Habitat selection by wood mice apodemus sylvaticus (L.) and bank voles clethrionomys glareolus (schr.), and their abundance and distribution in four gorge woodlands in county Durham

Sinclair, Anne Catherine

Habitat Selection by Wood Mice *Apodemus sylvaticus* (L.) and Bank Voles *Clethrionomys glareolus* (Schr.), and their Abundance and Distribution in Four Gorge Woodlands in County Durham

by
Anne Catherine Sinclair

A dissertation submitted in part fulfilment of the requirements for the degree of Master of Science in Advanced Ecology.

Department of Biological Sciences,
University of Durham, 1994

ACKNOWLEDGEMENTS

I would like to thank my supervisor Dr Phil Hulme for all his help and advice throughout the project, Gill Thompson, who made data collection in the field so much easier and more enjoyable, and to Dr Chris Thomas for discussions about multivariate analysis.

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

CONTENTS

SUMMARY

1.) This study was carried out to investigate the abundance, distribution and habitat selection of wood mice and bank voles in four woodlands in the coastal denes and limestone gorges of County Durham.

2.) Field work was carried out between April 25th and June 18th at Horsleyhope Ravine, Greta Gorge, Hawthorn Dene and Castle Eden Dene. Each site was visited twice, the second visit taking place four weeks after the first.

3.) Small mammals were trapped for four nights in the first session and three nights in the second session. Twenty-two habitat variables were recorded at each trap point in each site in session one, repeat measurements of eight variables were taken in session two to account for any seasonal changes. Point quadrat vegetation structure measurements were recorded at each trap point in each site in session two.

4.) Both species of rodents had very variable distributions and abundances both within (between sides) and between study sites. Bank voles tended to be captured significantly more on the lower slopes of a site, while wood mice were captured significantly more on the middle and upper slopes of a site. Both species were significantly differently distributed within a side of a site with respect to slope, although chi-square showed only one significant negative association.

5.) Significant trap site fidelity was shown by both species of rodent at each site, although there was some change in use of traps between sessions. There were significant changes in vegetational cover between sessions at all sites.

6.) Both wood mice and bank voles generally tended to avoid short dead and live vegetation and show positive associations with medium and tall, dead and live vegetation. No single habitat variable or group of variables could successfully explain bank vole and wood mouse distribution using univariate statistics. Discriminant analysis suggested that bank voles were found in areas of dense medium to tall herbaceous vegetation, while wood mice were found in areas with an open ground layer and cover from woody vegetation.

7.) Certain plant species present in the study sites fitted the structural requirements of bank voles and wood mice, and corresponded well with the discriminant analysis results and the actual distributions of the two species. It is suggested that small mammal community structure within a site is dependent on the habitat structure and species composition of that site.

INTRODUCTION

1.1 Habitat selection

The evolution of habitat preferences has been determined by and determines the morphological structure and behavioural functions of an organism, and affects its ability to obtain food and shelter successfully in the habitat. Factors causing habitat selection could be structural features of the landscape, food abundance and foraging opportunities, breeding site prevalence, or the presence of other species as competitors or predators. The choice of suitable habitat affects the potential for survival and reproduction, and therefore it must be a product of many generations of natural selection, such that natural selection favours those individuals who will select and exploit the habitat patch or combination of patches where the difference between costs and benefits is maximised (Partridge 1978). Those factors that are important as cues in the process of habitat selection are not necessarily important to individuals of a species at all time, nesting sites for instance are not a priority out of the breeding season. Likewise these factors can vary in space and time themselves, and their variations can be in different directions and on different scales. This causes actual habitat selection by individuals to be dynamic, with continual adjustment being made as the habitat changes. The combined effect of dynamic habitat selection by individuals of a species in several areas or at several times can therefore often lead to a variable picture of that species' optimal habitat.

Habitat selection is thought to be important in structuring populations and communities. MacArthur (1958) first noted this during his study of five species of warbler in relatively homogeneous conifer forests, which were able to coexist due to their using different feeding habitats, allowing partitioning of resources. A study of rodents in second growth mesic forest in eastern Tennessee by Dueser and Shugart (1978) concentrated on variables of habitat structure and composition to ascertain each species' particular microhabitat configuration and therefore the structure of the rodent community in that forest. Theories of how habitat selection allows coexistence in a community have been based around the effects of interspecific and intraspecific competition.

Interspecific competition is explained by Gause's theory (1934), more recently termed 'competitive exclusion', which states that when closely related species occur together in one habitat they are ecologically separated, otherwise the better adapted species for that habitat replaces the less well adapted species. A good example of this is seen in the coexistence of five or six species of *Parus* (Tit) in many areas of deciduous woodland in southern Britain and western Europe (Perrins, 1978). Competition between them restricts each species to a certain foraging microhabitat, much like the warblers of MacArthur (1958), in that blue tits (*Parus caeruleus*), for instance, search for food on twigs and buds, while great tits (*P. major*) search for food on the ground and on thick branches (Gibb 1954). Montgomery (1980) carried out various studies at Woodchester Park, Gloucestershire, which have shown that interspecific competition from yellow-necked mice (*Apodemus flavicollis* Melc.) can effect the habitat selection of wood mice (*A. sylvaticus* L.). He studied the interactions between sympatric populations of wood mice and yellow-necked mice, and found that wood mice occurred more frequently in areas with sparse high canopy and dense ground cover, while yellow-necked mice avoided dense ground cover, preferring a dense low canopy. Schroder and Rosenzweig (1975,) through their work on North American desert rodent communities, suggested that species actually avoid interspecific competition through habitat selection, and that the pressure of natural selection should eliminate interspecific competition entirely. Interspecific competition however, is always a threat in any community, and its continual presence maintains each species' habitat specialisations. Other interspecific effects to be considered are those between the habitat selector and its predators or parasites, since these can also determine which habitat is finally selected.

Intraspecific competition or density-dependent population pressure can affect the inherent value of a habitat (Svärdson 1949; Fretwell 1972; Grant 1975) when the reproductive success and survivorship of a species declines with an increase in density, due to increasing competition for limited resources. Fretwell (1972) proposed two models to explain habitat selection in terms of density-dependence. One was the 'ideal-free' distribution whereby a species will occupy an expanding number of habitats of decreasing suitability as the population density increases, with the average fitness across all the occupied habitats remaining equal. The second theory was the 'ideal-despotic' distribution whereby aggressive behaviour amongst conspecifics becomes greater at higher densities or in more favourable habitats. Socially dominant individuals occupy the highest quality habitat preventing further density-dependent resource depletion through territoriality while forcing subordinate individuals into lower quality habitats where they have a lower fitness than in the good quality habitats. Several studies have been carried out to test these models (Krebs 1971; Whitham 1978), and a recent study by Halama and Dueser (1994) on the white-footed mouse (*Peromyscus leucopus*), which is commonly regarded as an 'ecological equivalent' of *Apodemus* spp. in the Nearctic (Montgomery, 1989), suggested that the ideal-despotic distribution model was exhibited in this species, with fitness being highest in woodland and meadow areas and lowest in pasture.

In summary, habitat selection through partitioning of microhabitat space within a habitat allows for the coexistence of ecologically similar species, and has occurred through many generations of natural selection, with inter- and intraspecific competition playing important roles in its development and maintenance. Habitat selection in individuals can vary spatio-temporally depending on the species' life strategy, and on the variation in the habitats themselves in space and time. The scale at which habitat selection is investigated can also lead to different interpretations of the habitat or microhabitat requirements of a species, large scale studies can give generalised impressions of what variables are selected for by individuals of a species, while small scale studies can elucidate the site specific or time specific variables that are important in habitat selection. Ultimately, the fact that habitat selection is dynamic, and that habitats are also dynamic and geographically changeable, will make any characterisation of a species' optimal habitat open to variation.

1.2 Ecology of wood mice and bank voles

The wood mouse is one of the two *Apodemus* species found in Britain, the other being the larger yellow-necked mouse. It is distributed over the whole of Britain and Ireland in a wide variety of habitats, except exposed mountainous regions. They are generally nocturnal, with peaks of activity at dawn and dusk in winter, changing to a single peak in summer (Miller, 1955),and are most active on dark nights. They feed mainly on seeds, fruits, nuts and arthropods, the first three food items being taken most often in the autumn and winter, and arthropods forming a larger part of the diet in spring and early summer (Watts, 1968).

The bank vole (*Clethrionomys glareolus* Schr.) is the only species of this genus to occur in Britain and Ireland, there are two other species in northern Europe and several others in North America. It is distributed throughout mainland Britain and on the islands of Handa, Raasay, Mull, Bute, Anglesey, Ramsey, Skomer, Isle of Wight and Jersey, and in south west Ireland. They are active throughout the 24 hour cycle, with noticeably more diurnal activity in the presence of *Apodemus* spp. (Brown, 1956). Their diet is mainly herbivorous, consisting of roots and leaves, fleshy fruits and seeds with soft testas.

The breeding season for both species lasts from March-April through to October, and in both cases, females maintain exclusive home ranges, while males have larger home ranges that overlap and can encompass several female home ranges (Wolton and Flowerdew, 1985). Data from nine years of intensive study in an oak wood in southern England (Gurnell, 1981, 1985) showed that the numbers of wood mice and bank voles were positively associated. Both species have overwintering populations of young born late in the previous year and a few parous adults, these populations experience a decline in numbers during the late winter and spring, but with the onset of breeding, population size increases to a peak in September or October and consists mainly of animals born that year.

1.3 Habitat selection by wood mice and bank voles

The wood mouse is a habitat generalist and opportunist, its preferred habitat being very varied, ranging from deciduous and coniferous woodland, to heathland (Lance, 1973), arable land (Green, 1979) and sand-dunes (Gorman and Zubaid, 1993).

The bank vole, however, is more specific in its habitat requirements, showing a definite preference for thick cover (Gurnell, 1985; Fernandez 1993; Southern and Lowe, 1968) and occupying deciduous and coniferous woodland, scrub, banks and hedges, and are not infrequent on open ground with a high herb layer or cover from banks and walls. Local distributions have been seen to change with seasonal alteration in ground cover (Kikkawa, 1964).

Habitat selection studies of British rodents have tended to concentrate on rather broad habitat categories. Some studies have shown that the wood mouse often has no preference for dense cover in woodland as opposed to the bank vole (e.g. Southern and Lowe, 1968), while others have shown that it does, for instance Corke (1971) showed it to have a preference for habitats with *Pteridium aquilinum* (bracken) and *Rubus fruticosus* L. (bramble) as opposed to deciduous trees with shrubs. However, further work showed that when bank voles are present in high densities, wood mice then avoid *P. aquilinum* and *R. fruticosus* (Corke, 1974). The work of Montgomery (1980) on interspecific competition between wood mice and yellow-necked mice suggested that wood mice occurred more frequently in dense ground cover. Other studies in Ireland where the bank vole is absent indicate that wood mice prefer areas with good ground cover (Fairley, 1967), and in Sweden where wood mice are subjected to more competition from yellow-necked mice they also prefer ground cover (Hoffmeyer, 1973). However, when yellow-necked mice are absent, and wood mice are found living with bank voles, it is the latter which is restricted to dense ground cover while the wood mouse is distributed randomly with respect to vegetation and cover (Evans, 1942; Kikkawa, 1964, Southern and Lowe, 1968).

1.4 Aims

Since few detailed studies of microhabitat selection on British woodland rodents have been carried out, this project aims to study the abundance, distribution and microhabitat preferences of wood mice and bank voles, in detail, using fine scale habitat parameters. This will enable quantification of the specific factors of habitat structure that are selected for by these two species, enabling the prediction of the distributions of wood mice and bank voles in a woodland once the habitat structure is known.

The main questions being asked in this project are:

1) What are the abundances and distributions of wood mice and bank voles at each study site? Is there variation in abundance and distribution within sites and/or between sites? Is there any variation with respect to seasonal changes?

2) What features of the habitat and its structure are selected for or against by wood mice and bank voles? Do these features changes with respect to seasonal changes? Are these features the same across the different sites? Do wood mice and bank voles use microhabitats in similar ways?

3) Can the patterns described in 1) be interpreted using the information gathered on microhabitat utilisation in 2)?

MATERIALS AND METHODS

2.1 Site descriptions

This study was undertaken in four natural *Taxus baccata* L. (yew) woodlands (all Sites of Special Scientific Interest) in County Durham (Figure 1): two coastal denes, Castle Eden Dene and Hawthorn Dene and two inland gorges, Greta Gorge and Horsleyhope Ravine. A survey and description of these woodlands in terms of past and present patterns of regeneration have already been carried out by Hulme (1994).

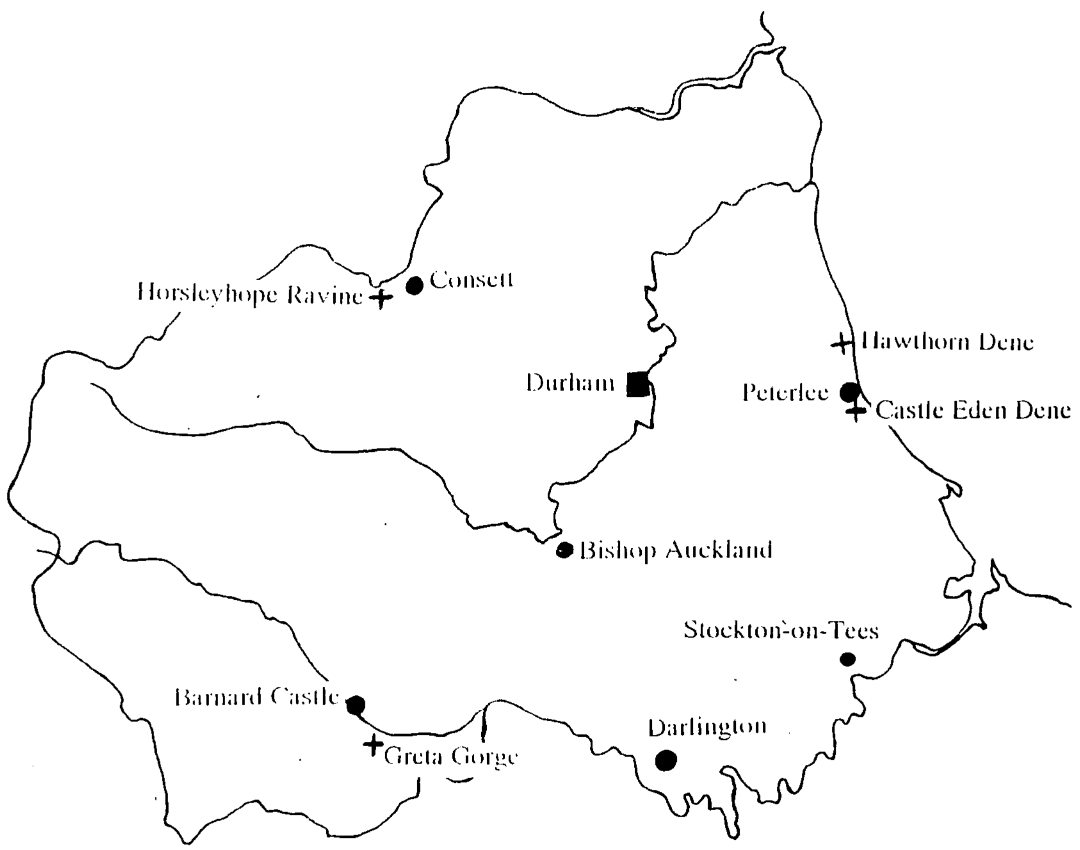


Figure 1. Map of Vice-county Durham to show the locations of the four study sites.

Castle Eden Dene (NZ434396) is the largest and biologically the richest of a series of steep sided wooded denes, formed as ravines in the Magnesium Limestone and boulder clay of the Durham coast. It also has the highest density of *Taxus baccata* of the four study sites. The specific area of study was the east and west slopes of the North Blunts Dene, this being a more comparable size to the other study sites. The site comprised areas of dense *Taxus baccata* woodland, interspersed with a canopy of *Quercus robur* L. (pedunculate oak) and *Betula pubescens* Ehrh. (birch) on the boulder clay soils of the upper slopes. Areas of boulder clay landslip also occur in the study area which have been colonised by a wide range of herbaceous ruderal and wetland plants, and also *Salix* sp. L. (willow) in the later stages of succession.

Greta Gorge (NZ063113) is the most eastern part of the Brignall Banks SSSI, which forms one of the largest expanses of semi-natural woodland in North East England. Sandstone, shale and more locally limestone is exposed in a series of crags, cliffs and boulder screes. The study area was situated on the east and west-facing slopes of Greta Gorge, with the east slope consisting of mainly *Acer pseudoplatanus* L. (sycamore) woodland with a *Hyacinthoides non-scripta* L. (bluebell) ground flora on the upper slopes, and an area of conifer plantation on the valley bottom, with a strip of deciduous woodland and areas of *Mercurialis perennis* L. (dog's mercury) and *Urtica dioica* L. (stinging nettle) along the streams' edge. The west-facing slope comprised areas of *Fagus sylvatica* L. (beech), *Quercus petraea* Matt. (sessile oak) and *Taxus baccata* woodland with *Luzula sylvatica* Hudson. (great wood-rush) and grasses as the dominant ground flora.

Hawthorn Dene (NZ435458) is second only to Castle Eden Dene in the extent and diversity of undisturbed semi-natural woodland that it supports on the Magnesium Limestone of County Durham. The study area was situated on north and south-facing slopes, with areas of *Crataegus monogyna* Jacq. (hawthorn) scrub on the upper slopes, and areas of *Fagus sylvatica*, *Acer pseudoplatanus* and *Taxus baccata* woodland with a ground flora dominated by *Allium ursinum* L. (wild garlic) and *Mercurialis perennis*, or *Anemone nemorosa* L. (wood anemone) and *Hyacinthoides non-scripta*, on the middle and lower slopes.

Horsleyhope Ravine (NZ063483) forms part of the Derwent Gorge SSSI which comprises an extensive area of woodland on sheltered slopes. The study site was situated on north and south-facing slopes of the ravine. Conifer plantation dominated the upper and middle parts of the north-facing slope, with *Salix* sp. and *Alnus glutinosa* L. (alder) on the lower slopes and *Allium ursinum* dominating the ground flora. The upper slopes of the south-facing side consisted of ancient *Quercus petraea* woodland with a ground flora of *Vaccinium myrtillus* L. (bilberry), *Calluna vulgaris* L. (heather) and *Deschampsia cespitosa* L. (tufted hair-grass). The middle and lower slopes were dominated by *Fraxinus excelsior* L. (ash) and *Acer pseudoplatanus* and a more sparse ground flora of *Luzula sylvatica* and *Mercurialis perennis*. *Taxus baccata* was very scarce at this site with only three individuals present within the study area.

