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INFLUENCES OF LARGE HERBIVORES ON SMALL RODENTS IN THE NEW FOREST, HAMPSHIRE

Submitted by

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ABSTRACT

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The distribution and ecology of small rodents within grazed New Forest habitats was compared to similar areas outside the New Forest.

Intensive live trapping was carried out for two and a half years (January 1982 to June 1984) in four New Forest deciduous woodlands, grazed by ponies deer and cattle, and two woodlands outside the New Forest, grazed only by deer. For one and a half years (January 1983 to June 1984) trapping was performed in two 5 ha enclosed New Forest woodlands, one grazed by deer the other free from grazing for 22 years. Less intensive trapping was carried out in four grazed New Forest *Calluna* heathlands, and two heathlands outside the New Forest, grazed only by deer, and on two acid-grassland areas within the New Forest.

Rodent diversity and abundance was greater in the woodlands and heathlands outside the New Forest. Within the intensively grazed woodlands this is due to the absence of bank voles (*Clethrionomys glareolus*), which can be attributed to habitat modification demonstrably caused by large herbivores. Small rodents were almost totally absent from New Forest heathlands, but this is due more to management practices than to grazing.

Woodland wood mouse (*Apodemus sylvaticus*) populations were low in all sites throughout the study, probably because mast crops were poor.

Demographic comparison of wood mouse populations revealed no differences between grazed and ungrazed sites, and were similar to those reported elsewhere.

The diet of tawny owls (*Strix aluco*) in the New Forest was studied by pellet analysis. This revealed that they prey more heavily on wood mice than elsewhere, but it is not clear if this is due to the absence of bank voles and other prey, or increased wood mouse availability due to modification of woodland habitats by large herbivores.

CONTENTS

CHAPTER 7 SPECIES DIVERSITY AND SIZE OF SMALL RODENT POPULATIONS 98

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CHAPTER 1

INTRODUCTION

1.1 LARGE HERBIVORE-SMALL MAMMAL INTERACTIONS

In recent time much attention has been paid to the role of large herbivores in shaping and maintaining vegetational communities (Harper 1977; Crawley 1983). With the wide range of effects that large herbivore grazing may have upon plant communities, it is not surprising to find that it may also affect other animals within the community. For small mammals, the influence of grazing may be due either to alterations to the physical structure of the habitat or to direct competition for resources.

As far as small mammals are concerned, the primary effect of grazing is the structural modification of vegetation. Shelter has been identified as an important factor in the habitat selection by small mammals (Hansson 1978), and habitat modification by the large herbivores is a major route of indirect interaction between the two groups of mammals. Probably the most dramatic effects of this are seen in grasslands where the abundance, diversity and distribution of small mammals may be altered by grazing (Phillips 1936; Baker 1937; Birney, Grant & Baird 1976; Grant & Birney 1979; Grant, Birney, French & Swift 1982); the degree of effect depends in part upon the habitat preferences of the small mammals (Longhurst 1960; Getz 1961; Rosenzweig 1973; Grant *et al.* 1982).

The large body of data on interactions between small mammals and large herbivores in grasslands is not complemented by the information on woodlands. Most data come from experiments in which the habitat is altered; examples include herbicide treatments (Borrecco, Black & Hoven 1979), logging (Martell 1983a & b) and burning (Halvorson 1982), where changes in the lower statum are unlikely to be the same as those resulting from grazing. However, these experiments, and studies on the effects of other large mammals (e.g. pigs Singer, Swank & Clebsch 1984), reveal changes similar to those seen in grassland communities.

Direct interaction between large herbivores and small mammals is less easy to quantify than indirect effects through habitat changes. From knowledge of the ecology of small mammals one can predict that the main direct interaction is for food, both in grasslands, where small and large herbivores may compete for plant species, and in woodland where there may be competition for seed between granivorous small mammals and large herbivores. Food supply is a controlling factor in small mammal demography and so any direct interaction which alters this for species can alter demographic aspects of populations.

1.2 EFFECTS OF LARGE HERBIVORES ON VEGETATIONAL COMMUNITIES

The effects of herbivory upon vegetation communities have been extensively studied (see reviews by Harper 1977; Crawley 1983; Gessaman & MacMahon 1985; Putman in prep.). Tansley (1939) recognized much of British vegetation as plagioclimax communities, this "deflected succession" resulting from grazing or other management practices. The effects of large herbivores are complex and variable within, and between, communities and are dependent upon the herbivore and the intensity of habitat use. It is apparent that large herbivores affect all aspects of the plant community, including species composition, structure and productivity. They may also affect environmental conditions in other ways through alteration of nutrient cycling, and through trampling, leading to soil compaction. Herbivory may be thought of as a process of selection leading to the gradual development of a stable vegetation community which is grazing adapted in the sense that it is a product of a particular grazing regime.

Large herbivores have a direct effect on plant species by removing part, or sometimes all, of the plant. Feeding is usually selective and directed at preferred species which are commonly highly palatable and more erect in structure making them easily grazed. Selective feeding may reduce the vigour and abundance of preferred species and in vegetation communities with a long history of grazing leads to the development of graze tolerant genotypes, often with a prostrate growth form (*e.g.* Petterson´s (1958) study of grazing adapted *Schoenus ferrugineus* and Gray & Scott´s (1980) study of *Puccinellia maritima*).

The effects of grazing are variable depending upon the intensity of grazing and the herbivore species but the reduction in vigour of preferred species modifies the competitive relationships between the species in the community. The effects upon species diversity are variable (Gessaman & MacMahon 1985), but, the species composition usually favours unpreferred species which benefit from the reduced competition. This is seen clearly in hill pastures (Chadwick 1960) where selection for *Agrostis* and *Festuca* species has led to the spread of unpalatable *Nardus stricta*. Similar effects are found in a range of vegetation communties: woodland (Jones 1959; Adams 1975; Mann 1978); grassland (Ketling 1954; Waser & Price 1981; Edwards & Hollis 1982); heathland (Grant, Hamilton & Souter 1981; Bakker *et al.* 1983) and bogs (Rawes 1983).

The effects of large herbivores are not restricted to the grazing of preferred species. Other physical actions, such as dunging, urination and trampling, may affect both preferred and unpreferred species but again vary depending upon the intensity and species of large herbivore.

Trampling results in soil compaction which affects drainage, soil respiration and root production and therefore plant growth of all species in the community (Piggott 1983). Dunging and urination alter nutrient cycling, but the effects may be beneficial, such as the release of nitrogen from faeces stimulating plant growth (Weeda 1967), or restrictive, such as the scorching of plants from potassium in urine, or the smothering of plants by faeces. Within the community, the behaviour of the herbivore also affects the return and local distribution of nutrients. Patterns of habitat use by herbivores causes translocation and uneven distribution of nutrients within the environment which results in stimulation of plant growth in areas of high nutrient input. However, this may be further complicated by the reluctance of herbivores to feed near dung (Odberg & Francis-Smith 1977) and lead to intensive grazing and nutrient removal from some areas and low grazing and high nutrient input in others, resulting in the creation of sub-communities with markedly different species composition (Edwards & Hollis 1982).

Although the effects of herbivory are very complex, the removal of plant tissue by grazing alters the physical structure of the vegetation and usually results in a reduction in living standing crop. As with alteration of species composition, this may be seen in grasslands (Ketling 1954; Bell 1971; Sinclair 1975), heathlands (Grant _et_ _al._ 1981; Welch 1984b) and woodlands (Bratten 1975; Piggott 1983).In woodland, browsing can prevent the establishment of seedlings and the development of saplings (Adams 1975). Herbivores may also affect the population dynamics of tree species by removal of seeds (Harlow, Whelan, Crawford & Skeen 1974). These effects usually lead to a very open herb and shrub layer in heavily used woodland.

The removal and restriction of growth of vegetation affects production by altering photosynthetic rates, transpiration rates, location of nutrient storage and growth rates. McNaughton (1979) lists nine mechanisms which may compensate for this loss of tissue, the net effect often being increased production, but again this is dependent upon the intensity of grazing and the particular plant species.

Therefore, the influences of large herbivores on the vegetation communities are very complex and they may be caused by direct or indirect actions on the plant species. It is apparent that they vary between and within communities and with the herbivore species and the intensity of use.

1.3 SMALL RODENTS AND THEIR HABITATS

In terms of numbers, both of individuals and species, the Rodentia are the most successful Order of mammals, accounting for over 41% of all mammalian species (Morris 1965); most of them are small (<100g) and short-lived (Bourliere 1975). Within the Rodentia the two most successful families are the Muridae (mice and rats) and Cricetidae (voles), members of which generally weigh less than 50g. These families are found occupying a wide variety of habitats world-wide (French, Stoddart & Bobek 1975) and it is their members that are usually considered to be the ´Small Rodents´.

Partridge (1978) uses the word habitat to describe ´the conglomerate of physical and biotic factors which together make up the place in which an animal lives´. Therefore a habitat must fulfil a number of ecological requirements for the animal, but, as not all habitats are equally favourable, the animal´s problem is selection of one that best satisfies its individual basic ecological needs. These requirements, namely food availability, shelter, mate availabilty, reduction of predation and competitive pressure, are crucial to the animal´s survival and reproductive success.

From the theories of habitat selection (Fleming 1979; Rosenzweig 1974) it appears that most mammals are habitat specialists. However, the selection processes used by small rodents are still not clear. Experimental studies (Wecker 1963; Hansson 1982) have shown that a combination of innate and learned behaviour is involved, but very little is known about what environmental factors are important. Two factors, shelter and food availability (Hansson 1975,1978; Taitt & Krebs 1981), are known to be important and it has been suggested (Price 1984) that for some species food availability has priority over predator avoidance.

These habitat characteristics are the same as those influenced by large herbivores. To understand the mechanisms of interactions it is important to understand the behaviour of small rodents in habitat selection. This section reviews the current understanding of four apsects: shelter, food availabilty, predation and the use of habitats.

1.3.1 Shelter

It has long been recognised that different species of small rodents select habitats with different degrees of cover (Phillips 1936; Baker 1937; Eadie 1953). Both species diversity and demography of the different species vary depending upon the amount of shelter available and the preference of each species. Shelter may be afforded in many ways, for example by boulders, trees, leaf litter and soil, but the most important factor for rodents appears to be the degree of vegetative cover available.

Differential selection for cover is seen clearly in grassland rodents as most of these species are primarily herbivorous and are restricted to some extent by their food requirements (Hansson 1971a & b). Work by French, Grant, Grodzinski & Swift (1976) and Grant & Birney (1979) has shown the importance of cover to grassland small mammals. Habitats with high plant biomass are characterised by a high but variable mammal diversity: grasslands with low cover have high biomass and high diversity. Experimental studies have shown that the diversity and biomass of rodents can be altered by decreasing the amount of vegetative cover. Removal of cover by mowing (LoBlue & Darnell 1959) resulted in the meadow vole (Microtus pennsylvanicus) moving from mown areas whereas the prairie deer mouse

(*Peromyscus maniculatus*) gave an opposite response. Segregation can also occur between closely related species, for example *M.montanus* and *M.pennsylvanicus* were found to be spending most of their time in vegetation of different composition (Douglass 1976). Other studies using *Microtus* suggest that a threshold level of vegetative cover is necessary for these species to increase in numbers and undergo multi-year cycles (Birney *et al.* 1976); below this threshold, increased vulnerability to predation increases mortality and prevents population increase (Getz 1970; Birney *et al.* 1976). By increasing the degree of cover and thus providing protection from predation, the spring decline in numbers of *M.townsendii* has been reduced (Taitt & Krebs 1983); but emigration too was found to be important. These studies suggest that *Microtus* select habitats of increased cover to reduce vulnerability to predation. However, Price (1984), tentatively suggests that it is foraging strategy of rodents that is more important in microhabitat selection, but her review does not include *Microtus* species. The selection of cover by herbivorous grasssland rodents would be an advantage to species which are diurnal and therefore susceptible to a high degree of predation.

The selection of different levels of cover by woodland species is not so easily demonstrated as for grassland species. Local distribution of forest small mammals is related to their selection for a number of biotic characteristics (Miller, Lowell & Getz 1977; Dueser & Shugart 1978) and vegetative cover is one important factor for small rodents. Studies on the effects of woodland disturbance (Martell 1983a & b) show how reduction of tree and ground cover can affect small mammal demography and distribution.

The three Northern European woodland species of small rodent, the wood mouse (*Apodemus sylvaticus*), the yellow necked mouse (*A.flavicollis*) and the bank vole (*Clethrionomys glareolus*) all exhibit variation in numbers and occurrence depending upon the available cover. Bank voles prefer dense cover whilst wood mice appear to have no preference (Newson 1960; Kikkawa 1964; Southern & Lowe 1968; Treussier 1976), although it has been suggested that in the absence of bank voles wood mice select areas of heavy cover (Fairley & Comerton 1972; Montgomery & Bell 1981). In the Mediterranean, Abramsky (1981) found that A.sylvaticus and A.mystacinus selected different habitats but that both preferred areas with vegetative cover. The yellow necked mouse displays no apparent preference for ground cover (Hoffmeyer 1973; Corke 1974) but is found predominantly in woodland, whereas the other two species successfully occupy other habitats (Corke 1971; Corbet & Southern 1977). Habitat selection in multi-species communities would appear to be complex and competition may be a controlling factor.

The preference for habitats with high cover may be analagous to the selection of thick vegetation by Microtus, which apparently reduces the risk of predation. In deciduous woodland, tawny owls (Strix aluco) catch voles more successfully from areas of intermediate cover and wood mice more successfully from open areas (Southern & Lowe 1982). Bank voles are primarily herbivorous (Hansson 1977) and diurnal whereas wood mice are more nocturnal (Brown 1956), therefore selection for cover by voles may be both anti-predator and food selection behaviour. Wood mice would obviously gain protection from nocturnal predators if they selected areas of cover.

1.3.2 Food availability

Small rodent species exhibit granivory, herbivory or omnivory (Hansson 1985). Whilst different species show morphological and physiological features characteristic with these feeding patterns (Voronstov 1962), they are not feeding specialists and vary their diet in relation to food availability (for voles see Martell 1981; Hansson 1971a,1985 and for woodland species see Watts 1968; Zemanek 1972; Hansson 1971a,1985). For example Watts (1968) showed that wood mice are almost exclusively granivorous in the autumn but switch to other foodstuffs, such as green plant material and invertebrates, when tree seeds have been exhausted.

The degree of feeding specialisation demonstrated by a species limits the range of habitats it may occupy. Microtus species are concentrated in, but not restricted to, grasslands and may select their habitats on the basis of food availability (Getz 1961). In comparison the less specialised feeding Clethrionomys and Apodemus are able to occupy a wider range of habitats, but their population performances in these areas are not as good as in preferred ones.

