingly caused mice to use one area of Fattening Pasture more than another, if trap success is taken as a measure of the level of habitat utilisation by animals.

These results may indicate that the rodent's activity was unaffected by the weather conditions studied. Alternatively, both habitats (crop and boundary) may be used equally in all weathers and therefore the outcome of these tests relates merely to habitat utilisation with no climate effects. However, it has been demonstrated that weather does influence activity (King,

1985), with increased levels of mouse movement during cloudy / dark and wet nights, and reduced activity in moonlight (Wolton, 1985) and on cold / wet nights (Gurnell, 1975).

At Great High Wood, capture success was again unrelated to vegetative cover (Table 4.7) and similarly, weather conditions did not affect trap success under any category of vegetation studied (Table 4.9). Woodmice were caught equally in traps located in all types of vegetation, in common with a similar study undertaken by Southern and Lowe (1968). There were too few suitable nights available to test the effect of strong moonlight or low temperatures on mouse activity.

ii) Bankvoles.

Bankvoles were caught significantly more often in traps placed in scrub vegetation (predominantly *Rubus*), regardless of the weather conditions studied both during the day and night. This suggests that the majority of their activity occured in denser ground cover, as has been reported elsewhere (Corbet and Harris, 1991). Southern and Lowe (1968) attribute the vole's dependece on dense vegetation to its diurnal activity.

Capture success under other forms of vegetation was found to be influenced by the prevailing weather conditions. Where weather was not considered (Table 4.7), equal numbers of voles were caught in traps placed under canopy cover and in the open. In comparison, capture success of traps in the open was significantly higher than for those under the tree canopy on rainy nights and days, and on cloudy nights, indicating greater vole activity in the open during cloudy and wet conditions. Similarly, vole captures were higher away from shrub vegetation on wet nights though not on wet days or merely cloudy nights.

King (1985) has reported that the noise of rainfall and the occasion of a dark night adversly affect the hunting success of 'sit and wait' predators such as the tawny owl (*Strix aluco*) by distracting the predator and reducing visibility. Hirons (1982) noted that rodents make less noise when running across sodden ground than across dry leaf litter. It is known that nocturnal predators such as tawny owls (which were observed at Great High Wood) catch relatively more of the nocturnally - active woodmice (Southern and Lowe, 1968). However, from the results obtained by this study it may be suggested that bankvoles utilise the additional 'environmental interference' provided by rainfall and cloud cover, particularly at night, in order to forage in areas otherwise too exposed to predation risk.

Though the various effects of vegetative cover have not been treated wholly independently here, a 'hierarchy' in habitat use by voles was discernable. Scrub vegetation was of paramount importance, as is indicated by its extensive utilisation both here and elsewhere (Southern and Lowe, 1968). Vegetation types will vary in importance, dependent on the time of day and current weather conditions, in addition to the seasonal changes in the quality of cover provided, as has been noted previously (Evans, 1942).

5.6. Range Overlaps.

Wolton (1985), using radio - tracking techniques, has reported that the home ranges of male woodmice overlap extensively, while female ranges are largely exclusive. Male ranges were found to overlap 5 - 10 female ranges. In contrast, trapping studies carried out by Kikkawa (1964) revealed random intra and intersexual range overlap in mice, while Crawley (1969) notes considerable overlap, again seemingly at random. The results of my investigation indicate a similar randomness of overlap in woodmice of both sexes at Fattening Pasture (Table 4.10). This may be a 'true' result or it may be an artifact of the data - collection methods used. At present, such variability in the outcome of overlap studies means that conclusions are difficult to reach regarding the extent and importance of range overlap. Since spacing behaviour is of importance in the study of population dynamics and social interaction in small mammals (Bujalska, 1991), it is necessary that a reliable measure of range overlap is established. At present, it seems as though this role will be taken by the use of radio - tracking studies, which appear to provide a more accurate account of small mammal activity than past methods.

At Great High Wood, intrasexual range overlap was higher in session 1 than in session 2 of trapping for both sexes of bankvole. However, this difference was not significant for males and could not be tested for females. In comparison, Cody (1982) has reported male vole range overlap as being consistantly great, while the extent of female sympatry fell during the summer. This latter result may have been due to females becoming more territorial in order to protect and provide food for their young, as territorial behaviour is known to relax in *Clethrionomys* under conditions of abundant food. An alternative hypothesis is that defence of a territory may reduce infanticide by rival voles, thought primarily to be adult females (Ostfeld, 1990). This theory does not therefore explain why the extent of *inters*exual sympatry fell significantly as the breeding season progressed at Great High Wood (Table 4.10). However, this apparent fall in the extent of range overlap of males and females may not necessarily be due to increased female territoriality. Smaller average range sizes of females in session 2 of trapping may have aided reduced sympatry, as may the smaller MMIs of females in session 2, although in neither of these measures did the values fall significantly from one session to the next.