2.2 Methodology

At each site, the area of study comprised two opposite facing slopes which were divided into upper, middle and lower zones. A linear transect was run along each zone which comprised ten sample points spaced at approximately 10m intervals, such that there were 60 sample points at each site. Small mammal trapping and vegetation surveys were carried out at each site once every four weeks from April 25th to June 18th so that two sessions were carried out at each site.

One Longworth live trap was placed at each point, with trapping periods lasting four days in the first session and three days in the second. Rodents caught were identified, aged, sexed, breeding condition noted, weighed and individually marked by fur clipping before being released near their point of capture. Marking the rodents allowed an assessment of habitat use by individuals that were subsequently recaptured.

At each trap point the following environmental variables were measured during the first session:

a) Trap position, for example, base of tree or next to fallen log.

b) Slope of the sampling point.

c) Percentage canopy cover within radius of 2m - vertical cover provided by woody vegetation over 7m in height.

d) Percentage shrub/understorey cover within radius of 2m - vertical cover provided by all woody vegetation under 7m in height.

e) Percentage herb cover within radius of 2m - vertical cover given by herbaceous, non-woody vegetation.

f) Percentage moss cover within radius of 2m - ground cover given by mosses or bryophytes.

g) Percentage litter cover within radius of 2m - ground cover given by leaf litter.

h) Percentage brash cover within radius of 2m - vertical cover given by twigs and small branches less than 2cm diameter.

i) Percentage soil cover within radius of 2m - proportion of bare soil exposed.

j) Percentage rock cover within radius of 2m - proportion of bare rock exposed.

k) Percentage fallen log/branch cover within radius of 2m - ground cover given by logs/branches greater than 2cm in diameter.

l) Percentage of herbs between 0-10cm in height, within radius of 2m.

m) Percentage of herbs between 10-20cm in height, within radius of 2m.

n) Percentage of herbs between 20-30cm in height, within radius of 2m.

o) Percentage of herbs between 30-40cm in height, within radius of 2m.

p) Percentage of herbs over 40cm in height, within radius of 2m.

q) Number of tree stumps within radius of 2m.

r) Number of trees within radius of 5m - individuals with greater than 10cm diameter at breast height (DBH) and over 7m. Thus some species considered as shrub or understorey species which had been able to grow uninhibited were included in this variable.

s) Number of saplings within radius of 5m - individuals with a DBH less than 10cm, but which were greater than 1.5m in height.

t) Number of shrubs within radius of 5m - shrub/understorey species under 7m in height. One bramble plant was taken as having a diameter of 1m.

u) Nearest tree species.

v) Dominant herb species within radius of 2m.

During the second session, variables c), d), e), l), m), n), o) and p) were measured again to account for any changes in vegetation cover due to spring growth.

During the second session, ten point quadrats were also taken at each sampling point, within a radius of 2m, so as to gain an estimate of vegetation structure. The point quadrat was randomly placed vertical to the direction of growth of the vegetation, which was categorised into dead or living plant material, and the heights of all touches for both categories were recorded.

2.3 Analysis

Rodent abundance and distribution within sites was examined using two-way analysis of variance (anova). Capture data, which consisted of counts was transformed to a normal distribution using the $\log_{10}(x+1)$ transformation. Three two-way anovas were carried out, the independent variables in each case were:

a) Side of study site captured on (north, south, east or west-facing) versus position captured on the slopes (upper, middle or lower) for each species of rodent at each site and for each session.

b) Time period (either session one or two) versus position captured on the slopes, for each species of rodent on each facing slope of eadh site.

c) Species (wood mice or bank voles) versus position captured on the slopes. for each facing slope of each site, in both time periods.

To investigate whether there was any association between bank voles and wood mice at each site and for each session, chi-square analysis, with Yate's correction for one degree of freedom, on two-way contingency tables of the numbers of traps catching mice only; voles only; both; or neither was carried out.

The Pearson product moment correlation was applied to $\log_{10}(x+1)$ transformed data of the counts of mice and voles at each trap site for each session to assess the trap site fidelity of the rodents between trapping sessions.

When the seasonal change in vegetation cover between the first and second trapping session was tested, a paired t-test was used on percentage cover data that had been transformed to normal using the arcsine transformation. This is because when data sample sizes greatly exceed 40, in this case they numbered 60, parametric tests are more appropriate than nonparametric tests.

Vegetation structure associations of mice and voles were examined using chi-square analysis of contingency tables on the dead and live vegetation structure data, obtained from the point quadrats taken in session two, between traps catching mice compared to those catching no mice; between traps catching voles and those catching no voles; and between those traps catching mice and those catching voles.

Further analysis to assess habitat selection by rodents was carried out using the Mann-Whitney U-test on habitat variables c) to t), to determine which of these distinguished between the microhabitats of mice and voles when the capture sites of each species were tested against those sites where they were not captured, and when the capture sites of each species were tested against each other. This nonparametric test was used instead of a parametric test because habitat variable data tends to deviate from a normal distribution, and because the sample sizes in many cases were less than 20.

Discriminant function analysis was used as a multivariate technique which would provide a better means of characterising and quantifying the differences in habitat selection between mice and voles, if it were the case that no single variable or group of variables could be found to explain the phenomenon successfully. The aim of discriminant function analysis is to find linear combinations of the variables (discriminant functions) that separate the sample groups, in this case: a) traps catching no rodents; b) traps catching only voles; c) traps catching only mice; d) traps catching both mice and voles. The correlation of each variable with the discriminant functions produced provides an indication of the importance of a variable in a function, and this then allows interpretation of the group separations along discriminant function axes. Group membership can also be predicted from the data, a high percentage of correctly classified cases being an indicator of effective discriminant functions. Discriminant analysis requires data to be multivariate normal, therefore habitat variable data needs transformation, and standardisation so that equal weighting on the variables is attained.

RESULTS

3.1 Summary of trapping data

Table 1 summarises the number of individuals, number of recaptures and total number of captures (including escapes) of wood mice and bank voles per night at each site for each session. At Horsleyhope Ravine similar numbers of wood mice and bank voles were caught during each session, with the ratio of wood mice versus bank voles being very similar at approximately 1.3, whereas at Greta Gorge more wood mice than bank voles were caught in the first session (mouse:vole ratio = 0.53) and more bank voles were caught in the second session (mouse:vole ratio = 1.71). Bank voles dominated captures at Hawthorn Dene during both sessions, their ratios were 4.69 and 12 for the first and second sessions respectively, and although wood mice were dominant at Castle Eden Dene in the first session, (mouse:vole ratio = 0.35) equal numbers of wood mice and bank voles were captured there in session two. The number of recaptures per individual was very similar for both wood mice and bank voles, showing that neither species was more trap happy or trap shy than the other, although within sites wood mice tended to be recaptured more often per individual than bank voles.

3.2 Spatial distribution of rodents

Histograms were plotted of mean abundance of wood mice and bank voles against slope at each site and for each session (Figs 2-5). Two-way analysis of variance showed that at Horsleyhope Ravine, bank voles were found significantly more often on the lower slopes than the upper slopes ($F_{(2,54)}=10.71$; $p<0.001$), and significantly more were distributed on the north-facing slope ($F_{(1,54)}=7.07$; $p<0.05$) in session one (Fig. 2b). In session two (Fig. 2d), bank voles again showed a significant preference for the lower slopes ($F_{(2,54)}=7.47$; $p<0.005$), but there was no significant difference in their distribution between the north- and south-facing slopes of the site. When an analysis was carried out on time period versus slope, it showed that differences in distribution of bank voles with respect to slope were more highly significant for the north-facing slope ($F_{(2,54)}=12.47$; $p<0.001$) than they were for the south-facing slope ($F_{(2,54)}=5.25$; $p<0.01$). Wood mice appeared to be more variable in their distribution, showing no significant differences with respect to slope or side of the study site in session one (Fig. 2a), while in session two (Fig. 2c) they showed highly significant differences with respect to slope position, preferring the middle slopes ($F_{(2,54)}=7.27$; $p<0.005$), and with respect to side of the study site, preferring the north-facing side ($F_{(1,54)}=13.77$; $p<0.001$). Further analysis showed that it was the significant difference in the distribution of wood mice with respect to slope on the north-facing

Table 1. Summary of wood mouse and bank vole capture data.

Site	Session	Wood mice				Bank voles				
		No. indivs /night	No. recaps /night	Total/ night	Recaps /indiv.	No. indivs /night	No. recaps /night	Total/ night	Recaps /indiv.	Ratio of mice:voles
Horsleyhope Ravine	1	3.25	5.5	8.75	1.69	4.75	6.5	11.5	1.37	1.31
	2	3.67	4.67	8.67	1.27	5.67	6.33	12	1.12	1.38
Greta Gorge	1	3.25	5.25	8.5	1.62	2.75	1.75	4.5	0.64	0.53
	2	2.67	2.67	5.67	1.00	5.67	4	9.67	0.71	1.71
Hawthorn Dene	1	1.75	2	4	1.14	9.25	9.25	18.5	1.00	4.69
	2	1.67	1	2.67	0.60	15	15.33	32	1.02	12.0
Castle Eden Dene	1	9	11.75	21.5	1.30	3.5	4	7.5	1.14	0.35
	2	7	6.33	13.33	0.90	7	6.33	13.33	0.90	1.00

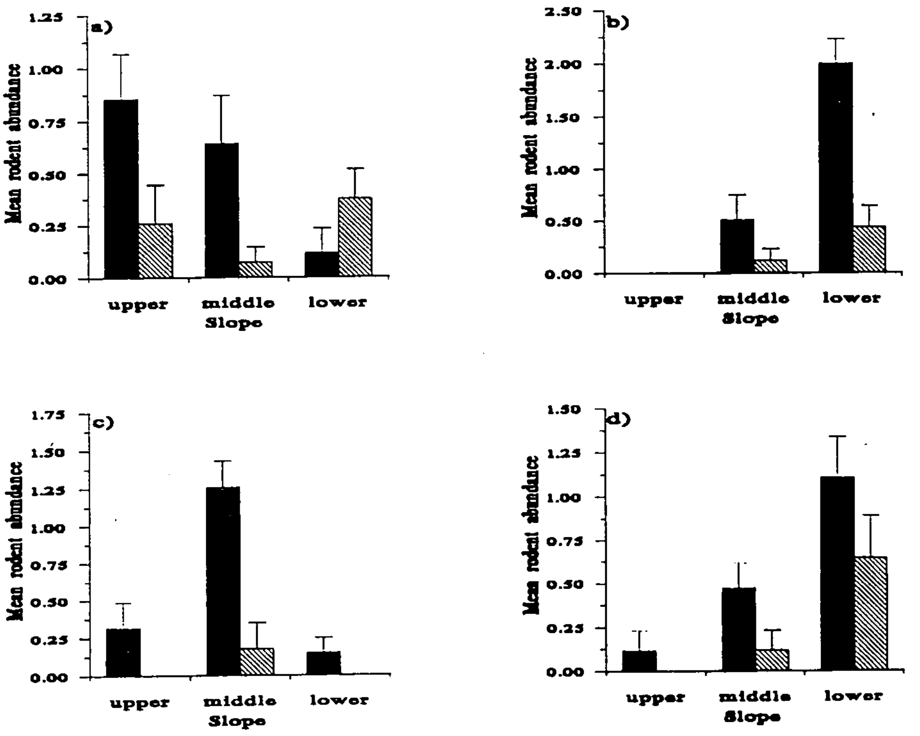


Figure 2. Distribution and abundance of rodents at Horsleyhope Ravine: a) Wood mice during session 1; b) Bank voles during session 1; c) Wood mice during session 2; d) Bank voles during session 2. ■ north-facing side; ▧ south-facing side.

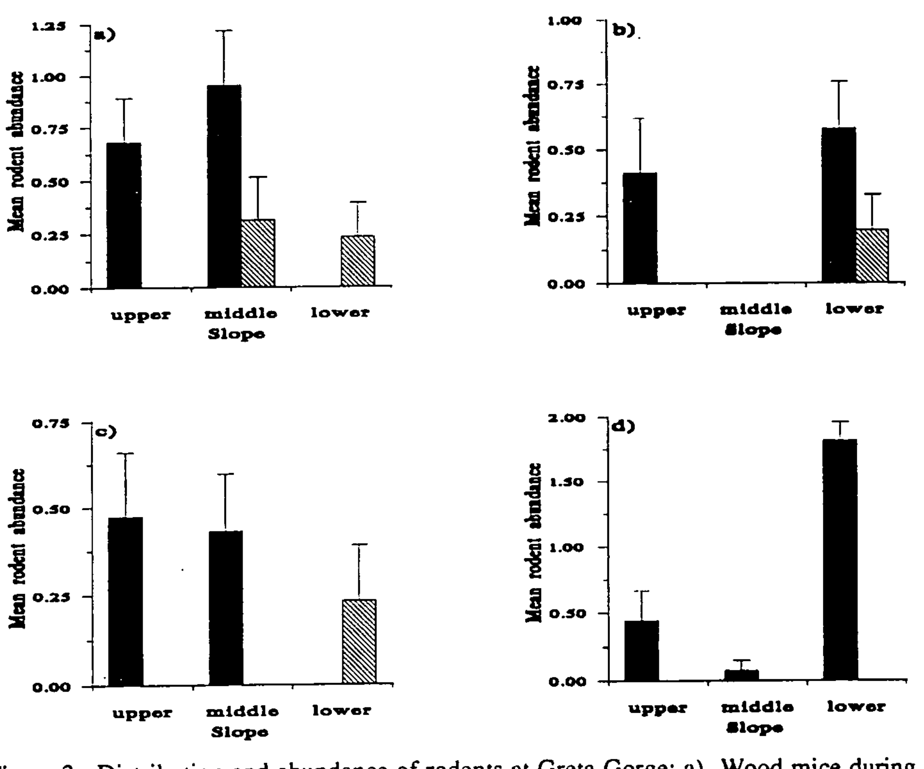


Figure 3. Distribution and abundance of rodents at Greta Gorge: a) Wood mice during session 1; b) Bank voles during session 1; c) Wood mice during session 2; d) Bank voles during session 2. ■ east-facing side; ▧ west-facing side.

side ($F_{(2,54)}$=5.00; $p<0.05$) which contributed to the overall preference for the middle slopes. In session one (Figs 2a-b), analysis of rodent species versus slope showed a significant interaction between slope and the distribution of wood mice and bank voles on the north-facing side of the study site ($F_{(2,54)}$=10.44; $p<0.001$), while in session two (Figs 2c-d), significant interactions between slope and the distribution of rodents was again seen on the north-facing slope ($F_{(2,54)}$=6.17; $p<0.005$) and to a lesser extent on the south-facing slope ($F_{(2,54)}$=3.19; $p<0.05$).

At Greta Gorge two-way anovas showed that wood mice exhibited no significant differences in distribution in session one (Fig. 3a), but in session two (Fig. 3c) there was a significant interaction between the part of the slope and the side of the study site that wood mice were distributed on ($F_{(2,54)}$=4.57; $p<0.05$). An analysis of time period versus slope revealed that on the east-facing slope there was a significant difference in distribution of wood mice with respect to slope ($F_{(2,54)}$=6.55; $p<0.005$). Bank voles were found to show significant differences in their distribution with respect to slope ($F_{(2,54)}$=3.91; $p<0.05$), and with respect to side of the site preferring the east-facing slope ($F_{(1,54)}$=5.02; $p<0.05$) in session one (Fig. 3b). In session two (Fig. 3d), bank voles showed a highly significant preference for the lower slopes ($F_{(2,54)}$=11.68; $p<0.001$), and for the east-facing slope ($F_{(1,54)}$=34.59; $p<0.001$), since no bank voles were caught on the west-facing side of the site, and there was a highly significant interaction between slope and side because of this fact ($F_{(2,54)}$=11.67; $p<0.001$). When rodent species versus slope were analysed for session one (Figs 3a-b), there was a significant interaction between slope and the distribution of wood mice and bank voles on the east-facing slope ($F_{(2,54)}$=6.17; $p<0.005$). In session two (Figs 3c-d) there was a significant difference between wood mouse and bank vole distributions on the east slope ($F_{(1,54)}$=4.61; $p<0.05$) and a significant interaction between slope and the rodent distributions ($F_{(2,54)}$=12.79; $p<0.001$).

At Hawthorn Dene during session one, wood mice (Fig. 4a) showed a significant difference in distribution with respect to slope, preferring the upper slopes ($F_{(2,54)}$=3.94; $p<0.05$), and with respect to the side of the study site, preferring the south-facing side ($F_{(1,54)}$=4.72; $p<0.05$). There was also a significant interaction between slope and side ($F_{(2,54)}$=4.72; $p<0.05$). Conversely, in session two there were no significant differences between slope or side for wood mice (Fig. 4c). Analysis of time period versus slope showed that over both time periods there was a significant difference in wood mice distribution with respect to slope on the south-facing side of the site ($F_{(2,54)}$=7.09; $p<0.005$). Bank voles showed significant differences in distribution with respect to slope ($F_{(2,54)}$=4.04; $p<0.05$), and with respect to the interaction between slope and side of the study site ($F_{(2,54)}$=4.14; $p<0.05$) in session one (Fig. 4b). During session two (Fig. 4d), only the interaction was significant

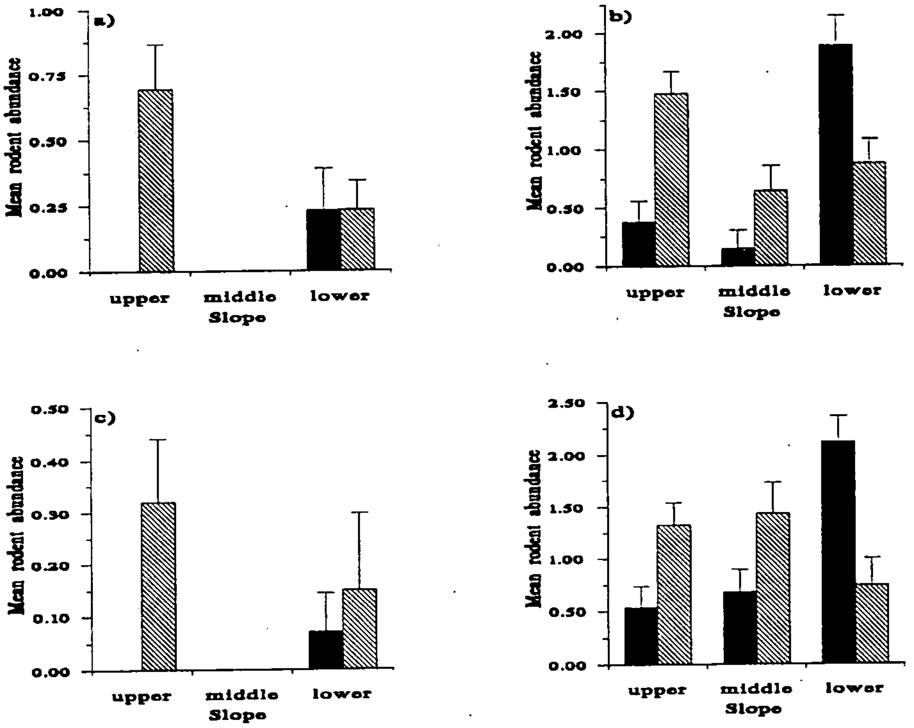


Figure 4. Distribution and abundance of rodents at Hawthorn Dene: a) Wood mice during session 1; b) Bank voles during session 1; c) Wood mice during session 2; d) Bank voles during session 2. ■ south-facing side; ▧ north-facing side.