The less specialised omnivores and granivores are opportunists that respond quickly to changes in habitat characteristics such as food. Wood mice make use of foods as they become available and bank voles will invade unpreferred habitats and make use of available foods (Hansson 1968,1979). Artificial manipulation of food supply results in immigration to food (Flowerdew 1972; Taitt & Krebs 1981; Abramsky 1978). Alteration of the productivity of an area, by adding water and nitrogen, leads to habitat changes followed by immigration of new species and a reduction in the numbers of previous occupants (Abramsky 1978).

The effects of diet upon demography and population success have been extensively investigated and it is now apparent, that in years of high food abundance, population structure is altered by greater juvenile survival (Smyth 1966; Bobek 1969; Watts 1970; King 1983), a longer period of fecundity in the adults (Zejda 1962; Smyth 1966; LeLoaurn & Schmitt 1972; Gashwiler 1979; Gurnell 1981; Merson, Kirkpatrick, Scanlon & Gwazdauskas 1983) and early fecundity in new recruits (Flowerdew 1972; Taitt & Krebs 1981).

Other morphological factors such as total body weight and fat content (Sawicka-Kapusta 1968; Pucek 1973) and relative weights of vital organs (Shvarts 1975) also vary in relation to food supply, for example spring plant growth (Batzli 1983) and availability of high energy foodstuffs such as tree seeds (Grodzinski & Sawicka-Kapusta 1970).

Wood mice, bank voles and field voles show annual fluctuations in population size (Hansson 1971a & b; Southern & Lowe 1982) with high autumn/winter and low summer numbers. The size of summer wood mouse populations is related to overwinter survival of animals and this is positively correlated to the size of the autumn mast crop (LeLouarn & Schmitt 1972; Vincent 1977; Flowerdew & Gardner 1978). Again artificially increasing food supply has been found to increase survival, breeding duration, weight at which sexual maturation occurs and body weight (Flowerdew 1972; Taitt 1981; Taitt & Krebs 1981).

As most species of small rodents are not dietary specialists, they are potentially competitors. Competition can be reduced by selection of different foods (Watts 1968) and plant parts (Batzli & Pitelka 1983), but it can be pronounced where the habitat of dietary specialists is occupied by those with more catholic diets. Although species must ultimately compete for certain foods, subtle differences in morphology, selection for habitat on the basis of other characteristics and seasonal variation in diet reduces this competition. The diets of more closely related species, for example, wood mice and yellow necked mice, overlap almost completely (Hansson 1985) but differences in habitat selection for other characteristics have already been noted. There seems to be little known on interspecific dietary competition, perhaps because it is not often a limiting resource, but Van Horne (1982a & b) did find dietary separation between adult and juvenile _P.maniculatus_ and _M.longicaudus_.

1.3.3 Predation

There are many rodent species occupying a wide variety of habitats, and under optimal conditions populations can achieve very high levels leading to high levels of production (Petrusewicz & Hansson 1975). Therefore rodents can form a large biomass in a habitat and it is not surprising to find they are a valuable food source to many avian (Newton 1979), mammalian (Corbet & Southern 1977) and reptilian (Beshkov & Gerasimov 1980) predators.

Most of these predators are not feeding specialists but opportunists taking advantage of the most abundant prey at any one time (e.g. weasels (Mustella nivalis) Erlinge 1975). However, small rodents can still be the main prey of some predators (e.g. Day (1966) estimated rodents to be 50% of the diet of weasels) and predation can directly affect the ecology of the prey. Small rodent offtake can be quite variable: Ryskowski, Goszcynski & Truszkowski (1973) estimated that, in arable habitats, the red fox (Vulpes vulpes) removed 39% of voles in populations at low density but only 3.2% in years of abundance. Similarly Southern & Lowe (1982) estimated that tawny owls removed 20-30% of bank vole standing crop from deciduous woodland in any two month period. It is rare though to have a one predator one prey system. King (1980), working in the same study area as Southern & Lowe (1982), estimated that weasels removed an average of 10% of the standing crop of bank voles and wood mice. The cumulative effect of predation on bank voles in this study site could therefore be very high; unfortunately, due to low wood mouse numbers during Southern & Lowe´s (1982) study, a comparison for this species is not possible. Erlinge and co-workers (1983) estimated that a number of avian and mammalian small rodent predators remove almost all the annual production of voles and mice in an agricultural system, and that about 80% of this offtake is caused by faculative predation.

Recently attention has been paid to the question of which part of the rodent populations are susceptible to predation, and how this affects rodent numbers. Some workers suggest that highest mortality is among those individuals emigrating from optimal habitats at times of population increase (Boonstra 1977; Abramsky & Tracy 1978). Boonstra's (1977) study suggests that up to 20% of the spring decline of M.townsendii populations is accountable to predation and, as previously noted, Taitt & Krebs (1983) have shown that predation does play an important role in this population change. Increased mortality has been attributed to a greater vulnerability of rodents unfamiliar with their surroundings (Metzgar 1967; Ambrose 1972) or those in unpreferred habitats (Thompson 1955; Getz 1970; Birney et al. 1976; Hansson 1977). This increased mortality reduces the population success in these areas and so restricts them to preferred ones.

It is therefore probable that predators do have a marked effect upon small rodent populations, but the importance of predation for demography is still unclear. Andersson & Erlinge (1977) suggest that the effects are dependent upon the nature and specificity of the predation. Andersson & Erlinge (1977) and Erlinge et al. (1983) suggest that predation may reduce rodent populations to levels lower than would normally be attained, restrict recovery of numbers and reduce the interval between population peaks.

1.3.4 Effects of competition

Small rodents have quite complicated social organisations and it is apparent that intraspecific competition is averted or reduced by differential habitat use, both seasonally within and between age and sex classes. Home range studies on wood mice and bank voles have revealed that these changes are related to periods of reproduction (Randolph 1977; Montgomery & Bell 1981). With recruitment there is increased intraspecific competition but adult and juvenile animals occupy different habitats, adult Peromyscus species remaining in preferred areas (Bock 1972; Van Horne 1982a). Laboratory studies on wood mice (Flowerdew 1974) suggest that in the presence of adults, juvenile and sub-adult wood mouse growth and survival is reduced. During periods of population increase, dispersal of animals reduces competition for resources (Wolton & Flowerdew 1985). Experimental control of M.townsendii dispersion (Boonstra & Krebs 1977) shows that if restricted, there is over exploitation of resources leading to a population crash; unrestricted populations did not show such drastic reduction in numbers.

Small rodents are successful because of their ability to utilise sub-optimal habitats if and when they become available. Population dispersion is often into such habitats (Hansson 1978,1979), but what may be sub-optimal for one species may be optimal for another and this can result in direct resource competition (Hansson 1983). Seasonal use of unpreferred habitats has been found to occur in wood mice (Kikkawa 1964; Corke 1974), bank voles (Bock 1972) and field voles (Hansson 1971b,1977). Bank voles and field voles have an inverse relationship regarding habitat occupation (Hansson 1983), but field voles will actively exclude the less specialised bank voles that attempt to immigrate into their preferred habitat. Immigration is not restricted to periods of high population increase but may occur in response to localised increased resource availability, such as food (see section 1.3.2).

Experimental studies with M.pennsylvanicus, C.gapperi and P.maniculatus (Grant 1969,1970a,1971) showed that, although these species do have different preferred habitats, in the absence of competitors, dispersal into unpreferred areas often occurs; on return of the normal occupant, however, the immigrants soon vacate. Grant's work was short term but it has been followed by some long term studies

(Redfield, Krebs & Taitt 1977). Basically the same results of immigration and competitive exclusion were found when *Microtus* populations were artificially maintained at low levels, but they also found *Peromyscus* extended its breeding season under these conditions in this unpreferred habitat.

If quite intense interspecific competition occurs in habitats where species are quite different, what happens in communities of closely related species or multi-species communities?. Current theory suggests microhabitat segregation with some utilisation of common resources (Pianka 1981) and this has been seen for *Microtus* (Douglass 1976) and *Apodemus* species (Hoffmeyer 1973) for the structure of the habitat selected. Manipulation of wood mouse and yellow necked mouse populations (Montgomery 1981) found that removal of the congener resulted in the remaining species making greater use of the available habitat but not changing its microhabitat associations. Montgomery (1980a & b) suggests that in the presence of bank voles these two species minimised competition by three dimensional habitat use with horizontal and vertical separation (this has been supported by other short-term studies, Brown 1981; Ward 1982; Cusworth 1983), a similar result to that found previously in other multi-species communities (Meserve 1976, 1977). In one such community Gliwicz (1981) found that *A.flavicollis* and *C.glareolus* limited *A.agarius* when all three species were present. In the absence of the other two, *A.agarius* density and reproduction increased, and there was decreased mortality and emigration. In addition to different use of space, the activity of small rodents can vary in time (Brown 1956), but this only reduces direct interaction and use of space, it does not reduce competition for resources such as food or nest sites.

1.3.5 Methodological limitations in habitat studies

It should be emphasised that apart from information on diet nearly all the above mentioned information on habitat selection comes from field studies using trapping techniques. However, no trap or trapping regime is completely effective and trapping of animals is subject to a wide range of bias (see Appendix 2 for discussion of this topic) and introducing traps into a habitat alters microhabitat characteristics. A good example is the use of bait: Teska (1980) suggests that when natural food is abundant animals are less attracted to traps than when it is scarce.

The main criticism of using traps to sample populations and make judgements on habitat selection is that one only knows where the animal was at the time of capture and does not know what the animal was doing: was it foraging or was it transient?. Some workers have used other techniques to examine habitat selection: Randolph (1973) used wool fibres in the diet; Webster & Brooks (1980) radioactively labelled animals and Lemen & Rosenzweig (1978) used labelled seeds, examining faeces to indicate where the animals had fed. The use of radiotelemtry is becoming more widespread (Wolton 1983; Ormiston 1985). This technique allows unrestricted movement of the animals, enabling one to study movement, activity and habitat use, and should provide further new information on these subjects.

1.3.6 Summary

Small rodents are primarily habitat specialists and in optimal habitats densities can be very high. However, their success lies in their ability to occupy sub-optimal habitats as and when they become available. The exact mechanisms of habitat selection are still unclear but it is obvious that rodents respond to a conglomerate of factors related to their morphology, physiology and social organisation. Intraspecific competition is reduced by social organisation whilst microhabitat selection in space, diet, time & competitive interaction are all responsible for reducing interspecific competition. Experimental studies have shown how small rodent communities can be affected by habitat manipulation, affecting abundance, diversity and population success.

1.4 AIMS OF THIS STUDY

The preceding sections have shown that large herbivores may have a profound influence upon the species composition, structure and productivity of vegetation. Evidence has been presented to show that through these effects they may in turn affect the ecology of small rodents. The New Forest, Hampshire, provides an excellent system in which to study such interactions. It has been subjected to large herbivore grazing since at least the Bronze Age, and the ecological history since the eleventh century is well known. Recent studies (*e.g.* Putman, Edwards, Pratt & Ekins 1981) have quantified some of the effects of large herbivores upon the Forest ecology. There have been a number of other ecological studies within the Forest, including work on reptiles (Spellerberg & Phelps 1977; Goddard 1981,1984), birds (Bibby 1979; Parr 1984; Tubbs & Tubbs 1985), badgers (*Meles meles*) (Packham 1983) and foxes (Dobson 1985).

Despite all this work, there have been no systematic studies of small rodents within the Forest (but see short term work of Hedges 1967) though some workers have noted the dramatic effects of a long history of large herbivore grazing (Tubbs 1968,1982), and the effects of such on small rodent populations are well documented (section 1.1 & 1.3).

The primary aim of this study is to compare the ecology of small rodents in vegetation subject to heavy use by large herbivores within the New Forest with that in similar areas where use is much lower. Through this comparison, and a knowledge of small rodent habitat selection, an attempt can be made to understand the influence of large herbivores upon the small mammal community.

The first part of the study investigates differences in small rodent diversity, abundance and distribution between New Forest sites and similar habitats outside the Forest perambulation. Work has concentrated on three vegetation communities which account for a large proportion of the Forest area open to grazing by cattle, ponies and deer; these are heathland, deciduous woodland and acid grassland adjoining the woodland. The study goes on to examine in detail the dynamics of small rodent populations in deciduous woodlands subject of different intensities of grazing and, finally, examines the predation pressure from tawny owls on the woodland small rodent populations.

The fieldwork for Chapter 11 of this thesis was done in conjunction with a study of New Forest raptors, conducted by Dr G Hirons, and the Chapter contains some data previously published (Hirons 1984). It is declared that all analysis and other fieldwork is my own original work.

CHAPTER 2

THE STUDY AREA AND STUDY SITES

2.1 THE NEW FOREST

The New Forest is a unique mosaic of plant communities including heathlands, grasslands, valley bogs, deciduous and coniferous woodlands. It covers 37,500 ha and is situated on the south coast of Britain between the River Avon, at Fordingbridge, and Solent Estuary (figure 2.1). The various communities of the Forest have been affected by over 900 years of heavy grazing by wild and domestic herbivores, and owe many of their unique features to past and present patterns of grazing. Due to this the Forest offers an ideal area in which to study the effects of intensive large herbivore grazing. This Chapter outlines the history, climate, geology, flora, management and large herbivore fauna of the area; it also summarises current knowledge on the effects of large herbivores on the vegetation.