Intersexual range overlap was greater for bankvoles than for woodmice at Great High Wood in session 1, but not in session 2, reflecting the reduction in bankvole intersexual sympatry later in the year. The fact that intersexual overlap is greater in voles than in mice may most readily be attributed to the different ways in which the two species utilise the habitat. Since the vast majority of vole activity is thought to occur within the areas of denser ground cover (classified as "scrub" above), one would expect a higher incedence of range overlap than in woodmice who utilise all areas of the woodland habitat almost equally (see above and Southern and Lowe, 1968). However, if it were the case that significant vole intersexual range overlap occured merely as an artefact of the concentration of animals in the scrub, rather than due to

active mate - seeking, one could assume that intrasexual sympatry may also be significant, again due solely to high densities of animals. This is not the case, so it may be suggested that either active mate - seeking resulted in significant intersexual range overlap, and / or that active intrasexual avoidance occured in the voles studied.

The use of range overlap as a means of controlling access to oestrous females has not yet been demonstrated for woodmice or bankvoles (Wolton and Flowerdew, 1985). Even so, high intersexual sympatry at the height of the breeding season during session 1 of trapping (16/4 to 10/5) would allow higher numbers of sexual encounters between males and females at this time than would occur later in the year. This later decrease in intersexual range overlap would force the males to increase their home range and MMIs in response to the reduction in the numbers of oestrous females.

Intersexual range overlap of woodmice at Fattening Pasture was higher than in the Great High Wood population, though not significantly so. This outcome may have been expected, due to the fact that most of the animals studied at Fattening Pasture tended to use the field boundary regularly. Although they also utilised the field surface to a similar extent, range overlap would occur where the mice entered and left the rough vegetation. In contrast, the mice in Great High Wood were found to use all areas of the habitat in a uniform manner, not moving regularly to any one particular site. There is no intrinsic reason why intersexual range overlap should differ between the two populations, the difference therefore possibly being due to patterns of habitat utilisation rather than greater mate - seeking activity by mice occupying farmland.

APPENDIX.

The disadvantages of using trapping techniques in investigations of small mammal populations relate primarily to experimental design and to the behaviour of the animals themselves.

Within the first category, Kikkawa (1964) has outlined some of the factors which can influence results due solely to the methods used during investigations, rather than to biological processes. The spacing of traps is of major importance in that wide spacing may mean that animals do not encounter traps regularly, while small distances between traps may cause underestimation of the range size. The same may be said for the size of the area trapped. If the area is too small, portions of an animal's range may be excluded, while edge effects may occur where animals are captured around the edge of the grid though their ranges occur mostly outside of it. If the trapping programme is carried out for an insufficient period of time, or the number of (re)captures of individuals is low, then the range may again be underestimated, though the minimum time period and number of captures needed varies between species.

Biological parameters which influence trappability are many. Trap shyness or addiction (Gipps, 1985), possibly caused by previous capture experiences, may distort home range sizes in that animals may avoid traps or be attracted to them (especially in order to obtain the bait food therein). "Social factors" (Kikkawa, 1964) such as species, sex and age group affect levels of movement and activity and so the assumption of equal trappability is often not valid.

Contamination of traps by the previous occupant by means of odour left by faeces and urine may attract other individuals (Montgomery, 1979). Alternatively, odour may serve to inhibit entry into traps, especially if the previous occupant was a dominant animal. Individual behaviour and the effect of weather conditions may have an impact on trap success.

These problems, amongst others, have led some authors to suggest that many errors are apparent in estimates of home ranges of animals. Kikkawa (1964) for example has stated that trap - revealed ranges approximate the truth for bank voles but not wood mice. Gipps (1985) meanwhile suggests the simultaneous use of more than one method of trapping in an attempt to overcome these problems.

Most of the mark - recapture techniques used to estimate, amongst other things, population densities and home range sizes, wrongly assume equal trappability. The increasing use of radio - tracking serves to overcome many of the problems encountered in the use of trap-based studies.

Practical problems encountered during the period of fieldwork were relatively few. They included the need to place some traps a short distance away from the location dictated by the grid in woodland due to the topography of the site and the requirement that they be hidden.

Difficulties in the handling and marking of animals were best overcome by practice and the use of a trial period. The "polythene bag" method is advised for those who have little experience in working with small mammals.