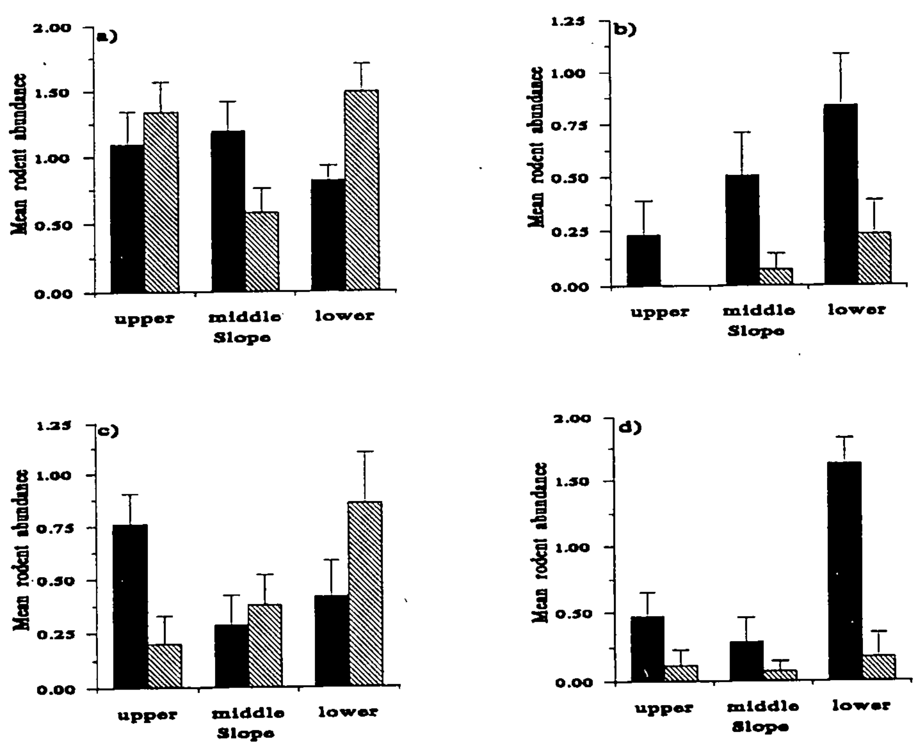


Figure 5. Distribution and abundance of rodents at Castle Eden Dene: a) Wood mice during session 1; b) Bank voles during session 1; c) Wood mice during session 2; d) Bank voles during session 2. ■ east-facing side; ▧ west-facing side.

($F_{(2,54)}$=3.47; p<0.05). Over both time periods there was a significant difference in the distribution of bank voles with respect to slope on the north-facing side of Hawthorn Dene ($F_{(2,54)}$=10.24; p<0.001). When rodent species versus slope was analysed for session one (Figs 4a-b), there was a significant difference in the distribution of rodents with respect to slope on the south-facing side ($F_{(2,54)}$=4.76; p<0.05), and a significant difference in the distribution of wood mice and bank voles ($F_{(1,54)}$=11.95; p<0.005). On the north-facing side, there was a significant difference in the use of the slope ($F_{(2,54)}$=8.88; p<0.001), a significant difference in wood mouse and bank vole distributions ($F_{(1,54)}$=13.75; p<0.001), and a significant interaction between the two ($F_{(2,54)}$=3.32; p<0.05). In session two (Figs 4c-d), on the south side there was no longer a significant difference in the use of the slope, but still a significant difference in the distribution of wood mice and bank voles ($F_{(1,54)}$=18.44; p<0.001). On the north side in session two, there were significant differences in the use of the slope ($F_{(2,54)}$=4.48; p<0.05) and in the distribution of wood mice and bank voles ($F_{(1,54)}$=33.50; p<0.001), but no longer a significant interaction between the two.

Castle Eden Dene data showed that there were no significant differences with respect to slope or side of study site that wood mice were captured on for either time period (Figs 5a & 5c), although wood mice did show a significant change in distribution with respect to time period on both the east-facing slope ($F_{(1,54)}$=5.66; p<0.05) and on the west-facing slope ($F_{(1,54)}$=6.35; p<0.05). Bank voles during session one (Fig. 5b), were captured significantly more often on the east-facing side of the study site ($F_{(1,54)}$=6.84; p<0.05). In session two (Fig. 5d), bank voles showed a significant preference for the lower slopes ($F_{(2,54)}$=4.01; p<0.05), and an even stronger preference for the east-facing side than in session one ($F_{(1,54)}$=11.79; p<0.005). When the two-way anova of time period versus slope was carried out for bank voles, it revealed that significant differences with respect to slope were found only on the east-facing slope ($F_{(2,54)}$=4.56; p<0.05). Two-way anovas of rodent species versus slope showed that in session one (Figs 5a-b) there was a significant difference in the distributions of wood mice and bank voles on the west-facing slope ($F_{(1,54)}$=27.61; p<0.001). In session two (Figs 5c-d), on the east-facing slope there was a significant difference in the use of the slope by all rodents ($F_{(2,54)}$=3.31; p<0.05), and a significant interaction between slope and species ($F_{(2,54)}$=3.47; p<0.05). On the west-facing slope there was a significant difference in the distribution of wood mice and bank voles ($F_{(1,54)}$=4.83; p<0.05) with many more wood mice than bank voles being captured on that side.

In general, the distribution and abundance of wood mice and bank voles was very variable between sites. Bank voles tended to be captured significantly more often during one or both sessions on the lower slopes of a site, often with a significant preference for a particular side of the site. For instance, bank voles were captured significantly more often on the lower north-facing slope of Horsleyhope Ravine, on the lower east-facing slope of Greta Gorge, on the lower north-facing slope of Hawthorn Dene, and on the lower east-facing slope of Castle Eden Dene. Wood mice tended to be distributed more randomly, with no significant differences with respect to slope or side of the study site at Horsleyhope Ravine and Greta Gorge in session one, at Castle Eden Dene in both sessions and at Hawthorn Dene in session two. During the remainder of sessions wood mice tended to significantly prefer the upper or middle slopes of a particular side of a site, such that at Horsleyhope Ravine wood mice preferred the middle north-facing slope, at Greta Gorge the upper and middle east-facing side, and at Hawthorn Dene the upper south-facing side. At all sites there were significant test results to indicate that wood mice and bank voles differed in their distributions within a side with respect to slope, in one or both sessions. The possibility of negative association between wood mice and bank voles was tested using chi-square (see section 3.3).

3.3 Rodent associations

Only the north-facing side of Horsleyhope Ravine, in session one, showed a significant association (χ^2 = 3.967, df = 1, $p < 0.05$) indicating that there was a negative association between wood mice and bank voles i.e. wood mice and bank voles were caught at different trap sites more frequently than expected by chance. In all other cases the null hypothesis was retained, whereby there were no associations, positive or negative, between wood mice and bank voles.

3.4 Trap site fidelity between trapping sessions

Table 2. Values of r and their significance levels for Pearson correlation between traps catching wood mice and bank voles in the first and second sessions. *p<0.05*; p<0.01; **p<0.001**. Degrees of freedom = 58 in all cases.

Site	Species	r
Horsleyhope Ravine	wood mouse	*0.27*
	bank vole	**0.47**
Greta Gorge	wood mouse	**0.78**
	bank vole	**0.45**
Hawthorn Dene	wood mouse	**0.66**
	bank vole	**0.47**
Castle Eden Dene	wood mouse	0.39
	bank vole	**0.58**

Pearson correlations carried out to investigate trap site fidelity were all significant (see Table 2.), indicating that rodents were using similar traps in the second session to those that were used in the first session. This result could lead one to suggest amalgamating the data for the first and second sessions, but was thought to be unwise since although the correlation coefficients are significant, they are not equal to 1. Therefore, data amalgamation, which could result in the loss of variation of the habitat variables that could explain these small differences in wood mouse and bank vole distribution, was not carried out.

3.5 Seasonal change in vegetation cover

Paired t-tests (Table 3) showed that % canopy cover, % shrub cover and % herbs >40cm changed significantly, and in a positive direction, at all sites between the first and second trapping sessions. Percentage herb cover changed significantly at Horsleyhope Ravine and Castle Eden Dene, while % herbs 0-10cm changed significantly at Horsleyhope Ravine and Hawthorn Dene. Percentage herbs 10-20cm changed significantly only at Hawthorn Dene, and % herbs 20-30cm only at Horsleyhope Ravine. Percentage herbs 30-40cm changed significantly at Horsleyhope Ravine and Greta Gorge. Seven out of eight variables changed significantly at Horsleyhope Ravine, four at Greta Gorge and Castle Eden Dene and five at Hawthorn Dene.

Table 3. Significant differences between first and second session vegetation cover. Values of t and significance levels for paired t-tests, $p<0.05$; *p<0.01*; <u>p<0.005</u>; **p<0.001**. Degrees of freedom = 59 in all cases.

Site	% canopy	% shrub	% herb	% herb 0-10cm	% herb 10-20cm	% herb 20-30cm	% herb 30-40cm	% herb >40cm
Horsleyhope Ravine	**5.60**	**7.20**	**4.78**	2.27	-	**3.70**	**7.43**	**3.46**
Greta Gorge	**4.38**	**3.51**	-	-	-	-	2.40	**6.77**
Hawthorn Dene	2.06	**5.66**	-	2.16	<u>2.95</u>	-	-	**3.77**
Castle Eden Dene	**4.45**	**4.20**	**4.40**	-	-	-	-	**3.30**

3.6 Habitat selection by rodents - Vegetation structure

Graphs of the total number of touches of dead and live vegetation against height class for each study site as a whole, for sample points where wood mice were captured at each site and for where bank voles were captured at each site, are presented in Figures 6-9. Wood mice showed significant differences in their choice of dead and live vegetation at all sites (Table 4). At Horsleyhope Ravine (Fig. 6b), Greta Gorge (Fig 7b) and Castle Eden Dene (Fig. 9b) wood mice tended to avoid low dead vegetation up to a height of 10-15cm, and preferred dead vegetation above 15-20cm in height. At Hawthorn Dene (Fig. 8b) however, wood mice showed no strong avoidance of any dead vegetation seemingly preferring most heights above 10cm. Wood mice tended to avoid low level live vegetation below 15cm and prefer medium and high live vegetation above 20cm at Horsleyhope Ravine and Hawthorn Dene, while they preferred short live vegetation at Greta Gorge and Castle Eden Dene, and avoided medium and high level live vegetation.

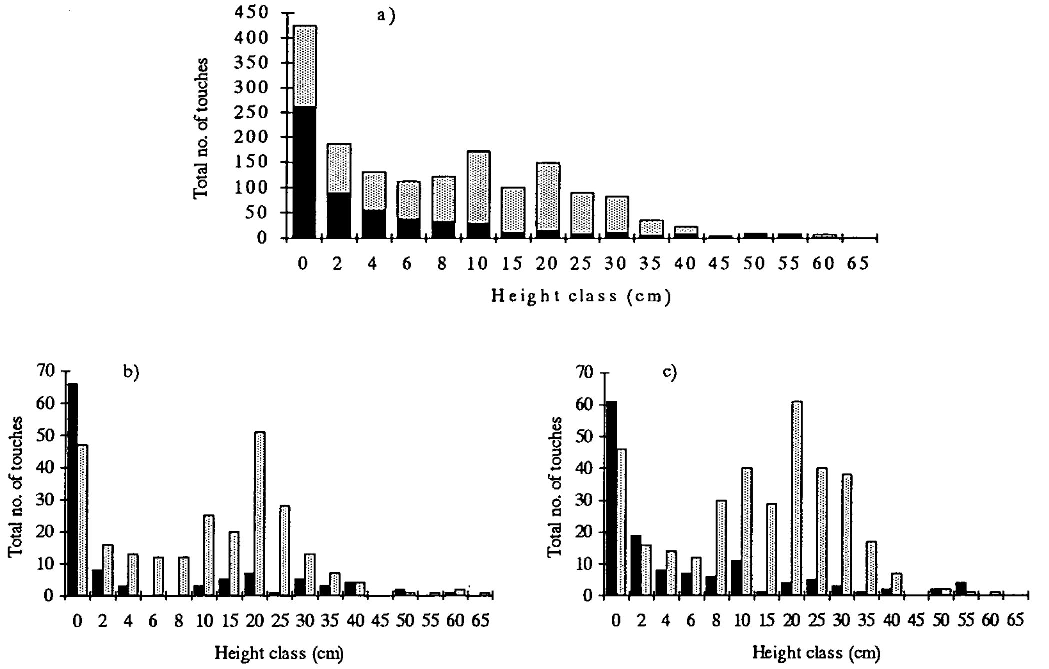


Figure 6. Total number of touches for dead and live vegetation at different height classes for a) the total study site; b) for trap sites where wood mice were captured and c) for trap sites where bank voles were captured at Horlseyhope Ravine. ■ - dead vegetation; ▨ - live vegetation.

Bank voles also showed significant associations with vegetation at all sites, except at Castle Eden Dene where they showed no significant association with dead vegetation (Table 4). At Horsleyhope Ravine (Fig. 6c), Greta Gorge (Fig. 7c) and Hawthorn Dene (Fig. 8c), bank vole habitats were characterised by an avoidance of low level dead and live vegetation below 10-20cm, and a preference for medium and high level vegetation above 20-30cm in height. At Castle Eden Dene (Fig. 9c) bank vole habitat was characterised by a preference for low level live vegetation below 8cm, and for vegetation above 45cm, while live vegetation between 10-25cm was avoided.

When the habitats of wood mice and bank voles were compared using chi-square, they were shown to be selecting similar habitats in most cases, except at Horsleyhope Ravine where wood mice were shown to avoid and bank voles to prefer low level dead vegetation, while medium height dead vegetation was preferred by wood mice and avoided by bank voles. At Greta Gorge wood mice and bank voles

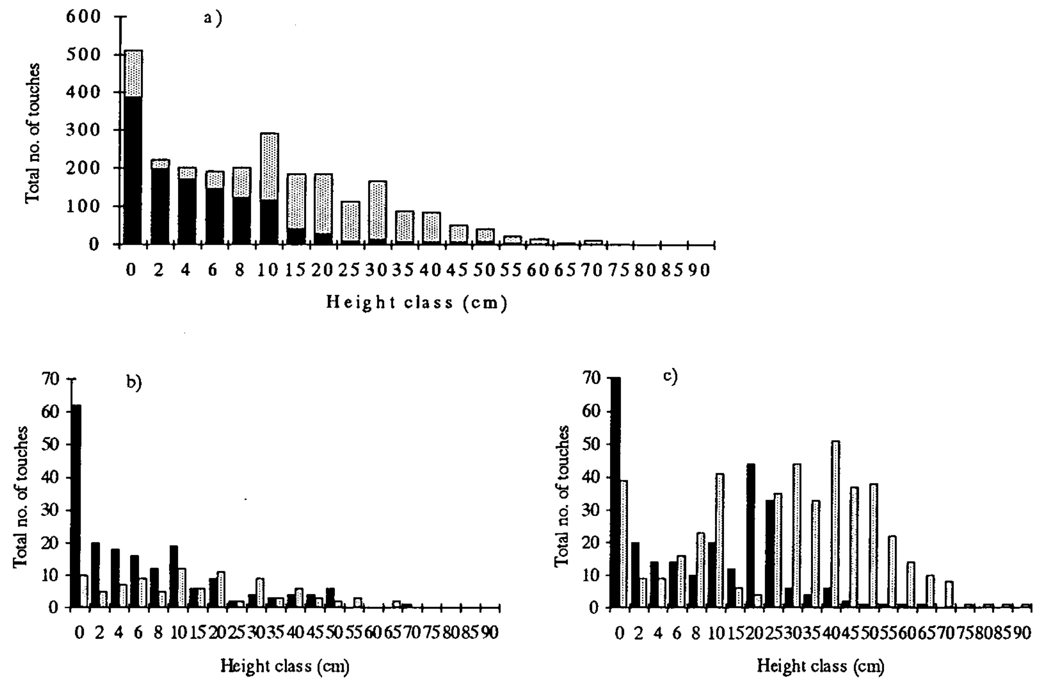


Figure 7. Total number of touches for dead and live vegetation at different height classes for a) the total study site; b) for trap sites where wood mice were captured and c) for trap sites where bank voles were captured at Greta Gorge. ■ - dead vegetation; ▩ - live vegetation.

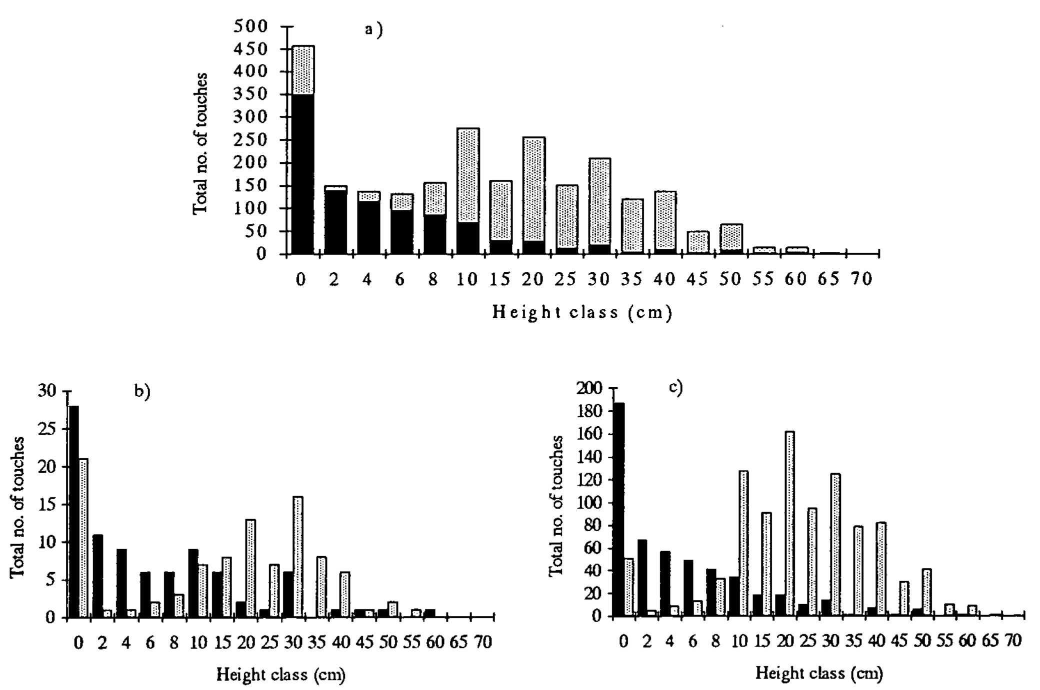


Figure 8. Total number of touches for dead and live vegetation at different height classes for a) the total study site; b) for trap sites where wood mice were captured and c) for trap sites where bank voles were captured at Hawthorn Dene. ■ - dead vegetation; ▩ - live vegetation.

were also shown to be associated with different aspects of the habitat, wood mice avoided medium height live vegetation and preferred short live vegetation, while bank voles did the reverse. A different but significant association was seen for live vegetation at Hawthorn Dene, where wood mice preferred and bank voles avoided very short vegetation, and wood mice avoided, while bank voles preferred short and tall vegetation.