2.1.1 History

The History of the New Forest has been documented for almost 900 years, from the Domesday Book (1086) to the present day (Countryside Commission 1984). Although the history of grazing can be followed from just prior to the Domesday Book when William I declared the area a Royal Hunting Forest, it is almost certain that pastoral agriculture was practised in the area since the Bronze Age when much of lowland Britain was disafforested. In 1086 the Forest covered 57,000 ha and much of the original afforestation is attributed to William I who managed the area for deer hunting. Due to poor soil quality (see section 2.1.3), it is unlikely that the Forest ever maintained a large arable agricultural community but with the advent of

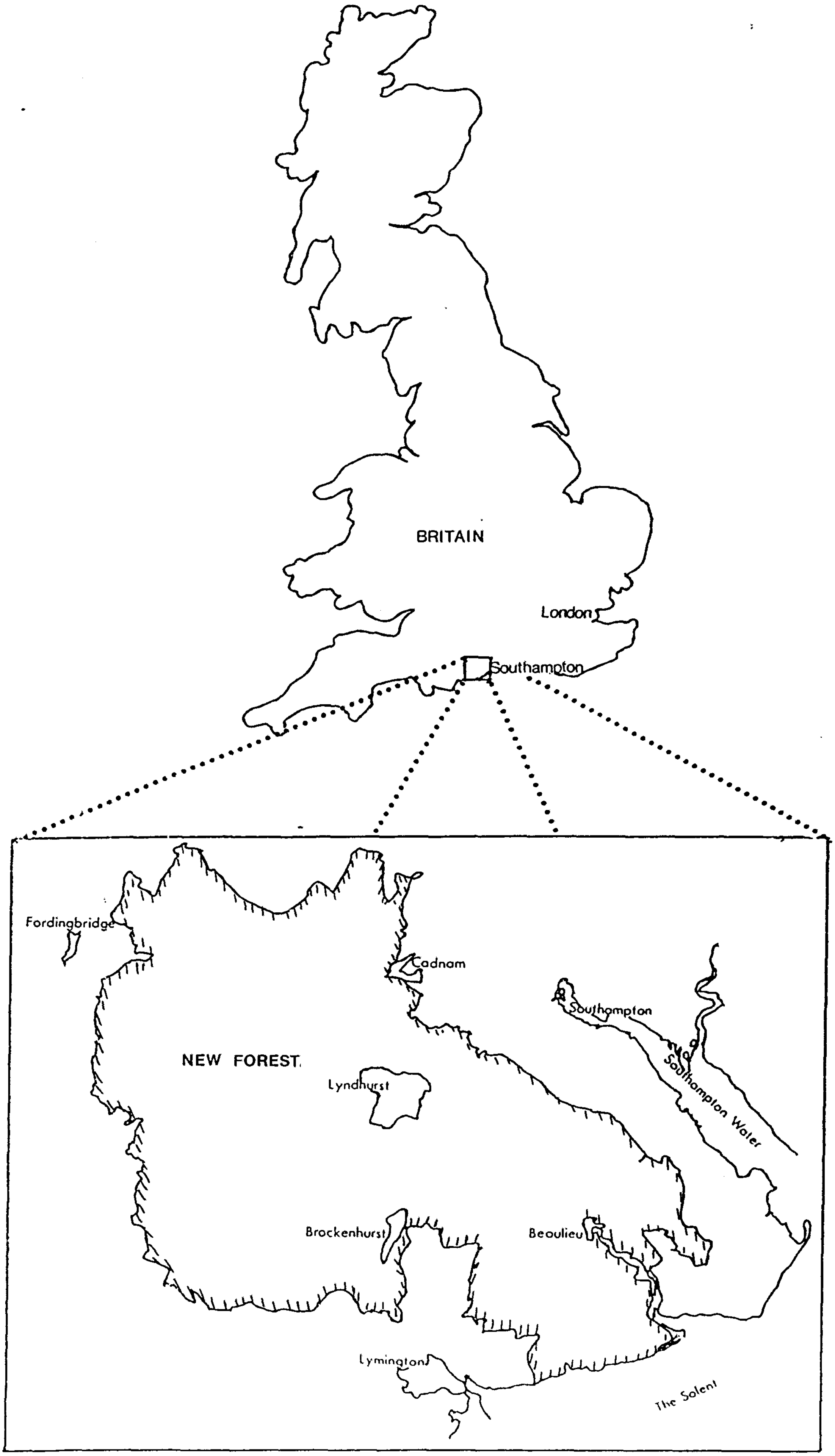


Figure 2.1 Maps showing the location of the New Forest on the south coast of Britain and its position in relation to Southampton. \\\\\ = New Forest boundary.

the Royal Hunting Forest the inhabitants lost their Common Law rights. However, they were accorded privileges by the Crown, including pasture, estover, marl and pannage (table 2.1), which are now embodied in law. Today, the rights of Commoners are safeguarded by the Verderer´s Court.

With time the economic priorities in the New Forest have changed. During the 15th Century the supply of timber for ships became important, and areas of woodland were enclosed to protect them from grazing by deer and commoners animals. This enclosure and resulting loss of grazing land led to conflict between the Crown and Commoners. A series of Acts enabled the enclosure of more woodland until the New Forest Act of 1877 finally stopped further loss of grazing for the commoners´ animals. During the 19th century the Deer Removal Act 1851 also led to an attempt to remove the Forest deer population. Although numbers were reduced to very low levels following this Act they have clearly increased since then to their present levels (see section 2.1.4).

In 1923 the Forestry (Transfer of Woods Act) passed management of the New Forest from the Crown to the Forestry Commission. This led to an attempt at economic management of the Forest by enforcing the right to enclose areas for timber production and by replacing slow growing hardwoods with fast growing softwoods. This again resulted in loss of grazing for commoners´ animals and resulted in two more Acts of Parliament: the New Forest Act 1949 and the New Forest Act 1964 which were passed to govern the Forestry Commission´s administration of the area.

The Forestry Commission now acts as a land agent, and the Verderers Court is responsible for the commoner´s interests and visual amenities. Today the Forest is designated as a Site of Special Scientific Interest (S.S.S.I.) and the Nature Conservancy Council (N.C.C.) provides advice on management activities which may affect its ecology and wildlife. Apart from its interest to naturalists and scientists, some 6 million holiday makers visit the area annually and, in an attempt to protect the Forest environment, these are now carefully "managed". A detailed description of the history of the New Forest and the present policy of administration can be found in Tubbs (1968) and the history of the New Forest Commoners in Countryside Commission (1984).

Table 2.1 The Rights of New Forest Commoners established by William I and officially recognized by Queen Victoria in 1854 (Right of Common 1858).

A commoner occupying a house with a garden plot has five Rights of Common throughout the New Forest. These rights extend outside the current perambulation of the Forest.

1. Common of pasture for cattle, horses and sheep on the Open Forest provided each animal is branded.

2. Common of mast is the Right to turn pigs onto the Forest during the Pannage season.

3. Common of turbary allows the commoner to cut turf for burning in his home. For every turf cut, the two adjacent turfs must be left so avoiding stripping the area.

4. Common of fuelwood (estover) is an allocation of one or more cords of wood.

5. Common of marl is the Right to take marl for dressing the land (now almost obsolete).

The New Forest covers approximately 37,500 ha and about half of this (19,000 ha) is Open Forest (the area open to grazing by commoners´ animals), 23% (10,522 ha) is residential or private land and the remainder is enclosed for sylviculture (Small 1979). Under the Rights of Common 1858 the whole of the Open Forest is available for grazing by commoners´ animals.

2.1.2 Climate

The New Forest has an oceanic climate with mild wet winters, where temperatures average 4^{o}c, and warm summers. Precipitation is low, the annual average is 750-875 mm, of which very little falls as snow, with rainfall being evenly distributed throughout the year. The Forest stretches approximately 25 miles north from the Solent to the River Avon and rainfall between coastal and inland areas varies considerably. Fisher (1973) showed that average precipitation bewteen 1916 and 1950 was 891 mm at Linwood (GR:179095) in the centre of the Forest but only 731 mm at Everton (GR:303937) in the south. Equivalent temperature data do not exist but temperature records for Southampton show a July maximum of 21.5^{o}c whilst coastal stations recorded 20^{o}c. It is probable that similar differences exist within the Forest.

2.1.3 Geology

The Forest lies in the Hampshire Basin, a chalk syncline which outcrops in the north and south; the highest sector being 128m above sea level in the north but considerably lower in the south at only 15-20m. The Forest is underlain by sedimentary rock laid down during a series of marine transgressions and retreats in the Tertiary Era. As a result of folding, the older Eocene strata are exposed in the North and the younger Oligocene strata are exposed in the south. Folding and erosion of these beds means the Forest has a patchwork of exposed beds of different ages (figure 2.2). Of the Eocene formations, Reading beds and London Clay are exposed outside the Forest but the Bagshot beds are exposed in the extreme north and the Bracklesham beds, Barton Sands and Barton clays are exposed over a broad central belt of the Forest. Most of these deposits are of low base status, especially the Barton Sands, and form acidic and relatively infertile soils. The southern area is underlain by the Headon beds from the Oligocene era and, although large areas of these beds are covered by gravels, they occur mainly as loams, clays and clay marls making this region the most fertile.

2.1.4 Vegetation and Management

There is no comprehensive account of the New Forest vegetation but information is available in Tubbs(1968) and Putman *et al.*(1981). The vegetation is an assemblage of communities: woodlands, heathlands, grasslands and bogs, whose distribution can be attributed to the considerable variations in edaphic factors over the area. The relative proportions of each vegetation are shown in figure 2.3. Of the 19,000 ha of Open Forest the Ancient and Ornamental deciduous woodlands (referred to for adminstrative purposes as A & O woodlands) occupy approximately 3,400 ha, and consist of beech (*Fagus sylvatica*) and oak (*Quercus petraea*) often with an understorey of holly (*Ilex aquifolium*), bracken (*Pteridium aquilinum*) in the shrub layer and brown bent (*Agrostis capillaris*) on the woodland floors. These woodlands are found at lower altitudes on the fertile clays and loams and are often fringed by *A.capillaris*/*Molinia caerulea* dominated acid grasslands. These natural grasslands occupy approximately 5,000 ha of the Open Forest and in many places have large coverings of bracken in the summer. A large proportion of the Open Forest, 8,200 ha, consists of

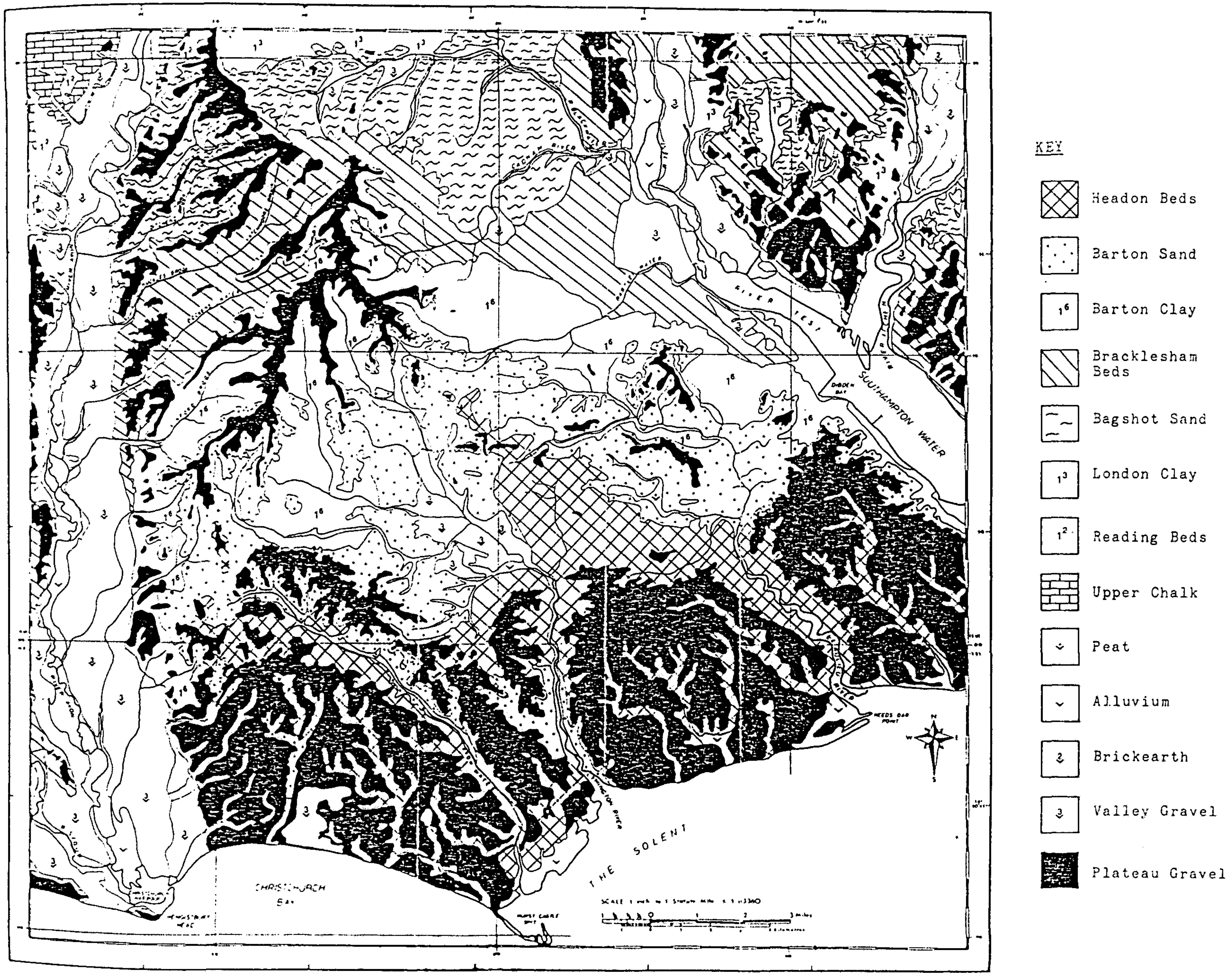


Figure 2.2 Geological map of the New Forest.

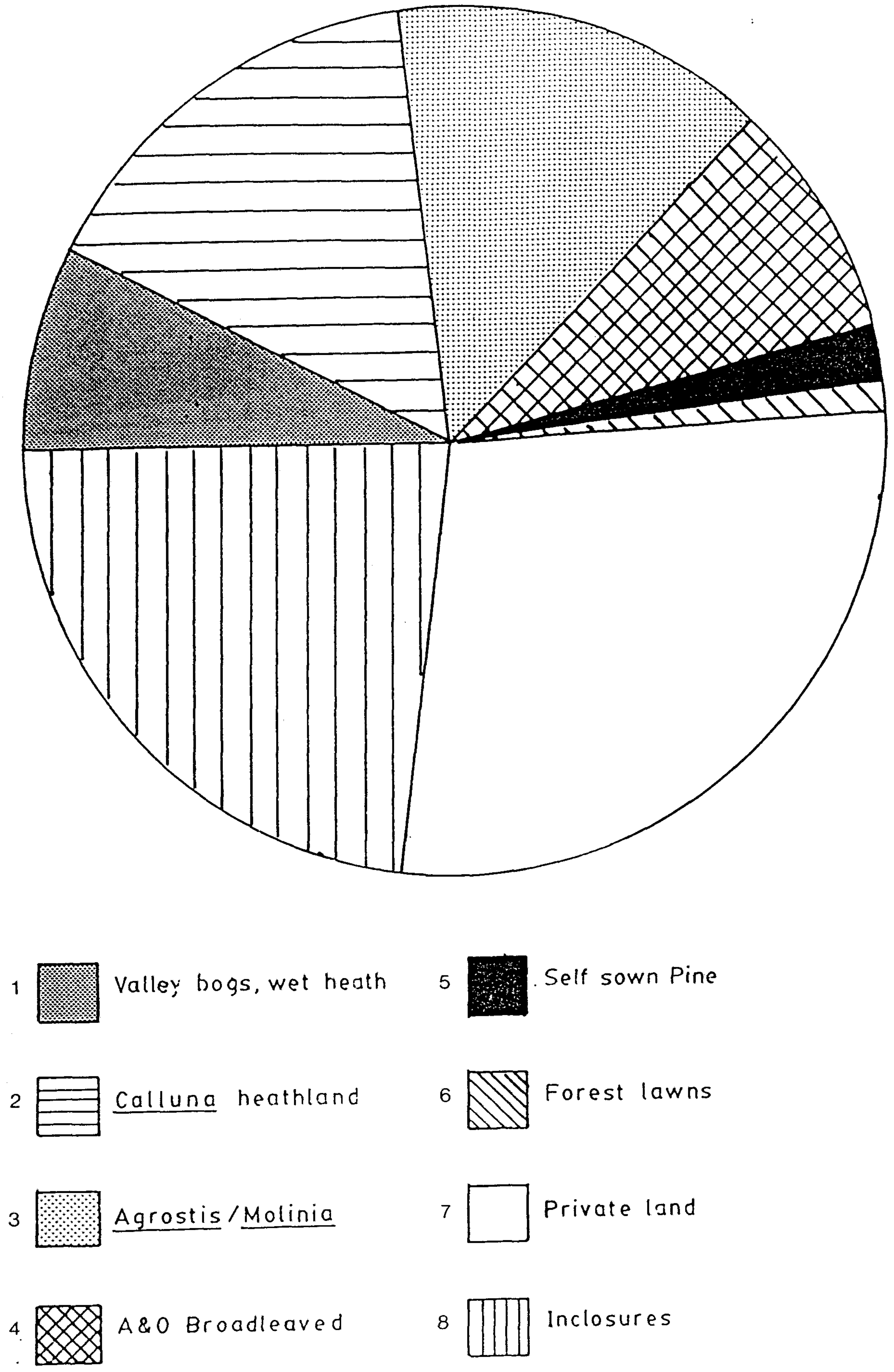


Figure 2.3 The relative proportions of the major vegetation communities within the New Forest. Communities 1 to 6 Open Forest. (Source: Countryside Commission 1984).

species poor *Calluna* dominated dry heaths, constituting the largest area of heathland in Hampshire, which occupy the heavily leached and base poor plateau gravels. In areas of poor drainage the *Calluna* heathland gives way to more complex heath and valley bog vegetation often dominated by *Molinia* and *Erica tetralix* but with many other species present; these wetter heathlands and bogs account for the remaining 3,200 ha of Open Forest.