The theft of a complete line of traps from the arable field site did not delay the project, but only because spare traps were on hand and those stolen were insured.

BIBLIOGRAPHY AND REFERENCES.

- Corbet, G.B. & Harris, S. (Eds) (1991). The handbook of British mammals. (3rd Edition). Blackwell, Oxford.
- Flowerdew, J.R., Gurnell, J. & Gipps, J.H.W. (Eds.) (1985). The ecology of woodland rodents: Bank voles and wood mice. *Symp. Zool. Soc.*, *Lond.* No.55. Oxford University Press, Oxford.
- Gurnell, J. & Flowerdew, J.R. (1990). Live trapping small mammals-a practical guide. *Mamm. Soc. Occ. Publ.* No.3. Mammal Society, London.
- Ashby, K.R. (1967). Studies on the ecology of field mice and voles (*Apodemus sylvaticus*, *Clethrionomys glareolus* and *Microtus agrestis*) in Houghall Wood, Durham. *J. Zool.*, *Lond.* 152: 389-513.
- Attuquayefio, D.K. & Gorman, M.L. (1986).in The ecology of woodland rodents: Bank voles and wood mice. (1985).
 (Floweredew, J.R., Gurnell, J. & Gipps, J.H.W., eds.).
 Oxford University Press, Oxford.
- Attuquayefio, D.K., Gorman, M.L. & Wolton, R.J. (1986). Home range sizes in the wood mouse *Apodemus sylvaticus*: habitat, sex and seasonal differences. *J. Zool.*, *Lond*. 210: 45-53.
- Bowers, M.A. & Brown, J.H. (1982). Body size and coexistance in desert rodents: chance or community structure?. *Ecology* 63: 391-400.
- Brant, D.H. (1962). Measure of the movements and population densities of small rodents. *Univ. Calif. Publ. Zool.* 62: 105-184.
- Brown, L.E. (1969). Field experiments on the movements of *Apodemus sylvaticus* L. using trapping and tracking techniques. *Oecologia* 2: 198-222.
- Bujalska,G. (1991). The ecology of territoriality in bank voles. *Trends in Ecology and Evolution*. Vol 6 (9): 300-301.
- Burt, W.H. (1943). Territoriality and home range concepts as applied to mammals. *J. Mammal.* 24:346-352.
- Campbell, I. (1974). The bioenergetics of small mammals, particularly *Apodemus sylvaticus* (L.) in Wytham Woods, Oxfordshire. PhD Thesis, University of Oxford.

- Charnov, E.L. & Finerty, J. (1980). Vole population cyclesa case for kin selection?. *Oecologia* 45: 1-2.
- Chitty, D. (1960). Population processes in the vole and their relevance to general theory. Canadian Journal of Zoology 38: 99-113.
- Cody, C.B.J. (1982). Studies on behavioural and territorial factors relating to the dynamics of woodland rodent populations. D.Phil. thesis. Univ. of Oxford.
- Crawley, M.C. (1965). Studies on the movements, population dynamics and food of *Apodemus sylvaticus* (L.) and *Clethrionomys glareolus* (Schr). Thesis, Fac. Sci., Univ. Durham.
- Crawley, M.C. (1969). Movements and home-ranges of Clethrionomys glareolus Schreber and Apodemus sylvaticus L. in north-east England. Oikos 20: 310-319.
- Dalke, P.D. (1942). The cottontail rabbits in Connecticut. Bull. Conn. State Geol. Nat. Hist. Surv. No.65: 1-97.
- Evans, F.C. (1942). Studies of a small mammal population in Bagley Wood, Berkshire. J. Anim. Ecol. 11: 182-197.
- Gaines, M.S. & McClenaghan, L.R. (1980). Dispersal in small mammals. *Annual Review of Ecology and Systematics* 11: 163-196.
- Gipps, J.H.W: (1985). in The ecology of woodland rodents:

 Bank voles and wood mice. (Flowerdew, J.R., Gurnell, J. & Gipps, J.H.W., eds.). Oxford University Press, Oxford.
- Grant, P.R. (1978). in Populations of small mammals under natural conditions. (D.P. Snyder, ed.). *Special Public. Series*, Vol.5. Pymatuning Lab. of Ecology, Univ. of Pittsburgh.
- Green, R. (1979). The ecology of wood mice (*Apodemus sylvaticus*) on arable farmland. J. Zool., Lond. 188: 357-377.
- Gurnell, J. (1975). Notes on the activity of wild woodmice, *Apodemus sylvaticus* in artificial enclosures. *J. Zool.*, *Lond.* 175: 219-229.
- Healing, T.D. & Nowell, F. (1985). in The ecology of woodland rodents: Bank voles and wood mice. (Flowerdew, J.R., Gurnell, J. & Gipps, J.H.W., eds.). Oxford University Press, Oxford.
- Hirons, G.J.M. (1982). The effects of fluctuations in rodent numbers on breeding success in the tawny owl *Strix* aluco, Mamm. Rev. 12: 155-157.