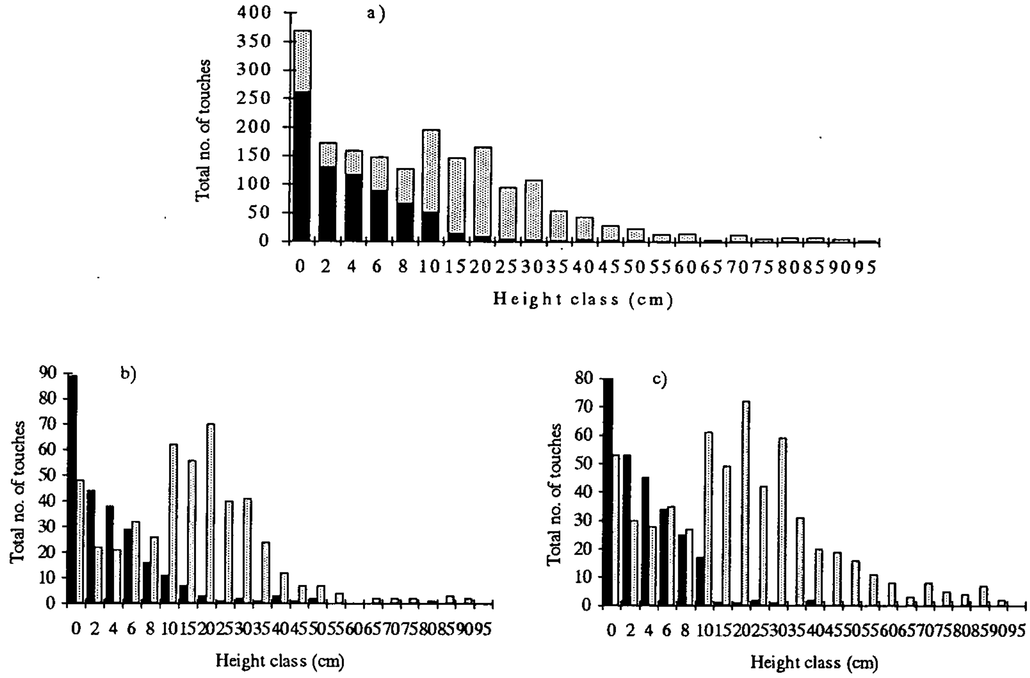


Figure 9. Total number of touches for dead and live vegetation at different height classes for a) the total study site; b) for trap sites where wood mice were captured and c) for trap sites where bank voles were captured at Castle Eden Dene. ■ - dead vegetation; ▨ - live vegetation.

Table 4. Significant chi-square values for dead and live vegetation and the structure associations with rodents. *p<0.05*; p<0.01, - indicates an insignificant test.

		wood mice vs no wood mice		bank voles vs no bank voles		bank voles vs wood mice	
Site	**Vegetation**	χ^2	**df**	χ^2	**df**	χ^2	**df**
Horsleyhope Ravine	dead	63.02	7	43.95	8	24.97	7
	live	41.27	11	72.72	11	-	-
Greta Gorge	dead	68.73	8	40.63	8	-	-
	live	35.57	11	48.68	16	*22.93*	11
Hawthorn Dene	dead	*15.44*	7	25.70	10	-	-
	live	38.59	9	59.13	14	43.02	10
Castle Eden Dene	dead	*19.12*	17	-	-	-	-
	live	*27.94*	17	54.87	18	-	-

A summary of the associations that wood mice and bank voles have with particular height classes of vegetation is given in Table 5, and, as has been seen these associations are very variable between sites although the overall tendency is for both wood mice and bank voles to avoid low level vegetation and prefer medium or tall vegetation.

Table 5. Summary table of height classes with strongest associations to wood mice and bank voles for dead and live vegetation.

		wood mice vs no wood mice		**bank voles vs no bank voles**		**wood mice vs bank voles**	
Site	**Vegetation**	**Avoid**	**Prefer**	**Avoid**	**Prefer**	**wood mice avoid/bank voles prefer**	**wood mice prefer/bank voles avoid**
Horsleyhope Ravine	dead	low	medium & high	low	medium & high	low	medium
	live	low	medium	low	medium & high	none	none
Greta Gorge	dead	low	medium & high	low	medium & high	none	none
	live	medium	low	low	high	medium	low
Hawthorn Dene	dead	none	low, medium & high	low	medium & high	none	none
	live	low & high	medium & high	low	medium & high	low & high	v. low
Castle Eden Dene	dead	low	medium & high	none	none	none	none
	live	high	low	low & medium	low & high	none	none

3.7 Habitat selection by rodents - Habitat variables

When the Mann-Whitney U-test was carried out on the habitat variables c)-t) for each site and each session, sixteen variables were found to distinguish between the microhabitats of wood mice and bank voles (Table 6.), while two variables, % rock cover and number of tree stumps showed no significant differences at all. By examining the number of variables showing significant results across the sites, it was seen that the four most important variables for wood mice (numbers in italics) was % herb cover, % soil cover, % brash cover and the number of trees. The four most important variables for bank voles (numbers underlined) however, were % moss cover, % herb cover, % herbs 30-40cm and % herbs >40cm. When wood mice habitat variables were compared to those of bank voles, the four variables showing the most significant differences between the two species' habitats were (numbers in bold) % herb cover, % soil cover, % brash cover, % herbs >40cm. Many of the variables changed in

Table 6. Differences between means of habitat variables for wood mice and bank voles, and traps where they were not caught as determined by the Mann-Whitney U-test. Direction of use of variable indicated by +, use variable more; -, use variable less. +/- p<0.05; ++/-- p<0.01; +++/--- p<0.005; ++++/---- p<0.001.

Variable	Species	HR1	HR2	GG1	GG2	HD1	HD2	CED1	CED2	sum
% canopy	mice			+		--				2
	vole					-	--			2
	m:v									0
% shrub	mice						+		+	2
	vole			+						1
	m:v									0
% moss	mice					+				1
	vole	++++	+					+	+	4
	m:v	-/+								1
% herb	mice			----	----	---	---			4
	vole	+	+		++++			+	+++	5
	m:v	-/+		-/+	---/+++	-/+	--/++		-/+	**6**
% litter	mice								-	1
	vole	-			-					2
	m:v									0
% soil	mice			++	+	+++	+++			4
	vole							--	----	2
	m:v					++/--	++/--	++/--	+++/---	**4**
%brash	mice	++				+++	++++			3
	vole									0
	m:v	+/-				+/-	+++/---			3
% log	mice			++	+					2
	vole									0
	m:v									0

Variable	Species	HR1	HR2	GG1	GG2	HD1	HD2	CED1	CED2	sum
% herb 0-10	mice				+					1
	vole					---	--			2
	m:v									0
%herb10-20	mice				--	--				2
	vole									0
	m:v									0
%herb20-30	mice			----						1
	vole	+								1
	m:v	-/+		--/++						2
%herb30-40	mice			----	-					1
	vole	+	+	+		+		++	+	6
	m:v			----/++++	-/+					2
% herbs >40	mice			--	-					2
	vole				+	+++		++	++++	4
	m:v			--/++	--/++			-/+	---/+++	4
no. trees	mice		++++			---	-			3
	vole					----	-			2
	m:v		+++/---					+/-		2
no. saplings	mice									0
	vole				+					1
	m:v									0
no. shrubs	mice									0
	vole			+				+++	++++	3
	m:v							-/+	-/+	2
	sum	10	5	14	14	15	11	10	12	

their relative significances within sites, with respect to the time period, for example wood mice showed a positive significant relationship to % canopy cover at Greta Gorge in session one, but no relationship in session two. A more striking example is shown by bank voles at Greta Gorge who showed no relationship with % herb cover in session one, but a very highly significant positive relationship with it in session two. By examining the columns of data, it can be seen that not only do the total numbers of significant variables change between time periods at a site, but those variables which show significance can also change. Horsleyhope Ravine in session two only had five significant variables, whereas in session one it had ten. Hawthorn Dene also had a reduced number of significant variables in session two, but Castle Eden Dene showed an increase and Greta Gorge had the same number of significant variables although they were different between the sessions. This data again shows that wood mice and bank voles are preferentially selecting or avoiding many variables depending on the particular habitat structure of the site which they inhabit, no single variable stands out as being the main factor determining wood mice and vole distribution.

3.8 Habitat selection by rodents - Multivariate analysis

In order to assess the main factors important in rodent habitat selection from such multivariate data, the 16 variables which showed significant differences in the Mann-Whitney U-test (Table 6), for all sites and for both time periods, were pooled

Table 7. Wilks' Lambda (U-statistic) and univariate F-ratio with 3 and 476 degrees of freedom for pooled data discriminant analysis.

Variable	Wilks' Lambda	F	Significance
% brash cover	0.948	8.710	0.000
% canopy cover	0.968	5.372	0.001
% herbs 0-10cm	0.987	2.133	0.095
% herbs 10-20cm	0.991	1.392	0.245
% herbs 20-30cm	0.981	3.121	0.026
% herbs 30-40cm	0.873	23.069	0.000
% herbs >40cm	0.904	16.832	0.000
% herb cover	0.846	28.803	0.000
% litter cover	0.969	5.028	0.002
% log cover	0.970	4.920	0.002
% moss cover	0.980	3.252	0.022
No. of saplings	0.982	2.913	0.034
No. of shrubs	0.945	9.171	0.000
No. of trees	0.926	12.680	0.000
% shrub cover	0.941	9.966	0.000
% soil cover	0.891	19.336	0.000

and analysed using discriminant analysis. From these 16 variables, only those which have significant values of Wilks' Lambda and the F-ratio are entered into the analysis, in this case all variables except % herbs 0-10cm and % herbs 10-20cm were significant (Table 7).

Three canonical discriminant functions were produced, the first two of which comprised 93.39% of the total variance (Table 8). The significance of the discriminant functions was tested using Wilks' Lambda, first on all three functions, and then with the first discriminant function removed. The significance levels associated with the first and second function were highly significant, indicating that they both contribute substantially to sample group differences, and that the means of each function are significantly different for each sample group. Discriminant function three only explained 6.61% of the total variance, and did not have a significant Wilks' Lambda or Chi-square value, therefore it was not used to explain rodent microhabitats.

Table 8. Summary information on canonical discriminant functions for pooled data discriminant analysis.

Fnctn	Eigenv.	Percent of Variance	Cum. Percent	Canonical Correlation	After Fnctn	Wilks' Lambda	Chi-square	df	Signif
					0	0.587	249.924	48	0.000
1	0.348	57.72	57.72	0.508	1	0.791	109.779	30	0.000
2	0.215	35.68	93.39	0.421	2	0.962	18.337	14	0.192
3	0.040	6.61	100.00	0.196					

Classification of the sample groups with respect to the discriminant functions, placed 51.25% of cases in the correct sample group (Table 9). Bank voles were most successfully classified with 56.3% being correctly placed, while wood mice, with only 49% correctly placed, were least successfully classified. Examination of the correlations between the habitat variables and the discriminant functions (Table 10) showed what the most important variables in each function are. Function one describes the amount of herbaceous cover available, ranging from open ground (% cover of soil) to areas of high level herb cover (% herb cover, % herbs 30-40cm, and % herbs >40cm). Function two described a more complex type of vegetative cover, ranging from low level cover (% litter cover, % herbs 0-10cm and % herbs 10-20cm) to higher level woody cover (% canopy cover, % shrub cover and % brash). The separation of the four sample groups and the sites along these two functions is shown in Figure 10. A highly significant amount of separation was found between wood mice and bank voles along the first function axis ($F_{(1,210)}$=174.13; p<0.0001), with bank voles being found in more herbaceous areas, and wood mice in the more open areas. Along the second axis, wood mice and bank voles were still significantly separated ($F_{(1,210)}$=4.23; p<0.05), bank voles being found in more herbaceous areas, and wood mice in areas with more shrubs and brash. Traps catching both species of rodent or neither were found between bank voles and wood mice along function one in areas with equal contributions from soil cover and herb cover. They were separated mostly by function two, where traps catching both rodent species were found in areas with more cover being contributed by shrubs and brash. Those traps catching no rodents were characterised by being in areas of intermediate herbaceous cover, with low growing herbs and litter.

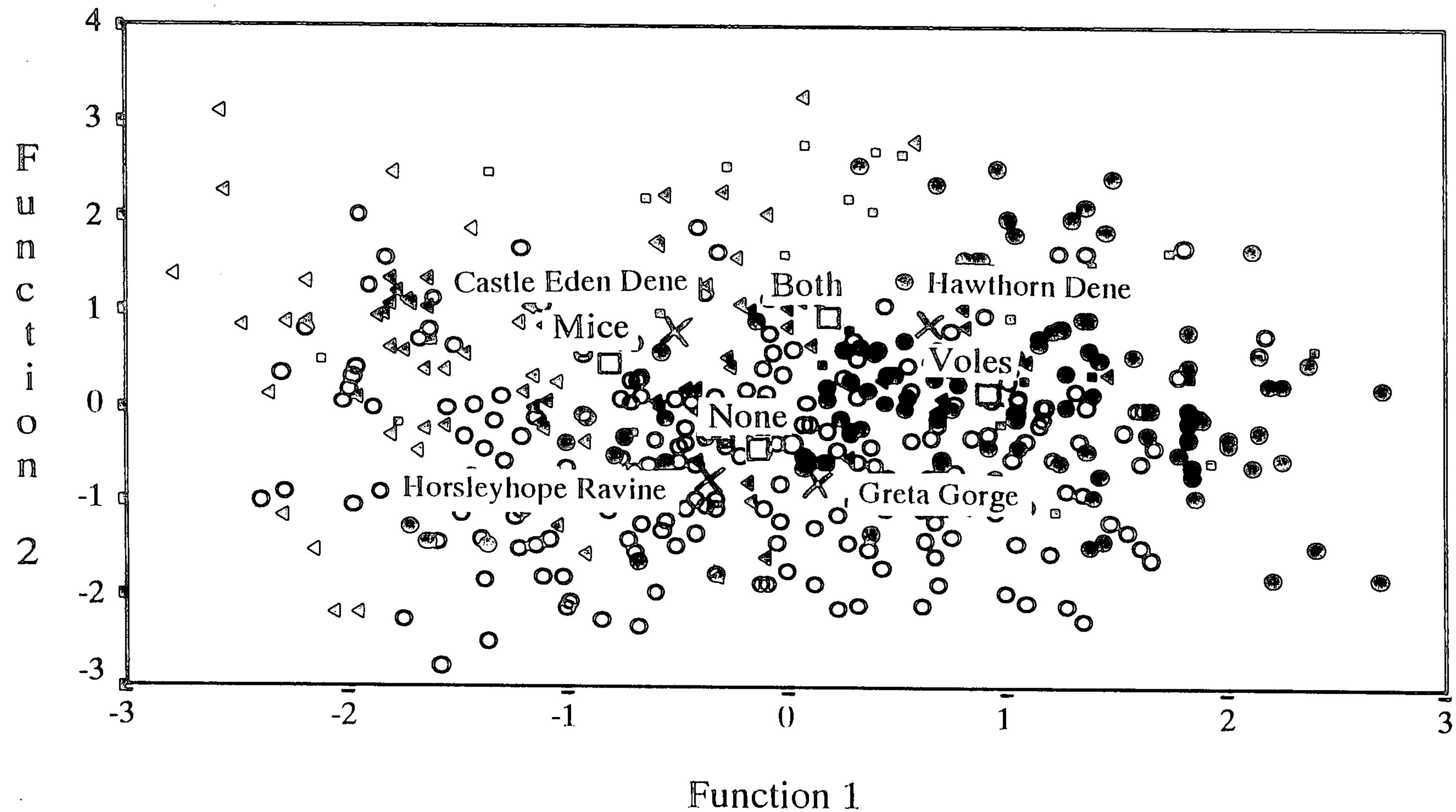
Table 9. Predicted sample group membership for pooled data discriminant analysis.

		Predicted Group Membership			
Actual Group	**No. of Cases**	**None**	**Bank voles**	**Wood mice**	**Both**
None	230	115 50.0%	50 21.7%	44 19.1%	21 9.1%
Bank voles	112	20 17.9%	63 56.3%	5 4.5%	24 21.4%
Wood mice	100	22 22.0%	10 10.0%	49 49.0%	19 19.0%
Both	38	2 5.3%	7 18.4%	10 26.3%	19 50.0%

A one-way analysis of variance on the discriminant functions for each site showed that there was a highly significant difference between all four sites for function one ($F_{(3,476)}$=23.67; p<0.0001) and for function two ($F_{(3,476)}$=49.92; p<0.0001). Site centroids were calculated using the means of functions one and two for each site, and these were plotted onto Figure 10. Both Horsleyhope Ravine and Greta Gorge had their function means near to the group centroid for traps catching no rodents, the Hawthorn Dene function means placed it near to the vole group centroid and Castle Eden Dene functions means placed it near to the wood mice group centroids.

Discriminant analysis at each site for each session, using the same habitat variables, produced higher percentages of correctly classified groups (Table 11), in all cases, they were over 20% higher than the percentage of correctly classified groups from the discriminant analysis on the pooled data set. Whereas only 50.0% of traps catching no rodents were correctly classified for the pooled data set, all the single site percentages were above 62.50% (CED session 1), with the largest number correctly classified at Hawthorn Dene in session one (84.00%). Several classifications for bank voles were 100% correct, at Horsleyhope Ravine session two, Greta Gorge session one, and Castle Eden Dene session one, this was also true for wood mice at Horsleyhope Ravine session two, and Hawthorn Dene sessions one and two, and for

Figure 10. Canonical discriminant function plot for pooled data discriminant analysis to show the separation of sample groups and study sites. Symbols used in the plots are defined as follows: □ Group centroids; o No rodents trapped; ● Voles only trapped; ◁ Mice only trapped; ■ Both species trapped; X Site centroids



traps catching both rodents at Greta Gorge sessions one and two, and Hawthorn Dene session two.