The Forest management policy has led to the creation of new vegetation community types and influences existing ones. The most obvious new communities are the reseeded lawns, areas of acid grassland fenced, ploughed, fertilised and cropped for potatoes and oats during the 2nd World War; these were later reseeded with ley and unfenced so opening them to grazing. Although the sown species have largely disappeared, the areas still comprise a very distinct vegetation type (Edwards & Hollis 1982). In the late 1960´s and early 1970´s attempts were made to improve grazing by swiping bracken from some areas and liming acid grasslands. This has led to distinct vegetational communities being created which are termed Commoners´ Improved Grassland. Rotational burning or cutting of heathlands has been practised since 1870 (Tubbs 1974) so heathland areas are a patchwork of different aged communities.

The New Forest Act of 1964 authorised the enclosure of up to 10,000 ha of the Forest for commercial sylviculture and at present this right is exercised upon just over 8,000 ha, 2,000 ha of deciduous woodland (primarily beech and oak), 4,500 ha of coniferous plantations of various species and 1,200 ha of mixed woodlands.

Management within the enclosed woodlands leads to intensive thinning, opening the understorey to use by deer and, sometimes, ponies. When deciduous plantations are deemed old enough these may be opened to grazing which leads to plantations having little understorey. Although Rights of Estover are controlled by the Forestry Commission, fallen trees are soon removed, so removing a valuable microhabitat for fauna and flora.

2.1.5 The large herbivore population

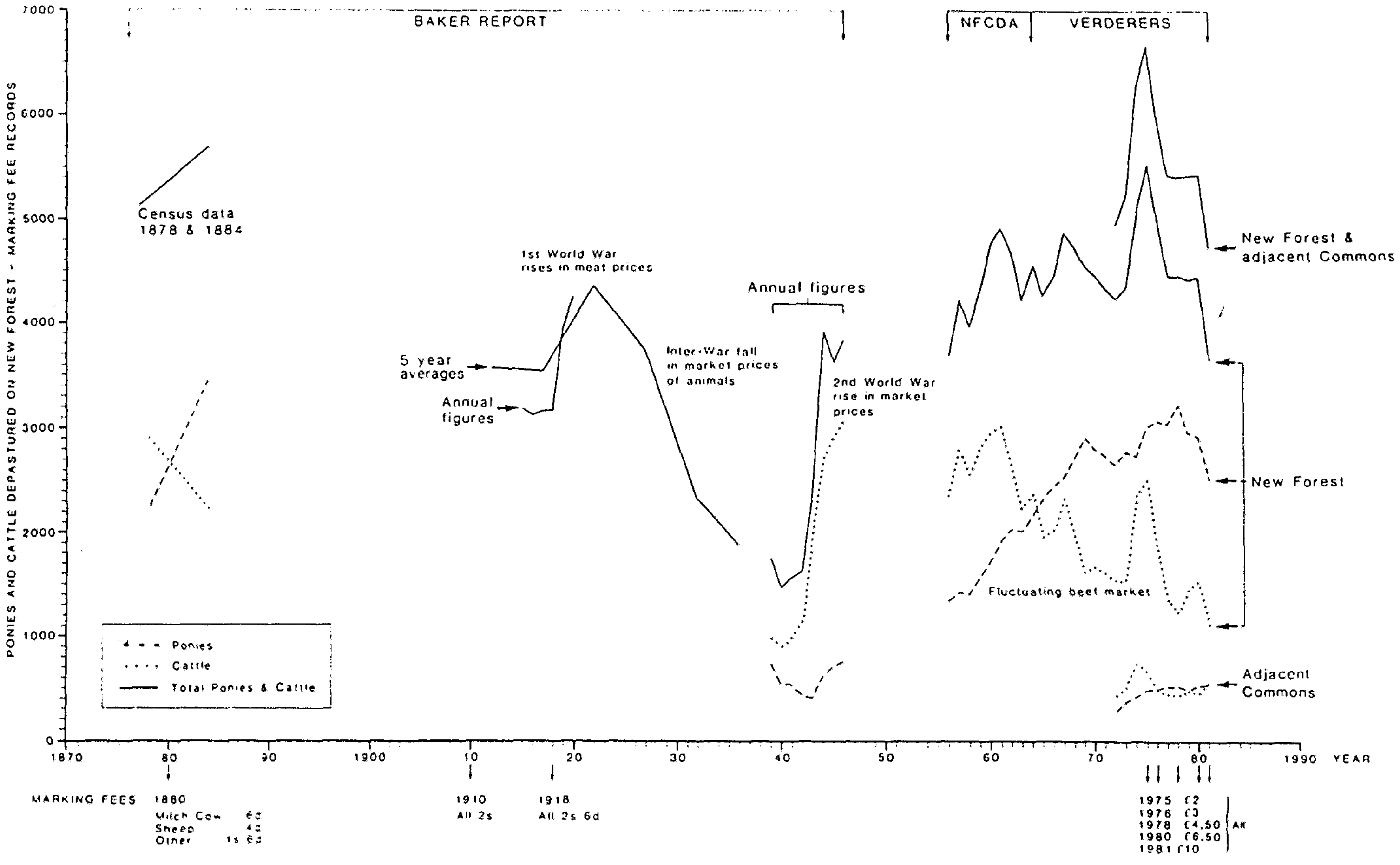
Commoners´ animals

Today cattle and ponies are the main commoners stock and have been depastured on the Forest ever since its designation as a Royal Hunting Forest. There are, however, small numbers of donkeys and pigs. The original rights of common allowed pasture for sheep, and these grazed the area in earlier times. The numbers of commoners´ animals have fluctuated, mainly due to economic conditions (Countryside Commission 1984). Despite these changes, it is apparent (figure 2.4) that there has always been a large population of free ranging stock, and the total number has increased in the past 40 years to a maximum of 5,500 in 1975. Whilst the number of cattle has fluctuated, the number of ponies has continually increased over most of this period, with the maximum number (3,200) in 1978. Since then the number of ponies has stayed around 3,000 whilst the number of cattle has again increased. In 1983, the mid point of this study, 2,997 ponies, 1,761 cows and 88 donkeys were depastured.

Deer

In previous times deer were probably the most abundant large herbivore in the New Forest with an average of 9,000 between 1789 and 1858 (Countryside Commission 1984). Numbers of deer have altered with time and management (section 2.1.2) but today it is estimated that at least 2,500 have access to the entire area. At least four species are present, fallow deer (*Dama dama*) accounting for more than 75% of total numbers, with smaller numbers of roe deer (*Capreolus capreolus*), sika deer (*Cervus nippon nippon*) and

Figure 2.4 Fluctuations in the numbers of commoners' large herbivores (cattle & ponies) depastured on the New Forest. Also shown are the marking fees and meat market prices which have affected numbers depastured. (Figure reproduced from Countryside Commission 1984).



red deer (Cervus elaphus). It is probable that there are also muntjac deer (Muntiacus reevesi).

2.1.6 Large herbivores and the New Forest vegetation

Introduction

The diversity of plant communities within the Forest has arisen principally from the topography and geology of the area, but grazing and browsing have considerably influenced them too. Tubbs (1968,1982) notes the Forest to be biologically impoverished and atributes a progressive loss of species over past centuries to intensive grazing. For example, the Open Forest woodlands have been subjected to grazing for hundreds of years and, due to the lack of natural regeneration, many are now in the same condition as those in other areas where intensive grazing is practised, such as Snowdonia (Smith 1983), with woodlands dominated by mature trees (figure 2.5) and sparse, species poor shrub and herb layers(in an ungrazed woodland outside the New Forest 259 species were recorded as opposed to only 40 within a grazed Forest woodland, Southampton University unpub.). At present grazing levels woodland regeneration scarcely occurs. Theoretically the statutory inclosures are ungrazed by domestic stock but ponies do gain access and recently attempts to evict them have reduced resulting in a decrease in shrub and herb layer vegetation in these woodlands too. There has been a great deal of interest in the effects of large herbivore grazing on the ecology of the Forest and the following sections review current knowledge on the effects of commoners´ animals and deer.

Effects of Commoners´ Animals

In 1977 the N.C.C. commissioned a study of the inter-relationships between commoners´ animals and the New

Figure 2.5 Size class distribution of established *Fagus sylvatica* trees within grazed (Open Woodland) and ungrazed (Enclosed Woodland) woodlands within the New Forest showing the reduced regeneration within grazed areas (Edwards unpublished).

Forest vegetation. This study investigated the use of all Forest vegetation communities by the animals and the impact of this use on these areas. The study was completed in 1980. A report of the work can be found in Putman et al. (1981) with a summary of their findings in 'The Food and Feeding Behaviour of Cattle and Ponies in the New Forest, Hampshire' (N.C.C. 1983). The salient points of the study are outlined below.

The project was divided into two: firstly a study of the behaviour (see Pratt, Putman, Ekins & Edwards 1985) and ecology of the common animals and their use of the Forest vegetation and, secondly, a study of the vegetation structure, standing crop, productivity and the effects of grazing. These studies revealed that cattle feed extensively on the grasslands, especially during the summer months, retiring to the open deciduous woodlands for night-time shelter. Most cattle are removed during the winter months but heathlands provide an important source of forage for those animals remaining.

Ponies also feed extensively on grasslands in the summer but there is considerable use of heathlands and bogs, the latter particulary during drought, where these animals feed on Molinia. Ponies use the open deciduous woodland and gorse for shelter at night but also use these as feeding areas, especially in the winter months. Although some open coniferous woodlands are available to both sets of animals they very rarely use them.

Assessment of offtake in deciduous woodlands showed that beech and oak are browsed in late summer whilst holly becomes an important food source in the winter months. In one study area it was found that 72% of accessible oak shoots and 53% of beech shoots were browsed. Most trees in the New Forest have a very clear browse line about 2m above ground level. Supplies of holly are often supplemented by the commoners' practice of cutting off holly branches as winter food for the ponies.

Grazing on the woodland floor, mainly A.capillaris, was found to be highest during October and November, after the intense grazing of grassland areas. Bramble (Rubus fruticosa) and bracken were also grazed in woodland glades (surprisingly as bracken is known to be toxic to horses). The study found production of bramble to be relatively high (320 g/m^2) in the woodland study areas, but in the autumn and winter months 60 to 70% of the current year's shoots were removed. Consumption of tree seeds by deer in other studies has been discussed (section 1.2); the N.C.C. study found that in good mast years acorns were consumed in large quantities by ponies. The practice of turning out pigs for pannage, intended to reduce overabundance of acorns, is quite localised so there are many areas where the ponies have unrestricted access to the acorn crop.

The findings of the effects of large herbivores within the deciduous woodlands quantified previous indirect observations of the restriction of woodland regeneration by grazing. Peterken & Tubbs (1968) identified periods of regeneration which coincided with times of low grazing pressure. Two notable periods are the late 1850's to early 1960's, after the 1851 Deer Removal Act was enforced, and the late 1930's to early 1940's, when an all time low was reached in large herbivore numbers (figure 2.4). However, large herbivore numbers have gradually increased over the past 30 years and there has been no opportunity for regeneration of woodland or ground flora. If large herbivores are excluded from New Forest woodlands, regeneration can occur rapidly (Mann 1978) and allow the development of a diverse and structurally complex ground flora, with favoured food species such as bramble, holly, beech and birch all present. This of course creates an ideal habitat for small rodents, affording food and shelter.

Intensive large herbivore use is responsible for the characteristically short (<3cm) vegetation of the New Forest grasslands (Pickering 1968; Putman et al. 1981; Edwards &

Hollis 1982). Productivity and offtake studies have revealed that most of the annual production (91% on acid grasslands) in these areas to be removed during the April to October growing season, with little vegetation available as winter forage. Apart from the obvious structural simplicity of the grassland vegetation, species composition has altered in favour of low growing prostrate herbs (Edwards & Hollis 1982; Hollis 1985), these species neither favoured nor easily grazed by large herbivores

Vegetation studies revealed that above ground plant biomass was greatest in the latrine areas of grassland habitats where the vegetation is less closely grazed. It was subsequently found (Edwards & Hollis 1982; Hollis 1985) that cattle and ponies exhibit separation of habitat use arising because ponies tend to create latrine areas which they then avoid when feeding. The pony latrine and non latrine areas differ in plant biomass, species composition and soil chemistry. This behaviour of ponies leads to a transfer of nutrients from grazing to latrine areas.

New Forest grasslands do not therefore offer a suitable habitat for small rodents. Many acid grasslands, however, do have an annual growth of bracken that can become quite dense depending upon the use by large herbivores. In the winter months this soon dies back and the vegetation affords little ground cover.

Cutting and burning of heathland is practised to rejuvenate it for grazing. Putman *et al.* (1981) found little evidence of *Calluna* browsing in the more extensive heathland tracts and they appear to have little affect on the vegetation over these areas. Areas associated with grasslands are, however, heavily used by cattle, but it appears that the animals make greater use of the *Molinia* in this habitat. Ponies apparently make little use of dry heathland but do utilise *Juncus* in the wetter heathlands and valley bogs. These studies suggest that management rather than grazing plays the dominant role in modifying diversity and complexity of this community.