- Jefferies, D.J., Stainsby, B. & French, M.C. (1973). The ecology of small mammals in arable fields drilled with winter wheat and the increase in their dieldrin and mercury residues. J. Zool., Lond. 171: 513-539.
- Kikkawa, J. (1964). Movement, activity and distribution of small rodents *Clethrionomys glareolus* and *Apodemus sylvaticus* in woodland. *J. Anim. Ecol.* 33: 259-299.
- King, C.M. (1985). in The ecology of woodland rodents: Bank voles and wood mice. (Flowerdew, J.R., Gurnell, J. & Gipps, J.H.W., eds.). Oxford University Press, Oxford.
- Krebs, C.J., Gaines, M.S., Keller, B.L., Myers, J.M. & Tamarin, R.H. (1973). Population cycles in small rodents. *Science.*, N.Y. 179: 35-41.
- Macdonald,D.W., Ball,F.G. & Hough,N.B. (1980). The evaluation of home range size and configuration using radio tracking data.in A handbook on biotelemetry and radio tracking: Amlaner,C.J. & Macdonald,D.W. (eds.): 405-424. Permagon Press, Oxford.
- Madison, D.M. (1980). Space use and social structure in meadow voles, *Microtus pennsylvanicus*. *Behav*. *Ecol*. *Sociobiol*. 7: 65-71.
- Mazurkiewicz, M. (1981). Spatial organisation of a bank vole population in years of small or large numbers. *Acta theriol*. 26: 31-45.
- Montgomery, W.I. (1979). An examination of interspecific, sexual and individual biases affecting rodent captures in Longworth traps. *Acta theriol*. 24: 35-45.
- Montgomery, W.I., Wilson, W.L., Hamilton, R. & McCartney, P. (1991). Dispersion in the wood mouse, *Apodemus sylvaticus*: variable resources in time and space. *J. Anim. Ecol.* 60: 179-192.
- Ostfeld,R.S. (1990). The ecology of territoriality in small mammals. *Trends in Ecology and Evolution*. Vol.5 (12): 411-415.
- Pollard, E. & Relton, J. (1970). Hedges V. A study of small mammals in hedges and cultivated fields. J. appl. Ecol. 7:549-557.
- Randolph, S.E. (1977). Changing spatial relationships in a population of *Apodemus sylvaticus* with the onset of breeding. *J. Anim. Ecol.* 46: 653-676.

- Roebuck, A., Baker, F.T. & White, J.H. (1944). The grazing of winter cereals by the wood mouse (*Apodemus sylvaticus*). J. Anim. Ecol. 13: 105-109.
- Smal, C.M. & Fairley, J.S. (1980). Food of wood mice (Apodemus sylvaticus) and bank voles (Clethrionomys glareolus) in oak and yew woods at Killarney, Ireland. J. Zool., Lond. 191: 413-418.
- Southern, H.N. & Lowe, V.P.W. (1968). The pattern of distribution of prey and predation in tawny owl territories. *J. Anim. Ecol.* 37:75-97.
- Stenseth, N.C. (1985). in The ecology of woodland rodents: Bank voles and wood mice. (Flowerdew, J.R., Gurnell, J. & Gipps, J.H.W., eds.). Oxford University Press, Oxford.
- Tansley, A.G. (1939). J. Ecol. 27: 513-530.
- Tertil, R. (1977). Impact of the common vole, *Microtus* arvalis (Pallas) on winter wheat and alfalfa crops. *EPPO Bull.* 7 (2): 317-339.
- Voigt, D.R. & Tinline, R.R. (1980). in A handbook on biotelemetry and radio-tracking. (Amlaner, C.J. & Macdonald, D.W., eds.). Permagon Press, Oxford.
- Watts, C.H.S. (1970). Long distance movement of bank voles and wood mice. J. Zool., Lond. 161: 247-256.
- Wolton, R.J. (1983). The activity of free-ranging woodmice, *Apodemus sylvaticus*. J. Anim. Ecol. 52:781-94
- Wolton, R.J. (1985). The ranging and nesting behaviour of wood mice, *Apodemus sylvaticus* (Rodentia: *Muridae*), as revealed by radio-tracking. *J. Zool.*, *Lond.* 206: 203-224.