Table 10. Pooled within-groups correlations between discriminating variables and canonical discriminant functions for pooled data discriminant analysis. **Bold** denotes the largest absolute correlation between each variable and any discriminant function.

	Function 1	**Function 2**	**Function 3**
% herb cover	**0.714**	-0.093	-0.224
% herbs 30-40cm	**0.635**	0.142	0.117
% herbs >40cm	**0.550**	0.060	-0.003
% soil cover	**-0.490**	0.417	0.135
% shrub cover	0.096	**0.500**	-0.379
% brash cover	-0.281	**0.348**	0.183
% litter cover	-0.134	**-0.341**	0.099
% canopy cover	-0.162	**-0.325**	0.223
% moss cover	0.145	**0.240**	-0.141
% herbs 0-10cm	-0.068	**-0.234**	-0.034
% herbs 10-20cm	0.029	**-0.197**	-0.066
% log cover	0.008	0.306	**0.522**
No. of shrubs	0.214	0.384	**-0.504**
No. of trees	-0.411	-0.234	**0.486**
No. of saplings	0.190	-0.076	**0.337**
% herbs 20-30cm	0.164	0.198	**-0.218**

Table 11. Summary of sample group classification results for individual site/time discriminant analyses

	HR		**GG**		**HD**		**CED**	
	1	**2**	**1**	**2**	**1**	**2**	**1**	**2**
None	75.90	68.60	66.70	71.10	84.00	78.30	62.50	76.00
Bank voles	61.50	100	100	91.70	62.50	83.90	100	80.00
Wood mice	75.00	100	90.90	88.90	100	100	83.30	83.30
Both	50.00	80.00	100	100	85.70	100	54.50	85.70
% correctly classified	71.67	80.00	76.67	78.33	76.67	83.33	73.33	80.00

A summary of the percentage variance explained by each function, the habitat gradient and the F values for a one-way anova between wood mice and bank voles for each function, for all sites, is presented in Table 12. The cumulative percentage variance for functions one and two for each analysis never exceeded the 93.39% of the pooled data analysis, with the largest cumulative percentage being 88.95% at Hawthorn Dene session one, and the smallest being 84.84% at Castle Eden Dene session one. The habitat gradients for all functions vary considerably between and within sites, and tend to be more complex than the habitat gradients for the pooled data set (see Appendix 2, for correlations between variables and functions). The overall trend was for the habitat gradients to be ones of cover, ranging either from open to closed cover or vice versa. Closed vegetative cover was either herbaceous or woody or a combination of the two.. Interpretation of habitat gradients became problematical when they consisted of a structural component, such as the number of trees, shrubs or saplings, at one end of the gradient to cover components at the other, since this mixture does not lend itself to simple biological interpretation.

Wood mice and bank voles were significantly separated by function one at all sites except Greta Gorge session one, and by function two at all sites except Greta Gorge session two, Hawthorn Dene session two and Castle Eden Dene session one. Function three significantly separated wood mice and bank voles at all sites except Horsleyhope Ravine session two, Greta Gorge sessions one and two and Castle Eden Dene session two. At Greta Gorge, wood mice and bank voles were separated significantly only by function two in session one, and only by function one in session two. At all the other sites wood mice and bank voles were separated significantly either by all three discriminant functions, or by two of the functions.

Examination of the discriminant function plots (Appendix 3) for the individual analyses showed that wood mice and bank voles were still being separated in habitat space by factors of cover, openness and herbaceousness or woodiness of the vegetation, despite the discriminant functions being so variable.

Table 12. Summary information for individual site/time discriminant analyses.

Site	Session		Function 1	Function 2	Cum. % var.	Function 3
Horsleyhope Ravine	1	% variance	45.68	39.85	85.54	14.46
		function gradient	open ground → herb cover	tall herb cover → canopy cover		shrub cover → brash cover
		mice vs voles anova	$F_{(1,27)}=23.99$; $p<0.0001$	$F_{(1,27)}=4.59$; $p<0.05$		$F_{(1,27)}=7.74$; $p<0.01$
	2	% variance	56.52	31.55	88.07	11.93
		function gradient	herb cover → numbers of trees and shrubs	open ground → tall herb cover		medium herb cover → shrub cover
		mice vs voles anova	$F_{(1,18)}=100.56$;$p<0.0001$	$F_{(1,18)}=10.93$; $p<0.005$		$F_{(1,18)}=2.02$; not signif.
Greta Gorge	1	% variance	51.06	33.84	84.89	15.11
		function gradient	open ground with shrub cover→ short herb cover	canopy cover → tall herb cover		medium herb cover → log cover and no. trees
		mice vs voles anova	$F_{(1,17)}=0.04$; not signif.	$F_{(1,17)}=67.33$; $p<0.0001$		$F_{(1,17)}=0.72$; not signif.
	2	% variance	65.93	20.78	86.72	13.28
		function gradient	canopy cover → herb cover	short herb cover → log and brash cover		open ground → litter and medium herb cover
		mice vs voles anova	$F_{(1,19)}=137.51$;$p<0.0001$	$F_{(1,19)}=0.06$; not signif.		$F_{(1,19)}=0.00$; not signif.
Hawthorn Dene	1	% variance	64.31	24.64	88.95	11.05
		function gradient	no. of trees and herb cover → medium herb cover	tall herb cover → open ground and brash		shrub and tall herb cover → short herb and log cover
		mice vs voles anova	$F_{(1,26)}=6.08$; $p<0.05$	$F_{(1,26)}=4.39$; $p<0.05$		$F_{(1,26)}=15.00$; $p<0.001$
	2	% variance	62.79	24.49	87.29	12.71
		function gradient	number of trees → tall herb and shrub cover	short herb cover → tall herb cover		canopy and brash cover → number of saplings
		mice vs voles anova	$F_{(1,32)}=31.10$; $p<0.0001$	$F_{(1,32)}=3.20$; not signif.		$F_{(1,32)}=9.69$; $p<0.005$
Castle Eden Dene	1	% variance	57.53	27.30	84.84	15.16
		function gradient	tall herb cover → open ground and brash cover	short herb cover → tall herb and shrub cover		canopy cover → number of saplings
		mice vs voles anova	$F_{(1,31)}=66.93$; $p<0.0001$	$F_{(1,31)}=0.87$; not signif.		$F_{(1,31)}=7.45$; $p<0.01$
	2	% variance	52.72	34.16	86.87	13.13
		function gradient	litter cover → shrub cover	open ground → tall herb and shrub cover		short herb cover → log and brash cover
		mice vs voles anova	$F_{(1,26)}=18.83$; $p<0.0005$	$F_{(1,26)}=28.66$;$p<0.0001$		$F_{(1,26)}=2.00$; not signif.

DISCUSSION

4.1 Habitat selection

4.1.1 Discriminant analysis

The discriminant analysis of the pooled data set and the single site/time data sets showed that wood mice and bank voles exploited habitats which differed in structure and composition. Wood mice occurred in areas of open soil with low densities of herbaceous cover, and high incidences of shrub or brash cover, while bank voles were associated with dense herbaceous ground cover and lower incidences of shrub and brash cover. These habitat preferences agree with several previous studies of habitat selection by these two species (Evans 1942; Kikkawa 1964; Southern and Lowe 1968; Gurnell 1985).

There were, however, several anomalies between the two groups of discriminant analysis. Firstly, there was the variability of the discriminant functions in the single site/time analyses. This could be caused by the difference in habitat composition between the sites and by the seasonal change in vegetation structure causing a real difference in the habitat variables selected for or against by wood mice and bank voles. Conversely, the variability could be an artefact of discriminant function analysis, because the linear functions that are calculated from the habitat variables maximise the differences between sample groups, such that the variables that describe the function gradient are certainly statistically significant, but not necessarily biologically significant (Rexstaad *et al.* 1988). This second explanation is more likely to happen with small sample sizes since there is more variation within the data set than there would be with a large data set.

Two other anomalies between the pooled data analysis and the single site/time analyses were differences in the percentage of correctly classified cases and the cumulative percentage of variance being explained by the first two discriminant functions. The percentage of correctly classified cases in the single site/time analyses were high, because the habitat configurations of the traps catching wood mice, bank voles, both or neither were site and/or time specific. This specificity was unable to be expressed in the pooled data analysis, because the data had become generalised and this caused the low percentage of correctly classified cases. However, the pooled data analysis had a larger value for the percentage of variance explained by the first two discriminant functions because the large number of samples was able to reduce the standard deviation of the mean for each variable and therefore decrease the variation in the data. In the single site/time analyses the sample size was smaller, creating greater variability in the data which then decreased the percentage of variation which was successfully explained by the first two functions.

Further errors which may influence the accuracy of optimal habitat prediction for a species, especially on a small scale, occur when individuals of a species become trapped in an inappropriate habitat patch as they move through it to reach an appropriate patch (Schroder and Rosenzweig 1975).

4.1.2 Vegetation structure

Wood mice and bank voles were seen to be selecting similar habitats from that which was available at each site with respect to the structure of the vegetation. The pattern of a general preference for medium to tall vegetation be it dead or alive, and a general avoidance of short vegetation, was more rigorously adhered to by bank voles than wood mice, which showed more random choices of habitat structure. However, wood mice and bank voles showed no positive associations, and although they show similar preferences for medium and tall live vegetation, the discriminant function analysis indicated that bank voles preferred dense herbaceous vegetation, and wood mice preferred higher densities of woody vegetation. In this way the live vegetation structure preferences of wood mice and bank voles become segregated despite them seeming similar. In some cases, the preferred vegetation structure for wood mice and bank voles did differ. The only preferences for different heights of dead vegetation by wood mice and bank voles was at Horsleyhope Ravine, and can be interpreted as wood mice being trapped in areas of medium height brash with little leaf litter, while bank voles were trapped in areas with more leaf litter and no brash. Both at Greta Gorge and Hawthorn Dene, medium and tall live vegetation was avoided by wood mice and preferred by bank voles, vice versa for very low vegetation, and this could be due to populations of bank voles at these sites monopolising the areas of medium and tall vegetation which provides them with essential cover, while wood mice are restricted to the more open areas with sparse and short vegetation, this situation having been observed in a number of studies (e.g. Southern & Lowe 1968). At Castle Eden Dene, wood mice also avoided tall live vegetation, preferring the short vegetation, but this was not shown to significantly differ from the choice of vegetation structure by bank voles at this site. In this case, the abundance of open or sparse short vegetation under dense shrubby cover which occurred at heights above the point quadrat, meant that wood mice were more likely to have been caught in such habitat here rather than at any of the other sites.

The habitat preferences of both species would seem to suggest that some element of cover, whether it be dense herbaceous cover or woody cover at a short distance off the ground is needed. This is likely to be a strategy for predator avoidance since by having open space under dense cover rodents can move uninhibited and without noise, whereas short dense vegetation can hamper their movements (Simonetti 1989). This phenomenon was observed by Healing *et al.* (1983) on Skomer island where bank voles were trapped more often in dense *Pteridium aquilinum* with a sparse understorey of *Hyacinthoides non-scripta* and *Oxalis acetosella* L. (wood sorrel) through which they could move easily, and avoided areas with extensive mats of grasses especially *Holcus lanatus* L. (yorkshire fog) which created an impenetrable barrier to the bank voles.

4.2 Abundance and distribution

4.2.1 Relationship between rodent distributions and plant species present

With the knowledge of the preferred habitats of wood mice and bank voles, an attempt to explain their distribution and abundance at the four study sites can take place. Both distribution and abundance can be explained to some extent by the vegetation present, and the structure of that vegetation. As has already been discovered, bank voles were trapped more often in areas with a high percentage of medium-tall herbaceous cover which had an open structure at ground level. Species of plant present in the study sites that fit this structural description were most commonly *Mercurialis perennis*, *Allium ursinum* and *Urtica dioica*, plus some other less common species. These species have very small basal areas, but large leaf surface areas and provide the ideal structure for bank voles to move around without creating noise or movement of the vegetation which could attract predators. It is also interesting that these species of plant which appear to be so important structurally for bank vole habitats are thought to be unpalatable to rodents because of the toxins they contain to prevent grazing damage seed predation (Hulme, *pers. comm.*). A study by Fernandez (1993) also showed that bank voles were trapped in large numbers under *Calluna vulgaris*, because of it's ideal structure rather than because of its use as a food plant. Inevitably, plants species of the types just described formed the major part of the vegetation in areas of high bank vole captures at the study sites, with significant results most notably on the lower north-facing slope of Horsleyhope Ravine, the lower east-facing slope of Greta Gorge, the north-facing lower slope of Hawthorn Dene, and the lower east-facing slope of Castle Eden Dene. These areas are all in the valley bottoms of the study sites and on the slopes that receive the least sunlight. These shady conditions are preferred by *Allium ursinum* and *Mercurialis perennis* and show how climatic conditions can determine what plant species can grow and how these in turn can determine the composition of the small mammal community.

Wood mice were trapped more frequently in areas of more medium and tall woody cover, with the ground layer being fairly open with only sparse cover given by short herbaceous plant species. Live woody cover was given by shrub species such as *Crataegus monogyna* under which herb growth was limited because of a lack of light, those herbs which could survive included *Viola riviniana* Reich. (common violet) and

Hedera helix L. (ivy). This vegetation type was seen on parts of the upper south-facing slope of Hawthorn Dene, where wood mice were trapped significantly more often than by chance. Other cover which was categorised as being shrub cover was given by low branches from canopy trees, particularly *Taxus baccata*, often when they have fallen over but are still living. *Taxus baccata* has a very dense canopy, under which very little else grows, with the ground cover often being bare soil. Wood mice were trapped in large numbers at Castle Eden Dene with no significant preferences for slope or side of the site in either session, this being the site with the highest densities of *Taxus baccata* which cover much of the west-facing slope and parts of the upper and middle east-facing slope. Dead woody cover was comprised of brash, which was recorded most often in the areas of coniferous plantation on the upper and middle, north and east-facing slopes of Horsleyhope Ravine and Greta Gorge respectively. Herbaceous ground vegetation is also scarce under closed canopy conifers, except for species such as *Oxalis acetosella* and various species of Pteridophyte, due to a lack of light, and increased soil acidity from the coniferous leaf litter. Wood mice were most significantly associated with this vegetation type on the middle slopes of both sites in session two.

The discriminant function plot indicated that traps catching both species were characterised by a greater amount of shrub or brash cover, than for traps catching each species separately, and intermediate levels of herb cover. This habitat structure is difficult to quantify in terms of plant species because traps catching both species were relatively rare and no continuous blocks of vegetation emerged as being typical habitat for both species. Furthermore, no positive associations between wood mice and bank voles were detected, and it should not be considered as a normal occurrence.

There were two main types of area that caught neither species in the traps, both were typified by a very open woodland structure with well spaced mature trees, and very little or no understorey or shrub layer. One type consisted of a ground layer with leaf litter and short herbs such as *Anemone nemorosa*, *Oxalis acetosella*, and *Hedera helix*, or *Vaccinium myrtillus* and short grasses, seen on parts of the upper and middle north-facing slope of Hawthorn Dene and the upper south-facing slope of Horsleyhope Ravine respectively. The other type was in areas of dense almost continuous areas of *Luzula sylvatica*, with large accumulations of leaf litter which, in contrast to the species *Mercurialis perennis* and *Allium ursinum*, has a very large basal area and a lower leaf surface area, the opposite of the preferred vegetation structure of wood mice and bank voles. *Luzula sylvatica* therefore, provided little medium-tall cover while the dense growth at ground level prevented easy and secretive movements of both wood mice and bank voles. This second vegetation type was seen most obviously on the upper west-facing slope of Greta Gorge. It is possible that rodents may have been present in this vegetation type, and constructed runways through litter, with the only chance of capture being if a trap was placed in a runway. This is however unlikely since it has been shown that bank voles avoid areas of dense cover at ground level (Healing et al. 1983).

During the fieldwork and the subsequent data analysis, it became apparent that several trap sites which appeared to be ideal in structure and species composition for one or other of the two species, had no captures. Fleming (1979) concluded from a survey of published data on small rodent habitat choice, that the important cues appear to be food or foraging areas and/or shelter. One can assume from the vegetation structure of the trap sites in question that they are adequate with respect to the provision of shelter, and therefore maybe they are lacking in available food resources. Another explanation could be the proximity of these traps to predators or abnormal amounts of disturbance.

4.2.2 Relationship between rodent distributions and habitat structure of sites

The discussion of the previous paragraphs and the data from the analysis of spatial distribution highlight the fact that at all sites there are significant differences in the distributions of wood mice and bank voles with respect to slope. On the north-facing side of Horsleyhope Ravine and the east-facing side of Greta Gorge the highly significant separation of wood mice on the upper and middle slopes and bank voles on the lower slope could be due to the marked change in habitat from the mixed coniferous plantation with little herb layer on the upper and middle slopes to a distinctly deciduous strip of woodland along the stream bank with lush dense herbaceous vegetation. The two discrete habitats enhanced the microhabitat differences of wood mice and bank voles. The significant difference in distribution of wood mice and bank voles on the north-facing side of Horsleyhope Ravine was reinforced by the significant negative association shown in the tests of association with chi-square.

At Hawthorn Dene, both wood mice and bank voles showed significantly different distributions over the whole site in both sessions. Bank vole captures consistently outnumbered those of wood mice, and they dominated the whole site. There were no obvious shifts in gross habitat types as there was at Horsleyhope Ravine and Greta Gorge, with the whole site consisting of deciduous tree species, except for several *Taxus baccata* on the lower north slope, and large continuous expanses of suitable herbaceous and shrubby cover in the form of *Rubus fruticosus* for bank voles. The fact that the site consists of so much typical bank vole habitat explains their large abundance here. It appeared that wood mice lived where they were able, and work by Ashby (1967) in Houghall Wood suggested that there was no tendency for the density of wood mice to be locally reduced by high concentrations of bank voles, and concluded that the local anomalies in density were usually caused independently in the two species.

Castle Eden Dene, in contrast to Hawthorn Dene had larger abundances of wood mice than bank voles over the whole site except on the lower east-facing slope in session two. In this case the high coverage given by *Taxus baccata* determined much of the wood mouse distribution, while bank voles were found in well vegetated (by herbs) areas between stands of *Taxus baccata*.