The very detailed studies of Putman et al. (1982), Edwards & Hollis (1982) and Hollis (1985) have brought about new information on the effects of the commoners´ animals on the New Forest vegetation, and have confirmed that these animals do have a dominating effect on the vegetation, stopping regeneration within woodlands and maintaining the characteristically short New Forest grasslands. However these animals are not the only large herbivores influencing the Forest ecology.

Effects of deer

In 1983 it was estimated that 2,500 deer were present in the New Forest (Forestry Commission). As the Statutory Inclosures are accessible to deer, the actual density of these herbivores in the unenclosed Forest is considerably less than that of the commoners´ animals. However, the deer occupy and make use of habitats in ways different from the cattle and ponies as they tend to spend more time within the woodland areas.

There is little published information on the ecology of the New Forest deer population, but studies have given information on the relationships between fallow (Jackson 1974a & b; Parfitt in prep), roe (Jackson 1980) and sika (Mann 1983) deer and the Forest vegetation. As with the commoners´ animals, these deer species exhibit seasonal patterns of feeding and habitat use, diet being related to food availability and habitat use being related to food and shelter requirements. Both Jackson (1974a,1980) and Mann (1983) found fallow, roe and sika deer respectively spent most of their time feeding within the woodlands, with the greatest use of this habitat in the winter months. This is related to diet, all three species taking advantage of good acorn crops, deciduous leaf litter and deciduous and coniferous browse in these months. This intensive use of woodlands is in addition to that by the cattle and ponies creating the lack of vegetation and regeneration in these areas. As supplies of acorns decline, and especially in years when the crop is small, Calluna predominates the diet; in late winter holly also becomes important. Mann (1983) found that Calluna formed 20-30% of sika diet throughout the year, though this was taken from plants within the large plantation which formed his study area and not from the areas of open heathland. Parfitt (in prep) has found that the fallow deer in his study area make little use of large areas of heathland despite these being available to them. So it is suggested that they do not play a major role in the modification of this habitat.

Grasses form a large part of the deer´s diet and it is the major food between spring and autumn. The animals make little use of improved grasslands areas (Edwards & Hollis, 1982) but graze chiefly in woodland glades and rides. Mann (1983) found sika deer make extensive use of Molinia whereas Jackson´s (1974a) fallow deer population did not; again this is probably related to availablity within study areas.

The deer, therefore, do not greatly influence heathland vegetation nor significantly add to the effects of cattle and pony grazing on the grasslands. By extensive use of deciduous woodlands they are a contributing factor to the dominant influence of the large herbivore grazing; however deer have access to the enclosed plantations too, so their density within this habitat is much less than the other two species.

2.2 STUDY SITES

2.2.1 Site selection

The primary aim of this study is to compare aspects of the ecology of small rodent populations within grazed areas of the New Forest with those in ungrazed areas. The study was restricted to grazed deciduous woodland, heathland and acid grassland, which collectively represent 50% of the total forest area and are used extensively by large herbivores. The study of food and feeding behaviour of cattle and ponies in the New Forest (Putman _et al._ 1981) revealed the density of large herbivores to be unequally distributed over the Forest and within vegetation communities. This is related to physical barriers, fences, cattle grids and roadways, and to the uneven distribution of habitats created by edaphic and management factors. It was therefore decided to try and select study sites covering a range of large herbivore use, from high to low, in an attempt to look for subtle effects on rodents if different levels of grazing pressure exist. After some preliminary trapping, consultation with the Forestry Commission and the authors of the N.C.C. study, four sites were chosen within the New Forest which, it was hoped, would represent a range of different grazing pressures.

Within the Forest there are no large areas of these vegetation communities which are totally ungrazed, and so two control sites were selected outside the perambulation of the Forest where deer, but no domestic stock, graze and where the vegetation communities were deemed broadly similar; woodlands were chosen on the basis of oak being the dominant species and approximately the same age as the Forest woodlands. These two control sites were open to grazing by New Forest cattle and ponies up to the fencing of the Forest between 1963 & 1964 (Tubbs 1968). As the structure and species composition of plant communities is affected by grazing, it was inevitable that the communities inside and outside the Forest could not be exact equivalents; in particular the acid grassland community is confined to the New Forest and appears to be derived from woodland through heavy grazing (Tubbs 1968).

One limitation of the study was that there were no sites totally free of large herbivore grazing, and even low levels of grazing can significantly alter plant communities (Chapter 1). In 1983 two deciduous woodland deer proof fenced pens were added to the study sites, one totally free of large herbivores and one with a small population of fallow deer. These pens allowed a controlled comparison to be made between grazed and ungrazed woodlands.

2.2.2 Site descriptions

The following is a brief description of each vegetation type at each site. The characteristics of each vegetative strata within each woodland site are summarised in table 2.2. It must be noted that although New Forest plantations are called Inclosures the areas are opened to large herbivore grazing when the trees are large enough not to be affected by browsing.

New Forest Woodlands

1) Island Thorns Inclosure (GR:SU215 075). This is one of the largest deciduous plantations within the New Forest dominated by oak but with small areas of beech. The area was planted in 1852 and has been open to grazing for over 50 years. There is no understorey between the canopy and the ground vegetation with bracken (*Pteridium aquilinum*) dominating the shrub layer in the summer months but dying back in the winter leaving this stratum empty (plate 2.1) the ground flora is mainly *A.capillaris* which is kept very short by grazing (< 2cm).

Table 2.2 The main dominant vegetation of the different strata in the deciduous woodland study sites. Sites 1 to 4 Open New Forest, 6 & 7 enclosed New Forest Pens and 7 & 8 outside the New Forest. (P) = Plantation (A&O) = Ancient & Ornamental.

SITE & GRID REFERENCE		MAIN SPECIES	VEGETATION STRATA			
			>5m	2-5m	15cm-2m	<15cm
1. Island Thorns Inc	215155	Q.robur (P)	Pinus sp (few)	Nothing	P.aquilinum	A.capillaris
2. Backley Inc	225075	Q.robur (P) C.sativa (P)	T.baccata (few)	Nothing	P.aquilinum	A.capillaris
3. Matley Wood (A&O)	333078	Q.robur C.sativa	I.aquifolium Betula sp	I.aquifolium	P.aquilinum	A.capillaris
4. Sloden Inc (A&O)	215125	Q.robur I.aquifolium	T.baccata	I.aquifolium	P.aquilinum	A.capillaris
5. Ungrazed Denny Pen	330054	Q.robur (P)	Pinus sp	U.europeus	R.fruticosa U.europeus P.aquilinum	Mosses
6. Grazed Denny Pen	330054	Q.robur (P)	Pinus sp	Nothing	P.aquilinum	A.capillaris
7. Howse Copse	308001	Q.robur	F.sylvatica I.aquifolium	F.sylvatica I.aquifolium	R.fruticosa P.aquilinum	R.fruticosa
8. Pound Bottom Wood	220175	Q.robur	Betula sp (few)	Nothing	P.aquilinum	A.capillaris

2) Backley Inclosure (GR:SU225 075). This is the northern edge of a large mixed plantation, again dominated by oak but with a small area of sweet chestnut (Castanea sativa) on the north western edge. The plantation is approximately the same age as Island Thorns Inc, and, similarly, has no tree understorey with the shrub layer being dominated by bracken and A.capillaris in the ground layer.

3) Matley Wood (GR:SU333 078).This is a small (c.20 ha) Ancient and Ornamental Woodland dominated by oaks with scattered beech and sweet chestnut trees and an extensive understorey of holly which has a characteristic browse line (plate 2.2); there is no shrub layer apart from bracken. Ground vegetation is sparse with large bare areas. The wood perimeter is surrounded by silver birch (Betula pendula) trees.

4) Sloden Inclosure (GR:SU215 125). Although termed an Inclosure the area chosen for study is an Ancient and Oranmental woodland abutting a coniferous plantation. The canopy is dominated by oak with a few scattered yew trees (Taxus baccata) and a holly understorey, again with the browse line. The yew and holly trees cause extensive shading of ground vegetation and the ground flora is sparse, but openings in the canopy have led to small glades dominated by A.capillaris and bracken.

5) The Denny Pens (GR:SU333 054).These are two adjacent 5 ha deciduous woodland pens situated within the Denny Inclosure. Both pens are surrounded by a deer proof fence and were created approximately 22 years ago. The grazed pen has had, on average, 7 fallow deer resident during this time. The dominant canopy species of both pens is oak with scattered scots pine (Pinus sylvestris), but the grazed pen also has a small area (c. 1ha) of corsican pine (Pinus nigra) for experiments and to act as cover for the deer. This pen is similar to the other inclosures with no understorey and only bracken in the shrub layer (plates 2.3a & b).

Plate 2.1 Island Thorns Inclosure study site

Plate 2.2 Matley Wood, Ancient & Ornamental, study site

Plate 2.3 a Ungrazed Denny Pen study site

Plate 2.3 b Grazed Denny Pen study site

These pens were first studied by Mann (1978) who reported extensive regeneration in the ungrazed pen; since this time the canopy in this pen has closed, and many small trees have died. This regeneration has led to the presence of many holly, willow (*Salix*) and birch trees with gorse bushes in the more open sections. The ground vegetation is dominated by bramble and bracken, where the canopy is more open, or ivy (*Hedera helix*) where it is not.

Woodlands outside the New Forest

1) *Howse Copse* (GR:SU308 001). This block of woodland is the north eastern corner of a large unmanaged oak plantation just outside the south eastern boundary of the Forest. The woodland is a mixture of oak, beech, birch and holly. The canopy is lower and more open than the Forest plantations due to the loss of older trees (plate 2.4). The woodland shows signs of extensive regeneration with many young holly, beech, oak and birch trees, and there is a dense covering of brambles on the woodland floor approximately 0.5m in height.

2) *Pound Bottom Wood* (GR:SU220 175). This wood is part of an extensive oak and coniferous plantation, Cloven Hill Plantation, just outside the north eastern boundary of the Forest. The wood itself is approximately the same age as the two Forest plantations (Island Thorns Inc and Backley Inc) and similarly has no understorey, with bracken dominating the shrub layer, grasses the ground layer and bluebells (*Endymion non-scriptus*) in the areas near woodland rides.

New Forest Heathlands

1) *Island Thorns Heath* (GR:SU215 165). This is part of an extensive area of heathland running along the southern edge of Black Gutter Bottom valley and stretches from the B3078 west to the Forest boundary. Although the heathland is of different ages the study area was sited in an area

approximately 10 years old and locally known as The Butts. There is some invasion of Scots pine and a small area of gorse just on the northern edge of the area (plate 2.5).

2) Backley Heath (GR:SU215 075). This is part of another extensive heath running east-west just south of the A31. Again the area is a patchwork of different aged heathlands; the area chosen for study was just north of Backley Holmes reseeded lawn and was approximately 10 years old.

3) Matley Heath (GR:SU333 078). This is a large heathland stretching from the southern edge of Matley Wood to the London-Bournemouth railway line. The area of heathland chosen for study was less than 5 years old, having recently been cut, and approximately 500m outside the woodland, but abutted the acid grassland at this site and the area between the edge of the wood and the heath.

4) Sloden Heath (GR:SU213 122): this is part of a large tract of heathland running east-west along the southern edge of Sloden Inc and is on a south facing slope. The area of heathland chosen was a large uniform area of approximately 5 years old.

Heathlands outside the New Forest

1) Setley Common (GR:SU305 000). This piece of heathland is small, covering just under 3ha, and is quite close to the Forest boundary. The heathland is approximately 20 years old and has been free from large herbivores, except deer, since the Forest was fenced. The area had been invaded by pine and birch from the surrounding woodland but this had been removed approximately one year before commencement of this study.

Plate 2.4 Howse Copse study site outside the New Forest

Plate 2.5 Island Thorns Heath study site

2) Pound Bottom Heath (GR:SU215 185). This piece of heathland is slightly smaller than the above outside site (<2ha) and is on a south facing slope. The area is quite close to the Forest boundary but, again, is only subjected to grazing by deer which come from the surrounding plantations. The *Calluna* on the heath is over 20 years old, there is extensive scrub invasion from gorse, pine and birch (plate 2.6) and the heather is dying back in parts. The slope is well drained but the bottom part of the heath is wetter with less tree invasion and a greater abundance of *Molinia*.

Acid grasslands

1) Matley Wood (GR:SU337 078): This is a small area (<2ha) of acid grassland on the southern edge of Matley Wood and is bounded by two strips of gorse and heather. The grassland is characteristically close cropped *A.tenuis* which is covered by bracken in the summer months (plate 2.7).

2) Sloden Inc (GR:SU213 122): This is a small piece of grassland (<2ha) bounded by the Inclosure on three sides and a woodland ride on the other. The grass is short but the area has a thick covering of bracken in the summer leaving a thick bracken litter in the winter.

Plate 2.6 Pound Bottom Heath study site outside the New Forest

Plate 2.7 Matley Wood acid grassland study site

LARGE HERBIVORES & THE NEW FOREST AS A HABITAT FOR SMALL RODENTS

The influence of large herbivores on vegetation in general and the New Forest in particular has been discussed in sections 1.2 and 2.2 respectively. It has been suggested (section 1.1) that large herbivores may affect small mammals indirectly through structural modification of the habitat, and directly through competition for food. As this study aims to identify how the actions of large herbivores influence small rodent populations within the New Forest through the comparison of populations in grazed and ungrazed areas, the following Chapters quantify three factors:

1) Large herbivores have been identified as playing a dominating role modifying and maintaining the New Forest vegetation, Chapter 3 therefore quantifies large herbivore habitat use of the New Forest and outside sites enabling a ranking of sites on the basis of large herbivore habitat use.

2) As vegetation has been identified as being of great importance to small rodents and greatly affected by large herbivores Chapter 4 quantifies vegetational characteristics of the study areas and identifies differences attributable to herbivore grazing or other factors such as management.

3) Deciduous tree seeds are a valuable food source to both large herbivores and small rodents so both may be in direct competition. Chapter 5 therefore examines large herbivore offtake of tree seeds within the deciduous woodlands.

CHAPTER 3

ASSESSMENT OF LARGE HERBIVORE HABITAT USE

3.1 INTRODUCTION

This study compares small rodent populations between grazed New Forest sites and low grazed outside sites. Before the effects on the habitat and small rodent populations can be related to the effects of large herbivores, the intensity of habitat use by these species has to be quantified. The study sites from within the Forest (Chapter 2) were selected in the belief that they experienced a range of different grazing pressures and that differences in the physical characteristics of the sites and differences between the rodent populations themselves might be attributable to this.