4.2.3 Seasonal variation in vegetation and rodent distributions

The seasonal changes in vegetation structure were due to ongoing spring growth, with the emergence of leaves on trees and shrubs, and the increased coverage and height of herbs. Species contributing most to the overall increase in herb height over 40cm at all sites were mostly *Pteridium aquilinum* and *Urtica dioica*. The largest and most significant amounts of change in vegetational cover between the first and second trapping sessions, were seen at Horsleyhope Ravine. This is most likely to be because the site was first trapped in the last week of April when very little woody vegetation had come into leaf, excepting the evergreen species (*Picea abies* L. (norway spruce), *Taxus baccata, Ilex aquifolium* L. (holly)) and the growing season was just commencing.

The changes in vegetation cover could have caused some of the recorded changes in wood mouse and bank vole distribution and abundance. Trap site fidelity correlation coefficients for wood mice at Horsleyhope Ravine and Castle Eden Dene were relatively low, and may be linked to the overall increase in percentage herb cover at these sites causing them to change their distributions. Significant changes in their distributions were actually recorded in the spatial distribution data at these sites. Wood mice at the remaining two sites, Greta Gorge and Hawthorn Dene showed the highest trap site fidelities between sessions. An explanation for this is that they are restricted in the habitat available to them at these sites, limiting the amount of distributional change that is possible. The relatively similar correlations for bank voles at all sites indicates that once herbaceous cover is available, they are less likely to move away from it. Since bank voles are so reliant on vegetative cover, it would be interesting to know how their distributions change once species such as *Allium ursinum* and *Mercurialis perennis* die down at these sites. It has been suggested that changes in bank vole distribution are likely to happen as the vegetation changes with the seasons, such that the highest abundances of bank voles will be found in the areas of densest cover at the time of year concerned (Ashby 1967; Kikkawa 1964). Other reasons for changes in distribution, of wood mice or bank voles, at this time of year could be due to changes in the availability and distribution of food resources, and to the onset of the breeding season, when male wood mice especially tend to move large distances in search of mates.

4.3 Concluding remarks

Wood mice and bank voles are ecologically similar species with respect to body size and general ecology, and regularly co-occur in various types of woodland. Their coexistence is possible due to differences in their times of activity, and in their preferred choice of food and their habitat selection (Gurnell 1985). I conclude however, that their main source of separation is due to habitat selection, with their relative habitat configurations being significantly different. This kind of time, dietary and habitat separation means that interspecific competition is unlikely to occur for the majority of the time, although intraspecific competition may occur at high densities. The habitat selection of both species was similar at all sites, despite the discriminant analysis misleadingly suggesting that different cues were being used in the selection procedure. Shifts in distribution of rodents were seen with respect to time and seasonal habitat change at some sites, and as mentioned earlier, it would be interesting to see how bank vole distributions change once herbaceous cover becomes scarce in the autumn and winter. Finally, I would suggest that small mammal community structure within a site is dependent on the habitat structure and species composition of that site, and knowledge of these factors could enable predictions of the estimated abundances and distributions of wood mice and bank voles.

REFERENCES

Ashby, K. R. (1967) Studies on the ecology of field mice and voles (*Apodemus sylvaticus, Clethrionomys glareolus* and *Microtus agrestis*) in Houghall Wood, Durham. *Journal of Zoology, London* **152,** 389-513.

Brown, L. E. (1956) Field experiments on the activity of the small mammals (*Apodemus, Clethrionomys* and *Microtus*). *Proceedings of the Zoological Society of London* **126,** 549-564.

Corke, D. (1971) The local distribution of the yellow-necked mouse (*Apodemus flavicollis*). *Mammal Review* **1,** 62-66.

Corke, D. (1974) *The comparative ecology of the two British species of* Apodemus *(Rodentia: Muridae).* Ph.D. thesis, University of London.

Dueser, R. D. & Shugart, H. H. (1978) Microhabitats in a forest-floor small mammal fauna. *Ecology* **59,** 89-98.

Evans, F. C. (1942) Studies of a small mammal opulation in Bagley Wood, Berkshire. *Journal of Animal Ecology* **11,** 182-97.

Fairley, J. S. (1967) A woodland population of *Apodemus sylvaticus* (L.) at Seaforde, Co. Down. *Proceedings of the Royal Irish Academy* **65 B,** 407-424.

Fernandez, F. A. S. (1993) *Responses of rodent populations to spatial heterogeneity and successional changes within Sitka spruce* (Picea sitchensis) *plantations at Hamsterley Forest, County Durham.* Ph.D. thesis, University of Durham.

Fleming, T. H. (1979) Life history strategies. In: *Ecology of small mammals* (ed. Stoddart, D. M.), pp. 1-61. Chapman and Hall, London.

Fretwell, S. D. (1972) *Populations in a seasonal environment.* Princeton University Press, Princeton, N.J.

Gause, G. F. (1934) *The struggle for existence.* Hafner, New York.

Gibb, J. (1954) The feeding ecology of tits, with notes on the treecreeper and goldcrest. *Ibis* **96,** 513-543.

Grant, P. R. (1975) Population performance of *Microtus pennsylvanicus* confined to woodland habitat, and a model of habitat occupancy. *Canadian Journal of Zoology* **53,** 1447-1465.

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

Gorman, M. L. & Zubaid, A. (1993) A comparative study of the ecology of woodmice *Apodemus sylvaticus* in two contrasting habitats: deciduous woodland and maritime sand-dunes. *Journal of Zoology, London* **229,** 385-396.

Gurnell, J. (1981) Woodland rodents and tree seed supplies. In: *The worldwide fur-bearer conference proceedings* (eds Chapman, J. A. & Pursley, D.), pp. 1191-1214. R. R. Donnelly and Sons Co., Falls Chard, Virginia, U.S.A.

Gurnell, J. (1985) Woodland rodent communities. *Symposium of the Zoological Society of London* **55,** 377-411.

Halama, K. J., and Dueser, R. D. (1994) Of mice and habitats: tests for density-dependent habitat selection. *Oikos* **69,** 107-114.

Healing, T. D., Jewell, V. T., Jewell, P. A., Rowlands, I. W. & Gipps, J. W. (1983) Populations of bank vole (*Clethrionomys glareolus*) and long-tailed field mouse (*Apodemus sylvaticus*) on Skomer Island, Dyfed. *Journal of Zoology (London)* **199,** 447-460.

Hoffmeyer, I. (1973) Interaction and habitat selection in the mice *Apodemus flavicollis* and *A. sylvaticus*. *Oikos* **24,** 108-116.

Hulme, P. E. (1994) Survey and description of natural yew woodlands (*Taxus baccata*) in terms of past and present patterns of regeneration in the coastal denes and limestone gorges of County Durham. *Bulletin of the British Ecological Society* **25,** 28-34.

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

Krebs, J. R. (1971) Territory and breeding density in the great tit *Parus major* L. *Ecology* **52,** 2-22.

Lance, A. N. (1973) Numbers of wood mice (*Apodemus sylvaticus*) on improved and unimproved blanket bog. *Journal of Zoology, London* **171,** 471-473.

MacArthur, R. H. (1958) Population ecology of some warblers of northeastern coniferous forests. *Ecology* **39,** 599-619.

Miller, R. S. (1955) Activity rhythms in the wood mouse *Apodemus sylvaticus* and the bank vole *Clethrionomys glareolus*. *Proceedings of the Zoological Society of London* **125,** 505-519.

Montgomery, W. I. (1980) Spatial organisation in sympatric populations of *Apodemus sylvaticus* and *A. flavicollis* (Rodentia: Muridae). *Journal of Zoology, London* **192,** 379-401.

Montgomery, W. I. (1989) *Peromyscus* and *Apodemus*: patterns of similarity in ecological equivalents. In: *Biology of Peromyscus* (eds Kirkland, G. L. & Layne, J. L.), pp. 293-366. Texas Technical Press, Austin, Texas.

Partridge, L. (1978) Habitat selection. In: *Behavioural ecology: an evolutionary approach* (eds Krebs, J. R. & Davies, N. B.), pp. 351-376. Blackwell, Oxford.

Perrins, C. (1978) *British tits*. New Naturalist.

Rexstaad, E. A., Miller, D. D., Flather, C. H., Anderson, E. M., Hupp, J. W. & Anderson, D. R. (1988) Questionable multivariate statistical inference in wildlife habitat and community studies. *Journal of Wildlife Management* **52,** 794-798.

Schroder, G. D. & Rosenzweig, M. L. (1975) Perturbation analysis of competition and overlap in habitat utilisation between *Dipodomys ordii* and *Dipodomys merriami*. *Oecologia* **19**, 9-28.

Simonetti, J. A. (1989) Microhabitat use by small mammals in central Chile. *Oikos* **56**, 309-318.

Southern, H. N. & Lowe, V. P. W. (1968) The pattern of distribution of prey and predation in tawny owl territories. *Journal of Animal Ecology* **37**, 75-97.

Svärdson, G. (1949) Competition and habitat selection in birds. *Oikos* **1**, 157-174.

Watts, C. H. S. (1968) The foods eaten by the wood mouse (*Apodemus sylvaticus*) and the bank vole (*Clethrionomys glareolus*) in Wytham Woods, Berkshire. *Journal of Animal Ecology* **37**, 25-41.

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

Whitham, T. G. (1978) Habitat selection by *Pemphigus* aphids in response to resource limitation and competition. *Ecology* **59**, 1164-1176.

APPENDIX 1

Raw data and calculations for all significant chi-square tests on vegetation stucture associations with rodents.

A. Horsleyhope Ravine

1. Mice versus non-mice for dead vegetation

observed frequency(total number touches at each height category)

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-30cm	35-90cm	sum
mice	66	8	3	0	0	3	18	10	108
non-mice	194	79	51	36	31	24	21	12	448
sum	260	87	54	36	31	27	39	22	556

expected frequency

mice	50.5036	16.89928	10.48921	6.992806	6.021583	5.244604	7.57554	4.273381
non-mice	209.4964	70.10072	43.51079	29.00719	24.97842	21.7554	31.42446	17.72662

(o-e)^2/e

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-30cm	35-90cm	sum
mice	4.754879	4.686424	5.347233	6.992806	6.021583	0.960654	14.34477	7.674055	50.7824
non-mice	1.146266	1.129763	1.289065	1.685766	1.451632	0.231586	3.458114	1.849995	12.24219
sum	5.901145	5.816187	6.636299	8.678571	7.473214	1.19224	17.80288	9.52405	**63.02459**

2. Mice versus non-mice for live vegetation

observed frequency

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-40cm	40-90cm	sum
mice	47	16	13	12	12	25	20	51	28	13	7	9	253
nonmice	118	83	64	64	78	128	71	84	55	59	24	26	854
sum	165	99	77	76	90	153	91	135	83	72	31	35	1107

expected frequency

mice	37.71003	22.62602	17.59801	17.36947	20.56911	34.96748	20.79765	30.85366	18.96929	16.45528	7.084914	7.999097
non-mice	127.29	76.37398	59.40199	58.63053	69.43089	118.0325	70.20235	104.1463	64.03071	55.54472	23.91509	27.0009

(o-e)^2/e

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-40cm	40-90cm	sum
mice	2.288611	1.940425	1.20137	1.659877	3.569896	2.84123	0.030592	13.15484	4.299254	0.725541	0.001018	0.12524	31.8379
non-mice	0.678008	0.574857	0.355909	0.491743	1.057592	0.841723	0.009063	3.897161	1.273667	0.214944	0.000302	0.037103	9.432071
sum	2.966619	2.515282	1.557279	2.15162	4.627488	3.682953	0.039655	17.05201	5.572921	0.940485	0.001319	0.162343	**41.26997**

3. Voles versus non-voles for dead vegetation

observed frequency

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	25-35cm	40-90cm	sum
vole	61	19	8	7	6	11	5	9	8	134
non-vole	196	68	49	31	26	17	18	13	10	428
sum	257	87	57	38	32	28	23	22	18	562

expected frequency

vole	61.27758	20.74377	13.59075	9.060498	7.629893	6.676157	5.483986	5.245552	4.291815
non-vole	149.2669	51.78648	37.31673	23.60854	19.80071	12.94662	13.70819	9.900356	7.615658

(o-e)^2/e

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	25-35cm	40-90cm	sum
vole	0.001257	0.146586	2.299833	0.468589	0.348177	2.800357	0.042714	2.687207	3.203921	11.99864
non-vole	14.63139	5.076196	3.657847	2.314148	1.940899	1.269049	1.343699	0.970449	0.746499	31.95018
sum	14.63265	5.222782	5.957681	2.782738	2.289075	4.069406	1.386413	3.657656	3.950421	**43.94882**

4. Voles versus non-voles for live vegetation

observed frequency

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-40cm	40-90cm	sum
vole	46	16	14	12	30	40	29	61	40	38	17	11	354
nonvole	119	87	62	63	60	103	61	74	43	34	14	24	744
sum	165	103	76	75	90	143	90	135	83	72	31	35	1098

expected frequency

vole	53.19672	33.20765	24.50273	24.18033	29.01639	46.10383	29.01639	43.52459	26.75956	23.21311	9.994536	11.28415
non-vole	111.8033	69.79235	51.49727	50.81967	60.98361	96.89617	60.98361	91.47541	56.24044	48.78689	21.00546	23.71585

(o-e)^2/e

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-40cm	40-90cm	sum
vole	0.973609	8.916717	4.50184	6.135582	0.033343	0.808104	9.26E-06	7.016492	6.551272	9.419329	4.910337	0.007155	49.27379
non-vole	0.463249	4.242632	2.142005	2.91935	0.015865	0.384501	4.41E-06	3.338492	3.117138	4.481778	2.33637	0.003405	23.44479
sum	1.436858	13.15935	6.643845	9.054932	0.049207	1.192605	1.37E-05	10.35498	9.66841	13.90111	7.246706	0.01056	**72.71858**

5. Mice versus voles for dead vegetation

observed frequency

	0-2cm	2-4cm	4-6cm	6-8cm	10-15cm	15-20cm	25-35cm	40-60cm	sum
mice	66	8	3	0	3	12	9	7	108
vole	61	19	8	13	11	5	9	8	134
sum	127	27	11	13	14	17	18	15	242

expected frequency

mice	56.67769	12.04959	4.909091	5.801653	6.247934	7.586777	8.033058	6.694215
vole	70.32231	14.95041	6.090909	7.198347	7.752066	9.413223	9.966942	8.305785

(o-e)^2/e

	0-2cm	2-4cm	4-6cm	6-8cm	10-15cm	15-20cm	25-35cm	40-60cm	sum
mice	1.533329	1.360972	0.742424	5.801653	1.68841	2.567169	0.116391	0.013968	13.82432
vole	1.235817	1.096903	0.598372	4.675959	1.360808	2.069062	0.093808	0.011258	11.14199
sum	2.769146	2.457875	1.340796	10.47761	3.049218	4.636231	0.210199	0.025226	**24.9663**

B. Greta Gorge

1. Mice versus non-mice for dead vegetation

observed frequency

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	20-25cm	30-90cm	sum
mice	62	20	18	16	12	19	6	11	22	186
non-mice	323	177	152	130	110	96	34	25	18	1065
sum	385	197	170	146	122	115	40	36	40	1251

expected frequency

mice	57.24221	29.29017	25.27578	21.70743	18.13909	17.09832	5.947242	5.352518	5.947242
non-mice	327.7578	167.7098	144.7242	124.2926	103.8609	97.90168	34.05276	30.64748	34.05276

(o-e)^2/e

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	20-25cm	30-90cm	sum
mice	0.395453	2.946628	2.094375	1.500629	2.077746	0.211505	0.000468	5.958701	43.3295	58.515
non-mice	0.069065	0.514622	0.365778	0.262082	0.362874	0.036939	8.17E-05	1.040675	7.567406	10.21952
sum	0.464518	3.46125	2.460153	1.762711	2.440619	0.248444	0.00055	6.999375	50.89691	**68.73453**

2. Mice versus non-mice for live vegetation

observed frequency

	0-2cm	2-6cm	8-10cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-40cm	40-45cm	45-50cm	50-90cm	sum
mice	10	21	5	12	6	11	2	9	3	6	3	7	95
non-mice	117	84	75	166	140	146	104	145	81	74	45	84	1261
sum	127	105	80	178	146	157	106	154	84	80	48	91	1356

expected frequency

mice	8.897493	7.356195	5.60472	12.4705	10.22861	10.99926	7.426254	10.7891	5.884956	5.60472	3.362832	6.375369
non-mice	118.1025	97.64381	74.39528	165.5295	135.7714	146.0007	98.57375	143.211	78.11504	74.39528	44.63717	84.62463

(o-e)^2/e

	0-2cm	2-6cm	8-10cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-40cm	40-45cm	45-50cm	50-90cm	sum
mice	0.136614	25.30567	0.065246	0.017752	1.748152	4.94E-08	3.964883	0.29667	1.414279	0.027878	0.039148	0.061199	33.07749
non-mice	0.010292	1.906454	0.004915	0.001337	0.131701	3.72E-09	0.298703	0.02235	0.106548	0.0021	0.002949	0.004611	2.49196
sum	0.146906	27.21212	0.070162	0.019089	1.879853	5.32E-08	4.263586	0.31902	1.520827	0.029978	0.042097	0.065809	**35.56945**

3. Voles versus non-voles for dead vegetation

observed frequency

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	20-25cm	30-90cm	sum
vole	70	20	14	14	10	20	12	10	12	182
non-vole	315	177	156	132	112	95	28	26	28	1069
sum	385	197	170	146	122	115	40	36	40	1251

expected frequency

vole	56.01119	28.66027	24.73221	21.24061	17.749	16.73062	5.819345	5.23741	5.819345
non-vole	328.9888	168.3397	145.2678	124.7594	104.251	98.26938	34.18066	30.76259	34.18066

(o-e)^2/e

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	20-25cm	30-90cm	sum
vole	3.493709	2.616874	4.657101	2.468216	3.383121	0.638881	6.564399	4.330817	6.564399	34.71752
non-vole	0.594813	0.445529	0.792883	0.42022	0.575985	0.108771	1.117606	0.737333	1.117606	5.910746
sum	4.088521	3.062403	5.449985	2.888436	3.959106	0.747652	7.682005	5.068149	7.682005	**40.62826**

4. Voles versus non-voles for live vegetation

observed frequency

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-40cm	40-45cm	45-50cm
vole	39	9	9	16	23	41	35	44	33	51	37	38	22
non-vole	88	17	24	30	57	137	111	113	73	103	47	42	26
sum	127	26	33	46	80	178	146	157	106	154	84	80	48

	50-55cm	55-60cm	60-65cm	70-90cm	sum
vole	14	10	9	12	442
non-vole	20	10	11	5	914
sum	34	20	20	17	1356

expected frequency

vole	41.39676	8.474926	10.75664	14.9941	26.0767	58.02065	47.58997	51.17552	34.55162	50.19764	27.38053	26.0767	15.64602
non-vole	85.60324	17.52507	22.24336	31.0059	53.9233	119.9794	98.41003	105.8245	71.44838	103.8024	56.61947	53.9233	32.35398

vole	11.0826	6.519174	6.519174	5.541298
non-vole	22.9174	13.48083	13.48083	11.4587

(o-e)^2/e

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-40cm	40-45cm	45-50cm
vole	0.138765	0.032532	0.286872	0.067482	0.363008	4.993093	3.330688	1.006107	0.069679	0.012825	3.379561	5.451809	2.580407
non-vole	0.067105	0.015732	0.138728	0.032634	0.175547	2.414603	1.610683	0.486542	0.033696	0.006202	1.634317	2.636433	1.247855
sum	0.205871	0.048263	0.4256	0.100116	0.538555	7.407696	4.941371	1.492649	0.103375	0.019027	5.013879	8.088242	3.828262

	50-55cm	55-60cm	60-65cm	70-90cm	sum
vole	0.767983	1.858541	0.944061	7.527989	32.8114
non-vole	0.371388	0.898769	0.456537	3.64045	15.86722
sum	1.139371	2.75731	1.400598	11.16844	**48.67862**

5. Mice versus voles for live vegetation

observed frequency

	0-2cm	2-4cm	6-8cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-40cm	40-45cm	45-50cm	55-90cm	sum
mice	10	12	14	12	6	11	2	9	3	6	5	5	95
vole	39	18	39	41	35	44	33	51	37	38	36	31	442
sum	49	30	53	53	41	55	35	60	40	44	41	36	537

expected frequency

mice	8.668529	5.307263	9.376164	9.376164	7.253259	9.729981	6.191806	10.61453	7.07635	7.783985	7.253259	6.368715
vole	40.33147	24.69274	43.62384	43.62384	33.74674	45.27002	28.80819	49.38547	32.92365	36.21601	33.74674	29.63128

(o-e)^2/e

	0-2cm	2-4cm	6-8cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-40cm	40-45cm	45-50cm	55-90cm	sum
mice	0.204512	8.439894	2.280235	0.734257	0.216545	0.165771	2.837821	0.245578	2.348192	0.408865	0.699985	0.294154	18.87581
vole	0.043956	1.814004	0.490096	0.157815	0.046543	0.035629	0.609939	0.052783	0.504702	0.087878	0.150449	0.063223	4.057018
sum	0.248468	10.2539	2.770331	0.892073	0.263088	0.2014	3.44776	0.29836	2.852894	0.496744	0.850435	0.357377	**22.93283**

C. Hawthorn Dene

1. Mice versus non-mice for dead vegetation

observed frequency

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-35cm	40-65cm	sum
mice	28	11	9	6	6	9	15	4	88
non-mice	318	126	104	88	77	58	70	12	853
sum	346	137	113	94	83	67	85	16	941

expected frequency

mice	32.35707	12.8119	10.56748	8.790648	7.761955	6.265675	7.94899	1.496281
non-mice	313.6429	124.1881	102.4325	85.20935	75.23804	60.73433	77.05101	14.50372

(o-e)^2/e

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-35cm	40-65cm	sum
mice	0.586704	0.256245	0.232506	0.885909	0.399962	1.193253	6.254472	4.189462	13.99851
non-mice	0.060528	0.026436	0.023987	0.091395	0.041262	0.123102	0.645244	0.432207	1.444161
sum	0.647232	0.282681	0.256492	0.977304	0.441224	1.316355	6.899716	4.62167	**15.44267**

2. Mice versus non-mice for live vegetation

observed frequency

	0-2cm	2-8cm	10-15cm	15-20cm	20-25cml	25-30cm	30-35cm	35-40cm	40-45cm	45-65cm	sum
mice	21	7	7	8	13	7	16	8	6	4	97
non-mice	90	140	202	125	216	133	175	110	123	128	1442
sum	111	147	209	133	229	140	191	118	129	132	1539

expected frequency

mice	6.996101	9.265107	13.17284	8.382716	14.4334	8.823912	12.03834	7.437297	8.130604	8.319688
non-mice	104.0039	137.7349	195.8272	124.6173	214.5666	131.1761	178.9617	110.5627	120.8694	123.6803

(o-e)^2/e

	0-2cm	2-8cm	10-15cm	15-20cm	20-25cml	25-30cm	30-35cm	35-40cm	40-45cm	45-65cm	sum
mice	28.03121	0.553767	2.892615	0.017473	0.142353	0.377004	1.303733	0.042574	0.558319	2.242837	36.16188
non-mice	1.885594	0.037251	0.194579	0.001175	0.009576	0.02536	0.087699	0.002864	0.037557	0.15087	2.432526
sum	29.9168	0.591018	3.087194	0.018648	0.151928	0.402365	1.391432	0.045438	0.595876	2.393708	**38.59441**

3. Voles versus non-voles for dead vegetation

observed frequency

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-65cm	sum
vole	187	67	57	49	41	34	18	18	10	14	16	511
non-vole	159	70	56	45	42	33	10	8	1	4	2	430
sum	346	137	113	94	83	67	28	26	11	18	18	941

expected frequency

vole	187.8916	74.39639	61.36344	51.0457	45.07226	36.38363	15.2051	14.11902	5.973433	9.774708	9.774708
non-vole	158.1084	62.60361	51.63656	42.9543	37.92774	30.61637	12.7949	11.88098	5.026567	8.225292	8.225292

(o-e)^2/e

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-65cm	sum
vole	0.004231	0.735339	0.310277	0.081983	0.367928	0.156161	0.513739	1.066787	2.714226	1.826458	3.964749	11.74188
non-vole	0.005028	0.873856	0.368724	0.097426	0.437235	0.185578	0.610514	1.26774	3.22551	2.170512	4.711597	13.95372
sum	0.009259	1.609195	0.679	0.179409	0.805163	0.341739	1.124253	2.334527	5.939736	3.99697	8.676346	**25.6956**

4. Voles versus non-voles for live vegetation

observed frequency

	0-2cm	2-4cm	6-8cm	8-10cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-40cm	40-45cm	45-50cm	50-55cm
vole	51	14	13	33	128	91	162	95	125	79	82	30	41
non-vole	60	22	24	41	81	42	67	45	66	39	47	17	17
sum	111	36	37	74	209	133	229	140	191	118	129	47	58

	55-60cm	60-65cm	sum
vole	10	10	964
non-vole	3	4	575
sum	13	14	1539

expected frequency

vole	69.52827	22.54971	23.17609	46.35218	130.9136	83.30864	143.4412	87.69331	119.6387	73.91293	80.80312	29.4399	36.33008
non-vole	41.47173	13.45029	13.82391	27.64782	78.08642	49.69136	85.5588	52.30669	71.36127	44.08707	48.19688	17.5601	21.66992

vole	8.14295	8.769331
non-vole	4.85705	5.230669

(o-e)^2/e

	0-2cm	2-4cm	6-8cm	8-10cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-40cm	40-45cm	45-50cm	50-55cm
vole	4.937511	3.241616	4.468087	3.846219	0.064844	0.710094	2.401188	0.608801	0.24025	0.350118	0.017729	0.010656	0.600277
non-vole	8.277845	5.43464	7.490845	6.44827	0.108712	1.190488	4.025643	1.020668	0.402785	0.586981	0.029722	0.017865	1.006377
sum	13.21536	8.676257	11.95893	10.29449	0.173556	1.900583	6.426831	1.629469	0.643035	0.937099	0.047451	0.028521	1.606654

	55-60cm	60-65cm	sum
vole	0.423512	0.17271	22.09361
non-vole	0.710027	0.289551	37.04042
sum	1.133538	0.462261	**59.13403**

5. Mice versus voles for live vegetation

observed frequency

	0-2cm	2-8cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-40cm	40-45cm	45-50cm	55-65cm	sum
mice	21	7	7	8	13	7	16	8	6	3	1	97
voles	51	60	128	91	162	95	125	79	82	71	20	964
sum	72	67	135	99	175	102	141	87	88	74	21	1061

expected frequency

mice	6.582469	6.125353	12.34213	9.050895	15.99906	9.325165	12.89067	7.953817	8.04524	6.765316	1.919887
voles	65.41753	60.87465	122.6579	89.9491	159.0009	92.67484	128.1093	79.04618	79.95476	67.23468	19.08011

(o-e)^2/e

	0-2cm	2-8cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-40cm	40-45cm	45-50cm	55-65cm	sum
mice	31.5786	0.124892	2.312271	0.122019	0.56218	0.579764	0.749995	0.000268	0.519936	2.095631	0.440751	39.08631
voles	3.177515	0.012567	0.232666	0.012278	0.056568	0.058337	0.075466	2.7E-05	0.052317	0.210867	0.044349	3.932959
sum	34.75612	0.137459	2.544938	0.134297	0.618748	0.638101	0.825461	0.000295	0.572253	2.306498	0.4851	**43.01927**

D. Castle Eden Dene

1. Mice versus non-mice for dead vegetation

observed frequency

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	25-50cm	sum
mice	89	44	38	29	16	11	10	10	247
non-mice	171	86	78	59	50	39	10	3	496
sum	260	130	116	88	66	50	20	13	743

expected frequency

mice	86.43338	43.21669	38.56258	29.25437	21.94078	16.6218	6.648721	4.321669
non-mice	173.5666	86.78331	77.43742	58.74563	44.05922	33.3782	13.35128	8.678331

(o-e)^2/e

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	25-50cm	sum
mice	0.076215	0.014198	0.008207	0.002212	1.608551	1.901399	1.689207	7.460878	12.76087
non-mice	0.037954	0.00707	0.004087	0.001101	0.801033	0.946866	0.841198	3.715397	6.354706
sum	0.114169	0.021268	0.012295	0.003313	2.409584	2.848264	2.530405	11.17627	**19.11557**

2. Mice versus non-mice for live vegetation

observed frequency

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-40cm	40-45cm	45-50cm
mice	48	22	21	32	26	62	56	70	40	41	24	12	7
non-mice	61	20	22	27	35	83	77	88	52	65	30	28	20
sum	109	42	43	59	61	145	133	158	92	106	54	40	27

	50-55cm	55-60cm	60-65cm	65-75cm	80-95cm	sum
mice	7	4	0	6	6	478
non-mice	14	9	14	14	17	659
sum	21	13	14	20	23	1137

expected frequency

mice	45.47931	17.52414	17.94138	24.61724	25.45172	60.5	55.4931	65.92414	38.38621	44.22759	22.53103	16.68966	11.26552
non-mice	63.52069	24.47586	25.05862	34.38276	35.54828	84.5	77.5069	92.07586	53.61379	61.77241	31.46897	23.31034	15.73448

mice	8.762069	5.424138	5.841379	8.344828	9.669305
non-mice	12.23793	7.575862	8.158621	11.65517	13.33069

(o-e)^2/e

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-40cm	40-45cm	45-50cm
mice	0.139709	1.143186	0.521429	2.214104	0.011811	0.03719	0.00463	0.251996	0.067845	0.235539	0.095773	1.317754	1.615073
non-mice	0.100028	0.818494	0.373331	1.585246	0.008456	0.026627	0.003315	0.180424	0.048576	0.16864	0.068571	0.943481	1.156354
sum	0.239738	1.961679	0.89476	3.79935	0.020267	0.063817	0.007945	0.43242	0.116421	0.404179	0.164344	2.261235	2.771428

	50-55cm	55-60cm	60-65cm	65-75cm	80-95cm	sum
mice	0.354355	0.373915	5.841379	0.658877	1.392427	16.27699
non-mice	0.25371	0.267715	4.182289	0.47174	1.009985	11.66698
sum	0.608066	0.64163	10.02367	1.130618	2.402412	**27.94398**

3. Voles versus non-voles for live vegetation

observed frequency

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-40cm	40-45cm	45-50cm
vole	53	30	28	35	27	61	49	72	42	59	31	20	19
non-vole	56	12	15	24	34	84	84	86	50	47	23	20	8
sum	109	42	43	59	61	145	133	158	92	106	54	40	27

	50-55cm	55-60cm	60-65cm	65-70cm	75-80cm	85-95cm	sum
vole	16	11	8	11	9	9	581
non-vole	5	2	6	4	3	7	563
sum	21	13	14	15	12	16	1144

expected frequency

vole	55.43966	21.36207	21.87069	30.00862	31.02586	73.75	67.64655	80.36207	46.7931	53.91379	27.46552	20.34483	13.73276
non-vole	53.56034	20.63793	21.12931	28.99138	29.97414	71.25	65.35345	77.63793	45.2069	52.08621	26.53448	19.65517	13.26724

vole	10.68103	6.612069	7.12069	7.62931	6.103448	8.125874
non-vole	10.31897	6.387931	6.87931	7.37069	5.896552	7.874126

(o-e)^2/e

	0-2cm	2-4cm	4-6cm	6-8cm	8-10cm	10-15cm	15-20cm	20-25cm	25-30cm	30-35cm	35-40cm	40-45cm	45-50cm
vole	0.107358	3.49282	1.717753	0.830224	0.522389	2.204237	5.139861	0.870114	0.490966	0.479831	0.454846	0.005845	2.020266
non-vole	0.111125	3.615375	1.778025	0.859354	0.540718	2.281579	5.320207	0.900645	0.508193	0.496667	0.470805	0.00605	2.091153
sum	0.218484	7.108194	3.495778	1.689578	1.063107	4.485816	10.46007	1.770759	0.99916	0.976498	0.925651	0.011894	4.111419

	50-55cm	55-60cm	60-65cm	65-70cm	75-80cm	85-95cm	sum
vole	2.64875	2.911939	0.108583	1.489197	1.374635	0.094032	26.96365
non-vole	2.741689	3.014112	0.112393	1.54145	1.422868	0.097039	27.90945
sum	5.390439	5.92605	0.220976	3.030647	2.797502	0.191071	**54.87309**

APPENDIX 2

Pooled within-groups correlations between discriminating variables and canonical discriminant functions obtained from the discriminant analyses carried out on each site for each session. **Bold** denotes the largest absolute correlation between each variable and any discriminant function.

a) Horsleyhope Ravine, session 1

	Function 1	Function 2	Function 3
% moss cover	**.39517**	.04243	-.11342
% herb cover	**.38625**	.11107	-.05358
% herbs 20-30cm	**.36571**	.33108	-.22874
% log cover	**.30969**	-.23378	-.08499
% litter cover	**-.23529**	-.14709	.10284
% soil cover	**-.08841**	-.00057	.01871
% herbs 30-40cm	.34080	**.77538**	-.18048
% canopy cover	-.06276	**.09101**	.08101
% brash cover	-.04848	-.14531	**.56053**
No. of trees	.01166	-.07765	**.35532**
No. of shrubs	-.22117	-.26153	**-.32470**
% shrub cover	-.20992	-.12662	**-.23986**
% herbs 0-10cm	.08350	-.06994	**.21093**
% herbs 10-20cm	.10883	.16532	**.16585**
No. of saplings	.00409	-.15999	**.16364**

b) Horsleyhope Ravine, session 2

	Function 1	Function 2	Function 3
No. of trees	**.49178**	.08145	.32400
No. of shrubs	**.24099**	-.08482	-.04534
% herb cover	-.00278	**.42152**	-.38080
% moss cover	-.02094	**.36127**	.05764
% herbs 30-40cm	-.18143	**.28186**	.00078
% herbs 10-20cm	.07884	**-.19700**	.05132
% herbs >40cm	-.09954	**.15157**	.01773
% soil cover	-.01275	**-.12800**	-.10584
% herbs 20-30cm	.23577	.31539	**-.46611**
% litter cover	-.08259	-.14358	**.42143**
% shrub cover	.13185	.12256	**.38209**
% canopy cover	-.16452	.15274	**.35218**
% brash cover	.03463	.02152	**.31885**
% herbs 0-10cm	-.11266	-.08447	**.16857**
No. of saplings	.05301	.06067	**-.15355**
% log cover	-.09614	.07759	**-.11456**

c) Greta Gorge, session 1

	Function 1	Function 2	Function 3
% soil cover	**-.34999**	-.23554	-.03763
% shrub cover	**-.33320**	.28272	-.17588
% brash cover	**-.17280**	-.09040	.10738
% herbs 10-20cm	**.09888**	-.01546	-.06787
% herbs 30-40cm	.17833	**.74347**	-.04804
% herb cover	.31724	**.49409**	-.16327
No. of shrubs	-.18397	**.30393**	.13711
% herbs >40cm	.15158	**.29670**	-.13058
% canopy cover	-.21996	**-.24938**	-.01734
No. of saplings	.02522	**.21326**	.16686
% herbs 0-10cm	.02359	**.03308**	-.00086
% herbs 20-30cm	.28020	.34529	**-.36530**
No. of trees	-.10477	-.11558	**.33255**
% log cover	-.22385	-.22385	**.33219**
% moss cover	-.04172	.00579	**.22747**
% litter cover	.19848	-.21944	**.22568**

d) Greta Gorge, session 2

	Function 1	Function 2	Function 3
% herb cover	**.55822**	.06977	.13946
% herbs >40cm	**.34505**	.19128	.17033
% canopy cover	**-.10684**	-.04819	.02816
% herbs 10-20cm	.15957	**-.44747**	.19504
% brash cover	-.11679	**.42378**	.12353
% log cover	-.08466	**.37416**	-.27100
No. of shrubs	-.01680	**.22292**	.13534
% herbs 0-10cm	-.23853	.05993	**-.50671**
% herbs 20-30cm	.04017	-.06459	**.42116**
% litter cover	-.24429	-.03089	**.40296**
% soil cover	-.17754	.15778	**-.35290**
No. of saplings	.24165	-.07657	**-.34798**
No. of trees	-.00211	-.03476	**-.28137**
% herbs 30-40cm	.26324	.05592	**.28032**
% shrub cover	-.15533	-.19552	**-.26212**
% moss cover	.08837	.00410	**-.12976**

e) Hawthorn Dene, session 1

	Function 1	Function 2	Function 3
No. of trees	**-.48371**	.16115	.21444
% herbs 10-20cm	**-.31535**	-.22691	.08718
% herb cover	**-.30518**	-.18967	-.21163
% canopy cover	**-.29618**	-.05405	.14165
% herbs 20-30cm	**.18993**	.05138	.04248
% herbs 30-40cm	.07976	**-.39651**	-.32410
% brash cover	.31318	**.39130**	.01426
% soil cover	.21563	**.35189**	.22966
No. of shrubs	-.08481	**.25526**	-.25290
% moss cover	.18974	**.23417**	-.13661
% herbs 0-10cm	-.29620	.22214	**.54825**
% shrub cover	.17070	.30787	**-.41204**
% herbs >40cm	.14922	-.13986	**-.32321**
% log cover	.08978	-.31087	**.31200**
No. of saplings	.16218	-.22843	**.27828**
% litter cover	.06092	.02016	**.19786**