One can employ both direct and indirect methods to assess the size and habitat occupation of large herbivore populations. Direct observations can supply information on the size, structure and habitat use and there is a range of methods available depending upon the species under study e.g. transect sampling may be carried out from the air (Jolly 1969) or the ground (Sinclair 1972; Norton-Griffiths 1973; Mann 1983; Johnson 1984) but all these method have associated problems of practicability and limited accuracy (Neff 1968; Norton-Griffiths 1974).

Indirect methods, recording tracks or signs of animals, provide a continuous measure of habitat use independent of observer presence. The most commonly used method is measurement of faecal accumulation (Neff 1968; Putman 1984) and from these, data on population size, habitat use, sex structure and population biomass can all be obtained. There are however many potential sources of inaccuracy in using faecal accumulation. Putman (1984) summarises these as:

1) Heterogeneity in environment: non random use of the environment resulting in non random distribution of dung.

2) Non regular dunging: deposition rates vary for age and sex classes and seasonally.

3) Different mobility of animals: non regular distribution pattern of dung in different areas.

4) Differential search ability: recovery of dung in all habitats may not be equal.

5) Differential dung decay rates: between habitats, seasons and over time.

These factors may be eliminated or reduced by design of the sampling regime. Two basic methods are available for assessing population size and habitat use: assessment of the standing crop of faeces in random quadrats or examination of actual rate of accumulation of faeces in fixed plots (Neff 1968; Putman 1984). Although the methods do have limitations, they have been widely and successfully used for estimating population size (Dasman & Taber 1955; Harris 1959; Bailey & Putman 1981) and habitat use (Loudon 1979; Mann 1983; Johnson 1984).

3.2 METHODS

In this study the faecal accumulation method was employed to give an index of large herbivore habitat use between sites and vegetation communities. Sources of inaccuracy (section 3.1) from such a method were reduced through the experimental design and the aim of the investigation which was to obtain a comparative index of habitat use. Faecal accumulation was measured for one year

(1982) in cleared plots but this method tended to under represent the amount of dung within habitats, casual observation revealing large groups of animals to consistently use some areas. In 1983 Measurement was made along transects; at this time work was concentrated on the woodland areas (Chapters 2 and 7).

3.2.1 Cleared plots

In December 1981 six 100m^2 (10m x 10m) quadrats were established around the trapping grids within the woodland and heathland vegetations at each site and each quadrat was cleared of large herbivore dung. Starting in January 1982 quadrats were visited every 28 days (a period short enough not to be affected by differential rates of dung decay), any faecal piles present identified, recorded and removed. This method was continued until December 1982.

3.2.2 Cleared transects

From January 1983 faecal accumulation was measured at monthly intervals within woodlands along transects using each row of the trapping grids (95m) as a transect. Large herbivore dung was recorded and removed in a 1m width strip along each row.

3.3 RESULTS

3.3.1 Deciduous woodland

Monthly faecal accumulations for each species have been pooled into seasonal periods for both years on the basis of known periods of shifts in habitat occupation (Putman *et al.* 1981; Pratt *et al.* 1985). Only pony and deer dung were found within the woodlands. The seasonal variations are presented in table 3.1; the monthly data can

Table 3.1 The seasonal accumulation of large herbivore faeces (recorded as faecal piles) within New Forest (sites 1 to 4) & outside (sites 5 & 6) deciduous woodlands. 1982 data are the accumulation in six 100m^2 quadrats at each site; 1983 data from seven 95m x 1m transects at each site, all sites cleared monthly. Winter = January, February & March, Spring = April, May & June. Summer = July, August & September, Autumn = October, November & December. Actual monthly data are presented in Appendix 1.

Site	Winter	Spring	Summer	Autumn
Ponies 1982				
1. Island Thorns Inc	6	3	1	4
2. Backley Inc	-	-	0	1
3. Matley Wood	6	3	1	4
4. Sloden Inc	0	0	0	4
Ponies 1983				
1. Island Thorns Inc	7	3	0	0
2. Backley Inc	2	3	1	1
3. Matley Wood	14	13	-	-
4. Sloden Inc	8	2	4	5
Deer 1982				
1. Island Thorns Inc	7	0	3	2
2. Backley Inc	-	-	7	17
3. Matley Wood	0	1	0	3
4. Sloden Inc	0	0	0	3
5. Pound Bottom Wood	0	0	0	2
Deer 1983				
1. Island Thorns Inc	15	2	0	1
2. Backley Inc	21	11	6	7
3. Matley Wood	3	0	-	-
4. Sloden Inc	13	3	5	6
5. Pound Bottom Wood	26	3	4	2
6. Howse Copse	17	7	2	3
Combined Deer & Ponies 1982				
1. Island Thorns Inc	13	3	4	6
2. Backley Inc	-	-	7	18
3. Matley Wood	6	4	1	7
4. Sloden Inc	0	0	0	7
5. Pound Bottom Wood	0	0	0	2
Combined Deer & Ponies 1983				
1. Island Thorns Inc	22	5	0	1
2. Backley Inc	23	14	7	8
3. Matley Wood	17	13	-	-
4. Sloden Inc	21	5	9	11
5. Pound Bottom Wood	26	3	4	2
6. Howse Copse	17	7	2	3

be found in Appendix 1. These data show that a greater number of faecal piles were recorded using the transect method even though the actual area covered (459 m^2) was less than that covered by the quadrats (600 m^2).

Comparison of habitat use between sites was performed using the data from 1983 only. There are significant differences in the total (pony and deer combined) faecal accumulation between all sites and over time (2 way ANOVA: sites F ratio = 2.76, $p<0.01$; time F ratio = 17.99, $p<0.01$). Splitting the data into two groups, New Forest sites and outside sites, reveals no significant difference in total large herbivore habitat use between the New Forest sites if one considers deer and ponies to be equal.

Further division of the data into species reveals no significant differences in pony faecal accumulation between the New Forest sites or over time. There are however significant differences in deer faecal accumulation between all sites and over time (sites F ratio = 3.27, $p<0.07$; time F ratio = 12.30, $p<0.01$). Separation of these data into New Forest sites and outside sites reveals no significant differences between groups of sites. It is therefore reasonable to assume that differences in habitat use occur between New Forest and outside sites.

Comparison of deer faecal accumulation for pairs of sites reveals significant differences in three pairs: Backley Inc and Howse Copse, Island Thorns Inc and Howse Copse and Island Thorns Inc and Pound Bottom Wood (table 3.2). Paired comparisons of total faecal accumulation (table 3.2) reveals most sites to have the same level of accumulation except within Backley Inc where it was significantly greater than within Island Thorns Inc. When total accumulation within the Forest sites is compared to that within Pound Bottom Wood no significant differences are found but there are significant differences between Howse Copse and Backley Inc and Sloden Inc in the Forest (table 3.2). There are no significant differences between the two

Table 3.2 Paired comparisons (Mann Whitney U tests) of total monthly large herbivore (ponies & deer) faecal accumulation within deciduous woodland study sites (Sites 1 to 4 New Forest, 5 & 6 outside New Forest).

Site	Pound Bot.	Howse Cop.	Sloden Inc	Matley W.	Backley Inc
Deer & Ponies					
1. Island Thorns Inc	ns	ns	ns	ns	**
2. Backley Inc	ns	**	ns	ns	--
3. Matley Wood	ns	ns	ns	--	
4. Sloden Inc	ns	*	--		
5. Howse Copse	ns	--			
6. Pound Bottom Wood	--				
Deer only					
1. Island Thorns Inc	*	*	ns	ns	ns
2. Backley Inc	ns	**	ns	ns	--
3. Matley Wood	ns	ns	ns	--	
4. Sloden Inc	ns	ns	--		
5. Howse Copse	ns	--			
6. Pound Bottom Wood	--				

* $p<0.05$
** $p<0.01$

outside sites. Sites are presented in rank order of total pony and deer faecal accumulation in table 3.3.

Seasonal differences in faecal accumulation at each site are apparent (table 3.1 and Appendix 1). In both years accumulation was greater in the winter months than the rest of the year.

3.3.2 Heathland

Large herbivore faecal accumulation within the heathlands is presented in table 3.4; again these data have been pooled on a seasonal basis. Monthly data can be found in Appendix 1. Pony, deer and cattle dung were all recorded on the Forest heathlands with only deer on the outside one. Very little dung was recorded at any site but the data do show that total accumulation different within the Forest, it being greatest at Backley Heath and least at Sloden Heath. Accumulation was greater at all Forest sites, except Sloden Heath, than on the outside heath. The sites are presented in rank order in table 3.3.

3.4 DISCUSSION

Measurement of faecal accumulation is used here to derive an index of the level of large herbivore habitat use to allow comparison between areas and vegetation types.

Large herbivore occupation of New Forest woodland sites is restricted to ponies and deer, whilst cattle also use the heathland areas. The outside woodlands and heathland were only used by deer. There are no significant differences in pony, deer or total occupation between the New Forest sites, but one can rank them on the basis of large herbivore use (table 3.3), Backley Inc being the most heavily used. This is attributed to the large number of fallow deer which occupy this area. It is thought that this also explains the difference found between the use of Backley Inc and Island

Table 3.3 Rank order of woodland and heathland study sites on the basis of large herbivore (cattle, ponies and deer) habitat use, as determined by faecal accumulation (1=high use) (NF= New Forest).

WOODLAND

1. Backley Inc (NF)
2. Sloden Inc (NF)
3. Pound Bottom Wood
4. Howse Copse
5. Matley Wood (NF)
5. Island Thorns Inc (NF)

HEATHLAND

1. Backley Heath (NF)
2. Matley Heath (NF)
3. Island Thorns Heath (NF)
4. Pound Bottom Heath
5. Sloden Heath

Table 3.4 The 1982 seasonal changes in accumulation of large herbivore (cattle, ponies and deer) faeces from *Calluna* heathland within (sites 1 to 4) and outside (site 5) the New Forest (data from six 100m^2 quadrats at each site cleared at monthly intervals. See Appendix 1 for actual monthly data).

Site	Winter	Spring	Summer	Autumn
1. Island Thorns	2	6	6	2
2. Backley Heath	-	-	2	15
3. Matley Heath	13	5	3	1
4. Sloden Heath	0	2	0	1
5. Pound Bottom Wood	1	1	4	1

Thorns Inc (table 3.2), there being few deer in Island Thorns Inc.

Although no statistical comparisons were made on the heathland data, it is apparent (table 3.4) that use of this vegetation type is different over the Forest, the ranking of sites being similar to that found for woodland, this again is due to the large number of deer at Backley Inc. The similarity in ranking is expected to some extent because the heathland areas are in close proximity to the woodland and both ponies and deer utilise both habitats (Jackson 1974a; Putman *et al.*, 1981; Pratt *et al.* 1985). Although cattle do use the heathlands, it is clear from this study that they contribute little to the total large herbivore occupation. This again is consistent with findings of Putman *et al.* (1981) and Pratt *et al.* (1985).

The small differences in large herbivore occupation, as measured by faecal accumulation, over the Forest are due to a number of factors. Management of deer results in varying numbers as in areas where there are young plantations they are culled. Availability and accessibility of suitable habitat restricts distribution of all animals, with them spending more time in their preferred habitats. As with many grazing systems there is a historical aspect to the distribution of animals. In the Forest this is related to the distribution of residents and the number of animals each commoner depastures.

Deer occupation of all the Forest sites was greater than at Howse Copse (table 3.2) but similar to that at Pound Bottom Wood; the exception to this being Island Thorns Inc where the deer population was smaller than at the outside site. These differences are again due to distribution. Pound Bottom Wood is in the centre of a block of woodland which contains a large population of deer and where there is little control exerted on them. Howse Copse is part of a large area of woodland but is in the south where populations of deer appear to be lower.

There is only one species of large herbivore at the sites outside the Forest, whereas within the Forest at least two are present. Therefore the total large herbivore occupation of the Forest sites is expected to be greater. This is true for Backley Inc and Sloden Inc compared to Howse Copse but not for Island Thorns Inc and Matley Wood. This is due to the low numbers of deer in the latter two Forest sites where, effectively, only one species is present. Deer occupation within Pound Bottom Wood is not different from that at the Forest sites, even though only one species of large herbivore is present.

Although total large herbivore occupation might be the same, different effects upon the habitat would be expected depending upon the relative number of each species present. If, as one would expect, the main activity is grazing, one cannot say that because the total faecal accumulation is the same total grazing pressure is equal in all areas . The effects of large herbivores on vegetation varies with both the species present and their abundance (section 1.2) and so in the presence of two markedly different herbivores the effects upon the habitat will be greater than the same level of use by just one. The species use habitats differently, primarily by selection of different foodstuffs and in their use of other habitats (Jackson 1974a; Putman et al. 1981; Mann 1983; Pratt et al. 1985) so the time spent in these areas will be different. However, the primary difference in grazing pressure between the Forest and outside areas is the presence of ponies in the New Forest which have a much greater effect on the vegetation than equivalent numbers of deer.

Within the woodlands, at all sites there were seasonal changes in habitat occupation similar to those seen in previous studies (Jackson 1974a; Putman et al. 1981; Pratt et al. 1985). In the autumn of 1982 a slight increase in the use of woodland by both species was recorded, but this did not occur in 1983. At this time of year both species feed upon tree seeds, principally oak and beech (Jackson 1974a & b,1980; Putman *et al.* 1981); in both years the crop was poor, especially so in 1983 (Chapter 5) and so the animals probably made use of other foodstuffs: browse for the ponies and *Calluna* for the deer (see section 2.1.6). As faecal accumulation on heathlands was limited, seasonal patterns of use are not discernible at all sites, but at Backley Heath deer occupation did increase in the autumn of 1982. As noted above, in years of poor masting fallow deer use other foodstuffs (Jackson 1974a); in 1982 the crop was poor within Backley Inc and the increase in use of the heathland at this time may be indicative of this shift in habitat use. There was increased use of woodlands by both species in the winter months of both years (table 3.1), probably for use of browse, and decreased use in the spring and summer months, as food availability in other areas increases (Putman *et al.* 1981).

The primary aim here was to test the original subjective assessment that large herbivore occupation of the Forest heathlands and woodlands differs in intensity. Although differences do exist, there is no statistical confirmation of the original assessment. The Forest sites can therefore be viewed as having similar levels of large herbivore use. Due to the presence of more than one species it is apparent that the Forest sites are subjected to a greater and different kind of use than the two outside sites, and one would expect these differences to be reflected in the vegetation structure and species diversity of the different sites. This is investigated in the following Chapter.

CHAPTER 4

VEGETATION

4.1 INTRODUCTION

Large herbivores and management exert an overriding influence on the structure of plant communities (section 1.2) and especially on the ground and shrub vegetation which have been shown to be of great importance to small mammals (section 1.3). However, there appears to be no standard approach adopted to describe vegetation in small mammal investigations. Descriptions vary depending upon the aim of the study, but in the very least should give an adequate description of the area and, if examining microhabitat associations, measure variables which are known, or suspected, to affect small mammal distribution and abundance.