f) Hawthorn Dene, session 2

	Function 1	Function 2	Function 3
No. of trees	**-.48371**	.16115	.21444
% herbs 10-20cm	**-.31535**	-.22691	.08718
% herb cover	**-.30518**	-.18967	-.21163
% canopy cover	**-.29618**	-.05405	.14165
% herbs 20-30cm	**.18993**	.05138	.04248
% herbs 30-40cm	.07976	**-.39651**	-.32410
% brash cover	.31318	**.39130**	.01426
% soil cover	.21563	**.35189**	.22966
No. of shrubs	-.08481	**.25526**	-.25290
% moss cover	.18974	**.23417**	-.13661
% herbs 0-10cm	-.29620	.22214	**.54825**
% shrub cover	.17070	.30787	**-.41204**
% herbs >40cm	.14922	-.13986	**-.32321**
% log cover	.08978	-.31087	**.31200**
No. of saplings	.16218	-.22843	**.27828**
% litter cover	.06092	.02016	**.19786**

g) Castle Eden Dene, session 1

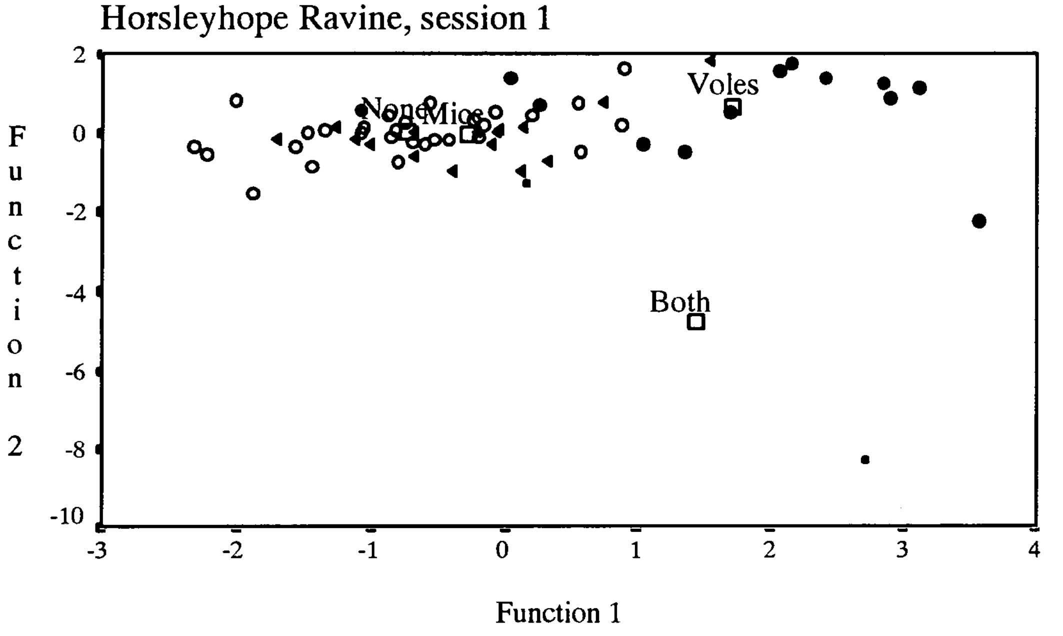
	Function 1	Function 2	Function 3
% soil cover	**.50893**	-.04154	-.03164
No. of trees	**.40564**	-.15223	.21413
% herb cover	**-.36244**	.19432	-.20644
% herbs >40cm	**-.35614**	.27652	.08416
% brash cover	**.30317**	-.01985	-.04975
% shrub cover	**.27719**	.16865	-.17922
% herbs 10-20cm	**-.25087**	.10119	.02373
% moss cover	**-.23699**	.14955	-.01623
No. of shrubs	-.24277	**.50782**	-.02052
% herbs 30-40cm	-.31800	**.40905**	.13569
% herbs 0-10cm	-.22178	**-.30554**	-.24422
% log cover	.11744	**-.17304**	.14644
No. of saplings	-.00810	-.24209	**.51363**
% litter cover	-.16972	-.11435	**.25571**
% herbs 20-30cm	.12469	.05404	**.13312**
% canopy cover	.07807	.02202	**-.08859**

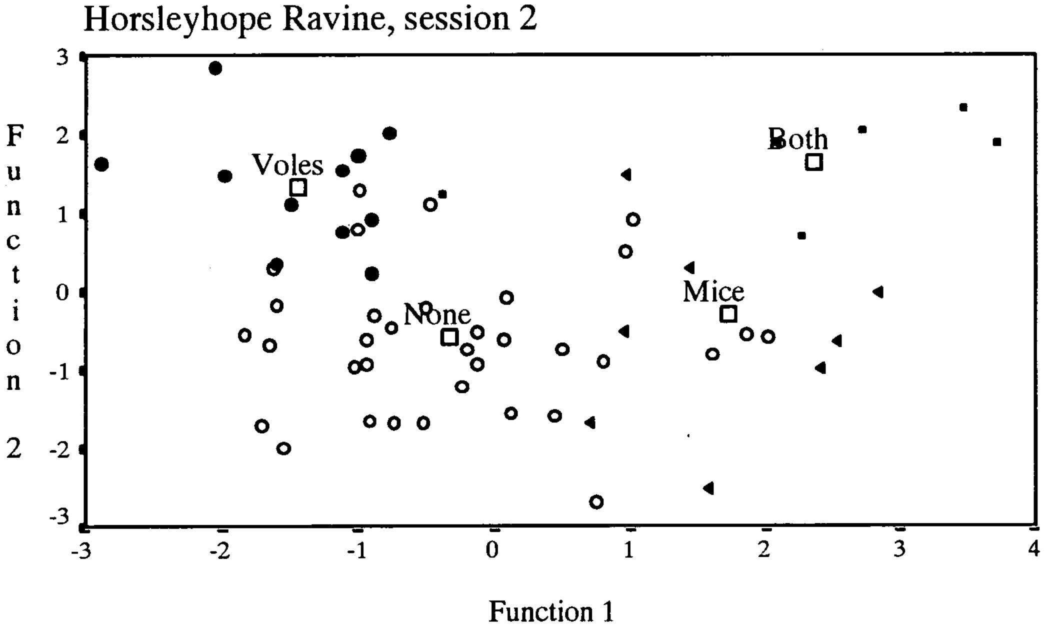
h) Castle Eden Dene, session 2

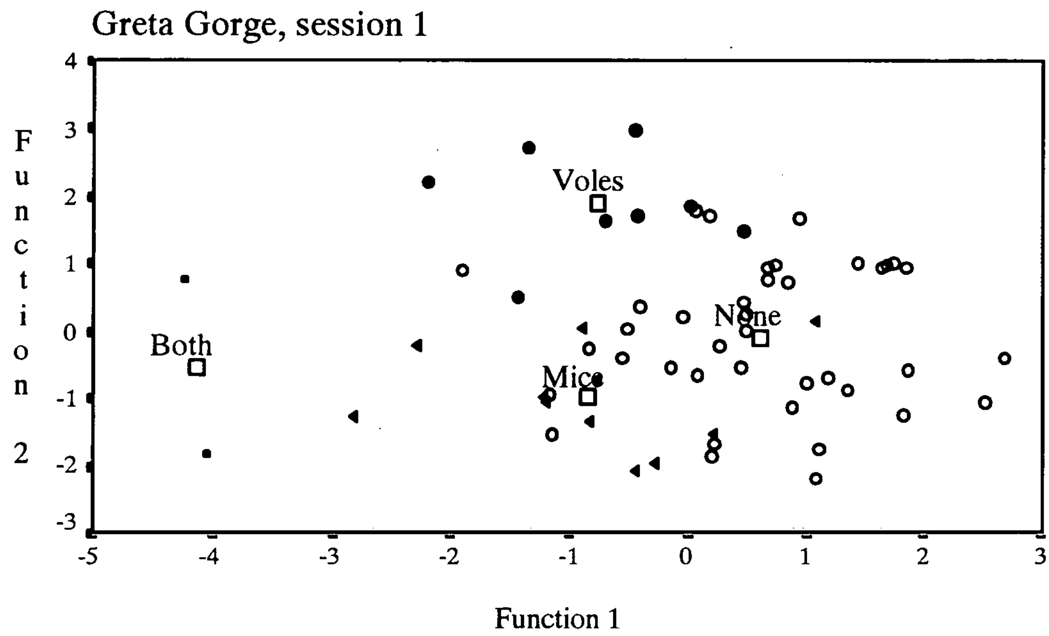
	Function 1	Function 2	Function 3
% shrub cover	**.37792**	.12554	.05333
% litter cover	**-.23277**	-.07870	-.20192
No. of shrubs	.23812	**.63746**	-.19031
% soil cover	.15253	**-.60695**	.32080
% herbs >40cm	-.13035	**.54823**	-.21127
% herb cover	.03442	**.46974**	-.30431
% herbs 30-40cm	-.00350	**.42196**	.26606
% moss cover	.00858	**.36977**	.24138
% herbs 20-30cm	.09890	**.13542**	-.02996
% brash cover	.04718	-.09113	**.40274**
No. of trees	-.16883	-.16824	**.36713**
% log cover	.07554	-.14627	**.30828**
% canopy cover	.03895	-.17851	**.24221**
% herbs 10-20cm	.06247	.02893	**-.21216**
% herbs 0-10cm	.03084	.14751	**-.17647**
No. of saplings	-.08757	.11873	**-.13434**

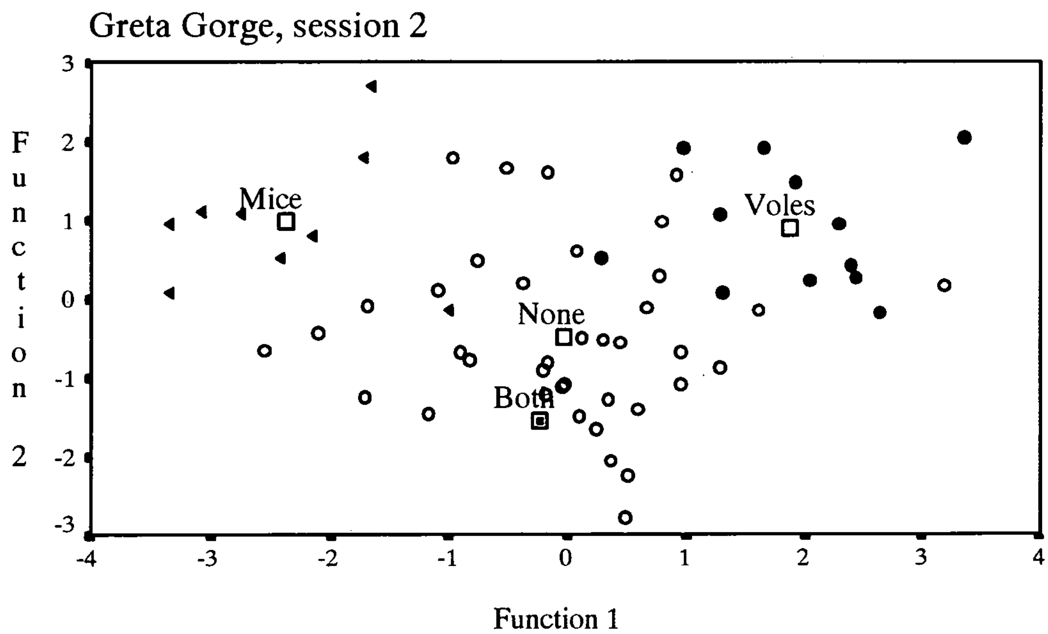
APPENDIX 3

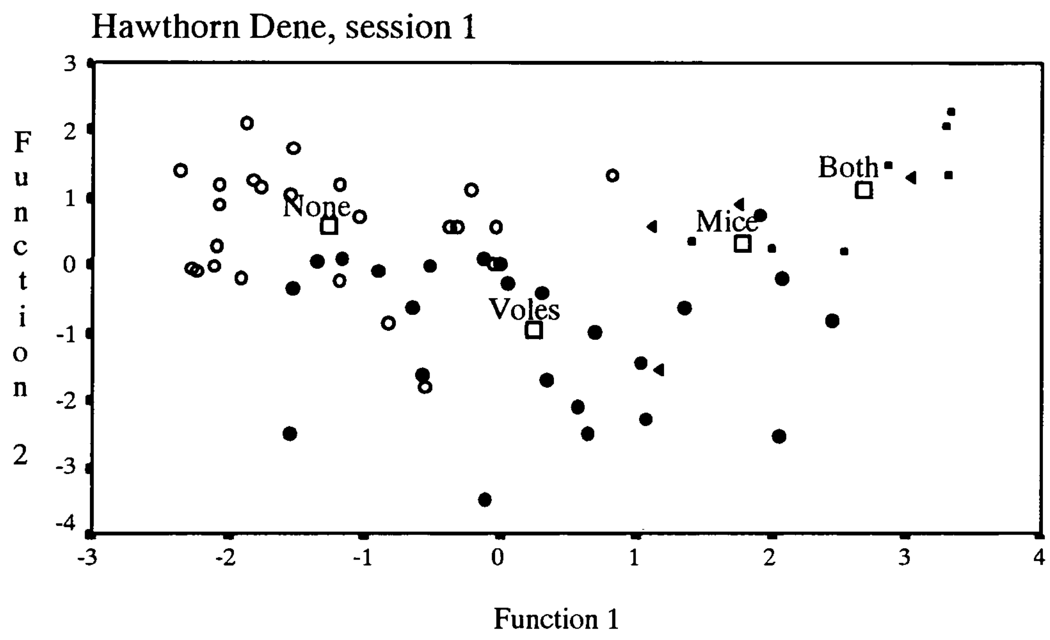
Canonical discriminant function plots, obtained after discriminant analysis was carried out on each site for each session. Symbols used in the plots are defined as follows: □ Group centroids; ○ No rodents trapped; • Voles only trapped; ◄ Mice only trapped; ■ Both species trapped.

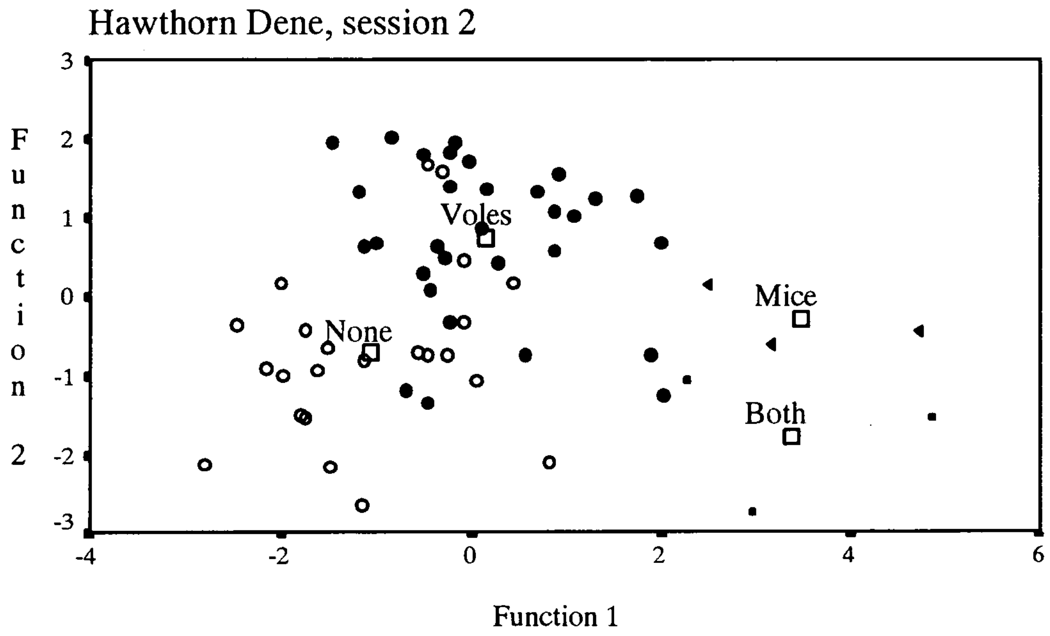




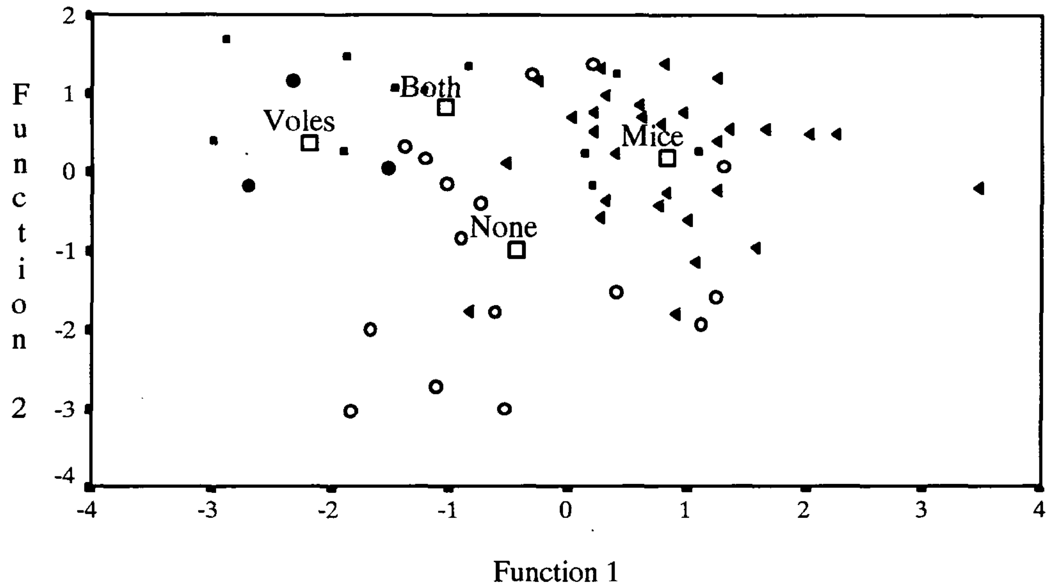

Greta Gorge, session 1
Function 2
Function 1
Voles
None
Both
Mice
4
3
2
1
0
-1
-2
-3
-5
-4
-3
-2
-1
0
1
2
3


Greta Gorge, session 2
Function 2
Function 1
Mice
Voles
None
Both
3
2
1
0
-1
-2
-3
-4
-3
-2
-1
0
1
2
3
4


Hawthorn Dene, session 1
Function 2
Function 1
None
Voles
Mice
Both


Hawthorn Dene, session 2
Function 2
Function 1
Voles
None
Mice
Both

Castle Eden Dene, session 1



Castle Eden Dene, session 2