Accounts, descriptive or quantitative, are generally derived from methods developed for botanical studies (Greig-Smith 1964; Kershaw 1973) and may range from simple to exhaustive lists of species, or simple presence and abundance of plants and of physical characteristics of the habitat (e.g. Dueser & Shugart 1978), some of which may be of little consequence to small mammals. The problem for such studies is to adequately characterise the habitat but also quantify those characteristics most relevant, especially as vegetation characteristics alone are not of prime importance (Hansson 1977). Some studies have attempted to include food potential, an important component of the habitat, into the site characterisation (Braithwaite & Gullan 1978; Monro 1985). Monro (1985) has recently described a method thought to be both comprehensive and quick to perform. Like most this is a subjective visual assessment; whilst such methods are relatively easy, in the same study area they may produce differing descriptions (Sykes, Horrill & Mountford 1983) and so differences between studies are likely to be difficult to interpret.

It is therefore difficult to quantitatively describe the habitat which small mammals perceive. This study aims to identify differences in habitat characteristics between sites that may be attributable to large herbivore grazing and may be responsible for differences in small rodent distribution and abundance between habitats. The main site characteristics have been described (Chapter 2, section 2.2) so here the structure of the dominant species in the field and shrub layers is examined, these two layers being the ones most affected by grazing (*e.g.* Putman *et al.* 1981) and found to influence distribution of small rodents (*e.g.* Montgomery 1980b).

4.2 METHODS

Kershaw (1973) distinguishes three components of vegetation structure: a) vertical structure (*i.e.* stratification), b) horizontal structure (*i.e.* spatial distribution of species populations and individuals) and c) quantitative structure (*i.e.* abundance of species). All these components may be affected by grazing or management (section 1.2). The vertical structure of the habitats has been described (Chapter 2) so the study of the vegetation at each site was divided into two sections: a cover analysis (*i.e.* Kershaw's (1973) quantitative structure of species but which gives information on horizontal structure) and an analysis of the physical structure.

4.2.1 Cover analysis

A detailed cover analysis of the dominant vegetation between 0 and 2m in height was performed over each trapping grid within the woodlands and heathlands during May 1983, recording the percentage cover over each 15m x 15m area surrounding each trapping station.

Analysis of cover data

Classification of vegetation data may be performed using simple tabular techniques or more datailed numerical methods, the latter being assumed to be more objective. There are many numerical methods (Mueller-Dombois & Ellenberg 1974) and selection of a method is dependent upon the quantity of data available and the aims of the study. The main purpose of the cover analysis here was to discover the major differences between grazed and ungrazed areas which may affect small rodents and to relate these to the effects of large herbivore grazing and management. It was therefore decided to subject the cover analysis data to a simple numerical classification to aid in the identification of differences between sites. The method chosen was TWINSPAN (Hill 1979a) a FORTRAN program for arranging multivariate data in an advanced two way table by classification of the individuals (quadrats) and attributes (species). This program first constructs a classification of the quadrats and then uses this as a basis for classifying the species. The output presents the species as a sequence which represents their similarity of occurrence in the quadrats.

TWINSPAN classifications present a linear ordering of the samples which can be difficult to interpret. Two way ordination methods give graphical representation of classications which are simpler to interpret; the classification of cover data was therefore extended and DECORANA (Hill 1979b), a FORTRAN program for Detrended Correspondence Analysis, used. DECORANA is based on reciprocal averaging (Hill 1973a), a multi dimensional ordination method where, as a minimum, two variables are selected; each quadrat is scored depending upon these variables so displaying the relative discontinuity between quadrats. Interpretation of these classifications requires knowledge above that used by the analysis and with this knowledge one can explain most major divisions that occur.

Both FORTRAN programs are available on the University of Southampton's ICL 2976 computer; details of the programs can be found in Hill (1979a & b).

4.2.2 Physical structure

Woodlands

There are a number of methods available for estimating the density of vegetation, for example, through measurement of light penetration (Mossman 1955) or through harvesting (Mueller-Dombois & Ellenberg 1974). Within all the woodland sites, except the Denny Pens, above ground biomass and species compostion were measured by harvesting all the ground vegetation in five randomly placed 1/4m^2 (50cm x 50cm) quadrats. This process was carried out in April, July and October of 1983 and January 1984. All vegetation harvested was removed, sorted into species and dried at 80°c for 48 hours. Dry weight of each species was then obtained.

Heathlands

In April 1982 two 2m transects perpendicular to each other were established about each trapping station at each heathland site. Along each transect the height of the heather was recorded at 20cm intervals.

4.3 RESULTS

4.3.1 Cover analysis

Cover data for each quadrat at all woodland sites were pooled and entered into the TWINSPAN and DECORANA programs, the results of the classifications are presented in table

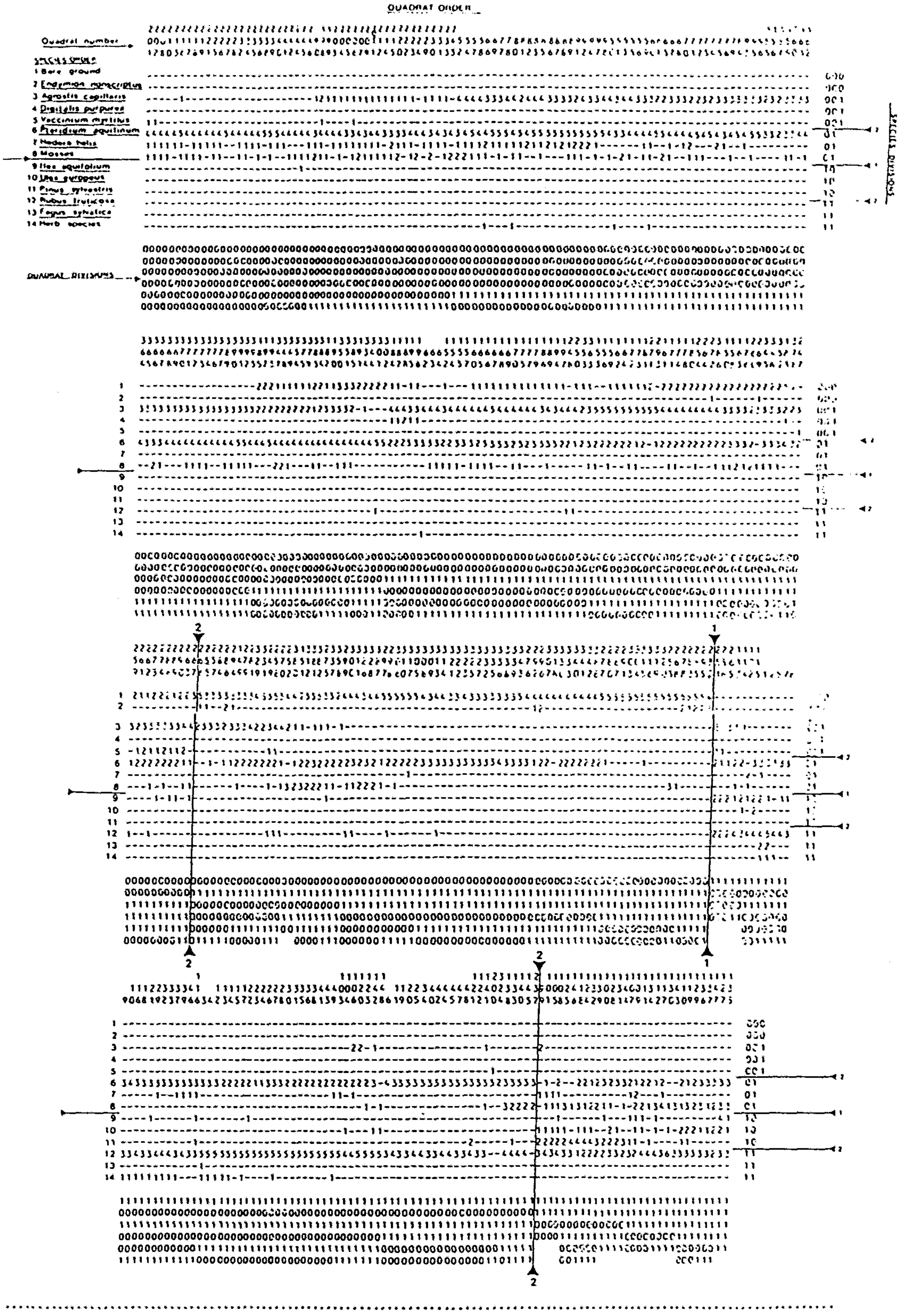
4.1 and figure 4.1 respectively. Heathland data were pooled and analysed in the same manner; the classifications are presented in table 4.2 and figure 4.2.

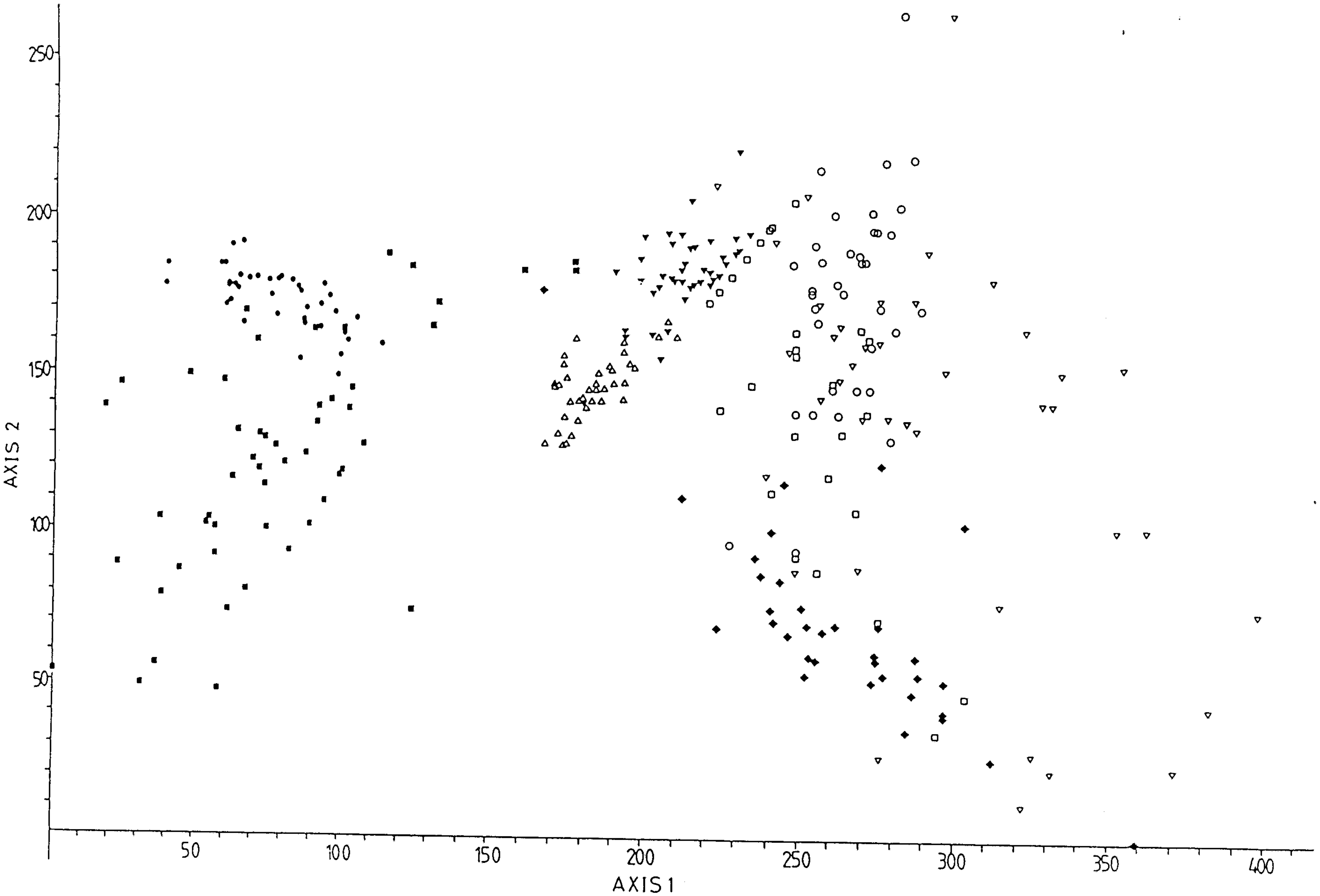
Woodland

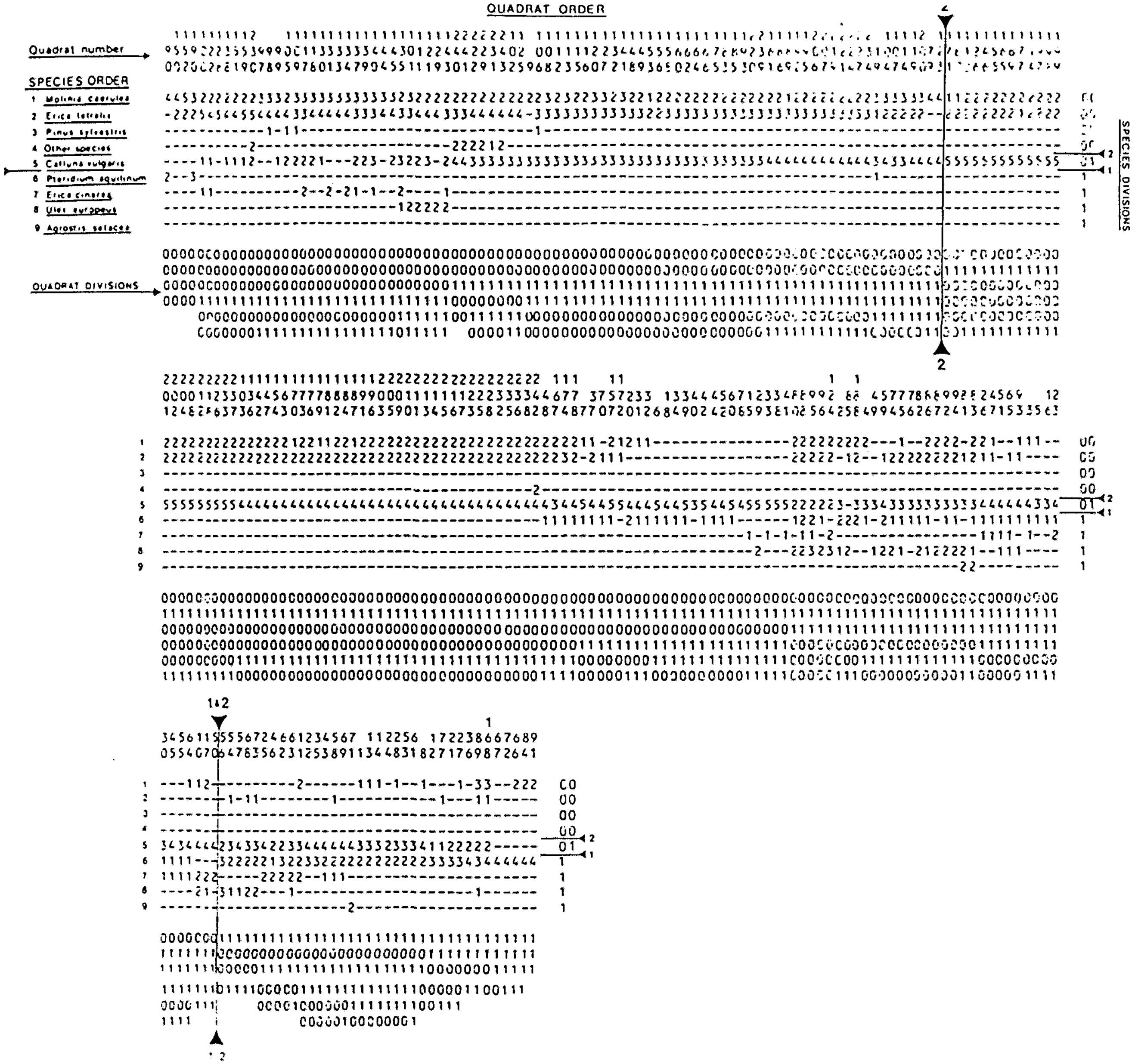
The major division of the TWINSPAN classification (table 4.1) has separated the two ungrazed sites, Howse Copse and the ungrazed Denny Pen, from the other sites. Reference to the ordering of species reveals that bracken, ivy and mosses are not involved in the major division and that these two ungrazed sites have been separated on the basis of the amount of bramble, holly and gorse cover. These sites also have more species than the grazed ones. The second division of the classification has separated the two ungrazed woodlands and produced two groups of grazed sites (Island Thorns Inc, Backley Inc, the grazed Denny Pen and the outside site Pound Bottom Wood in one group, Sloden Inc and Matley Wood in the another). These groupings are seen more clearly in the DECORANA classification (figure 4.1). The DECORANA classification also shows the intra-site quadrat variation. This is greatest at the grazed Denny Pen, Sloden Inc and Matley Wood; most of the other sites show close uniformity of quadrats.

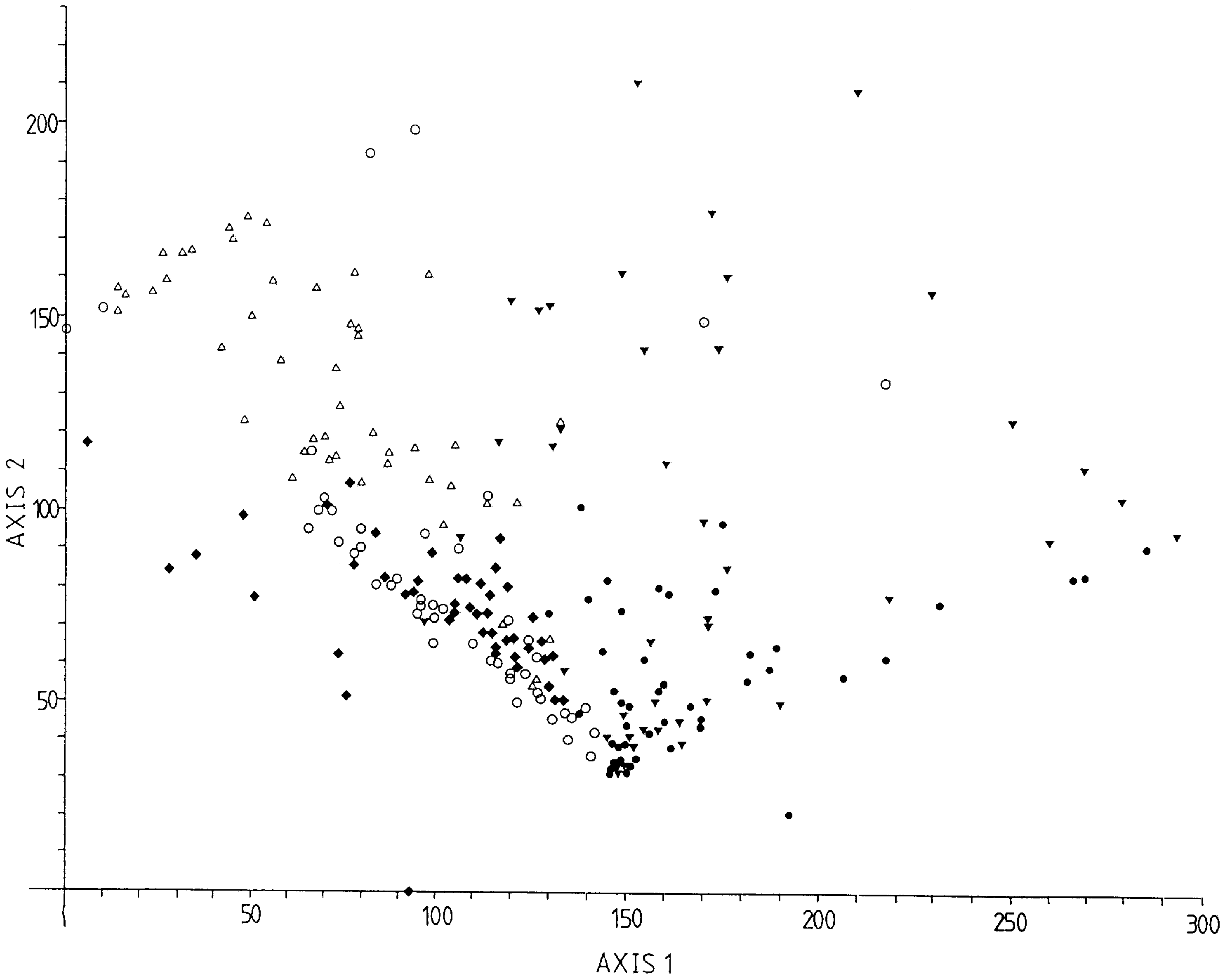
Heathland

Analysis of the heathland quadrats did not produce a clear separation of grazed and ungrazed sites (table 4.2), but the ordering of quadrats shows the two ungrazed areas to be similar. The major division of the classification has occurred on the basis of wet (*Erica tetralix* and *M.caerulea*) and dry (*E.cinerea* and *C.vulgaris*) heath species.


QUADRAT ORDER
Quadrat number
SPECIES ORDER
1 Bare ground
2 Endymion nonscriptus
3 Agrostis capillaris
4 Digitalis purpurea
5 Vaccinium myrtillus
6 Pteridium aquilinum
7 Hedera helix
8 Mosses
9 Ilex aquifolium
10 Ulex europaeus
11 Pinus sylvestris
12 Rubus fruticosa
13 Fagus sylvatica
14 Herb species
QUADRAT DIVISIONS
SPECIES DIVISIONS
1
2


AXIS 2
250
200
150
100
50
AXIS 1
50
100
150
200
250
300
350
400


QUADRAT ORDER
Quadrat number
SPECIES ORDER
1 Molinia caerulea
2 Erica tetralix
3 Pinus sylvestris
4 Other species
5 Calluna vulgaris
6 Pteridium aquilinum
7 Erica cinerea
8 Ulex europaeus
9 Agrostis setacea
QUADRAT DIVISIONS
SPECIES DIVISIONS
2
1+2


AXIS 2
200
150
100
50
50
100
150
200
250
300
AXIS 1

4.3.2 Physical structure

Woodlands

The seasonal changes in biomass of each species within the woodlands are presented in table 4.3 showing greater abundance of bracken within the two ungrazed sites, Howse Copse and Pound Bottom Wood, and the large biomass of bramble within Howse Copse. Also within the Forest sites Backley Inc shows a much greater biomass of grasses.

Heathlands

Results of the heathland structural analysis are presented as the height class distribution of the dominant vegetation (C.vulgaris) on the heathland sites (figure 4.3). It is apparent from these data that the ungrazed heathlands are structurally more varied and taller.

4.4 DISCUSSION

Large herbivore grazing affects many aspects of a habitat: it may alter species composition, structure, primary productivity and regeneration of vegetation and affect soil horizons and nutrient cycling (section 1.2). Analysis of large herbivore habitat use (Chapter 3) demonstrated the Forest is subjected to a greater and different use than the outside sites. One might therefore expect the differences to be reflected in the structure of the vegetation.

4.4.1 Deciduous woodland

The cover and biomass data have quantified the major differences between the grazed and ungrazed Forest sites and those outside that were identified in the general site

Table 4.3 Seasonal changes in the mean dry weight (g +/- S.E.) of ground vegetation harvested from five 1/4m^2 quadrats within New Forest (sites 1 to 4) and outside (sites 5 & 6) deciduous woodlands.

Site	Bracken	Grasses	Ivy	Mosses	Bramble	Holly	Litter
APRIL 1983							
1.Island Thorns Inc	37.04 (10.22)		0.64 (0.64)				116.77 (18.00)
2.Backley Inc	17.95 (10.22)						114.92 (25.27)
3.Matley Wood	1.20 (1.20)						
4.Sloden Inc	8.78 (5.93)			1.96 (1.26)			36.64 (24.52)
5.Howse Copse	54.91 (11.51)		5.70 (3.98)		52.35 (17.85)	15.13 (12.55)	164.75 (31.39)
6.Pound Bottom Wood	58.54 (18.73)	2.44 (1.54)	2.31 (1.48)	4.02 (4.02)			133.79 (12.74)
JULY 1983							
1.Island Thorns Inc	30.77 (13.88)	6.45 (3.33)	1.20 (1.20)	0.26 (0.26)			
2.Backley Inc	11.27 (5.51)	23.27 (6.66)					
4.Sloden Inc	2.54 (6.38)	7.69 (2.33)		0.38 (0.38)		0.18 (0.18)	
5.Howse Copse	72.60 (14.72)		3.62 (0.90)		68.43 (13.68)		
6.Pound Bottom Wood	21.51 (16.44)	14.81 (4.96)	18.41 (10.82)				
OCTOBER 1983							
1.Island Thorns Inc	56.33 (14.46)	7.24 (4.35)	1.13 (1.13)				
2.Backley Inc	48.71 (19.67)	38.67 (8.41)					
4.Sloden Inc	6.74 (5.45)	12.72 (3.21)		0.57 (0.41)			
5.Howse Copse	98.72 (18.70)				110.36 (13.67)		
6.Pound Bottom Wood	67.42 (13.33)	15.24 (5.42)					
JANUARY 1984							
1.Island Thorns Inc	42.76 (10.23)	4.85 (2.36)		1.38 (1.38)			
2.Backley Inc	22.98 (8.71)	23.17 (8.31)					
4.Sloden Inc	10.23 (5.87)	9.36 (4.21)					
5.Howse Copse	72.36 (9.87)				54.21 (16.01)	13.15 (12.33)	
6.Pound Bottom Wood	69.71 (10.22)	3.88 (1.96)		1.01 (1.01)			

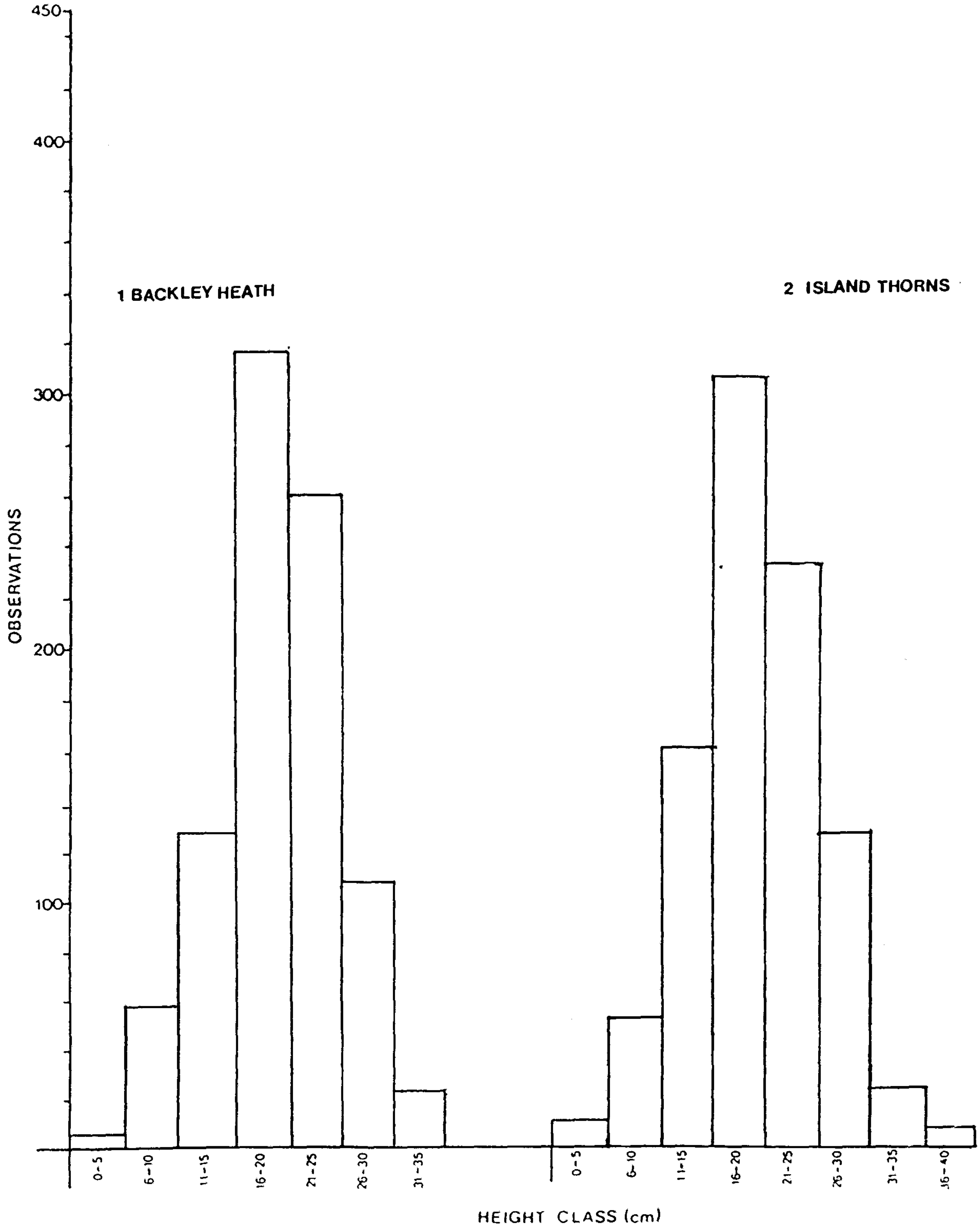
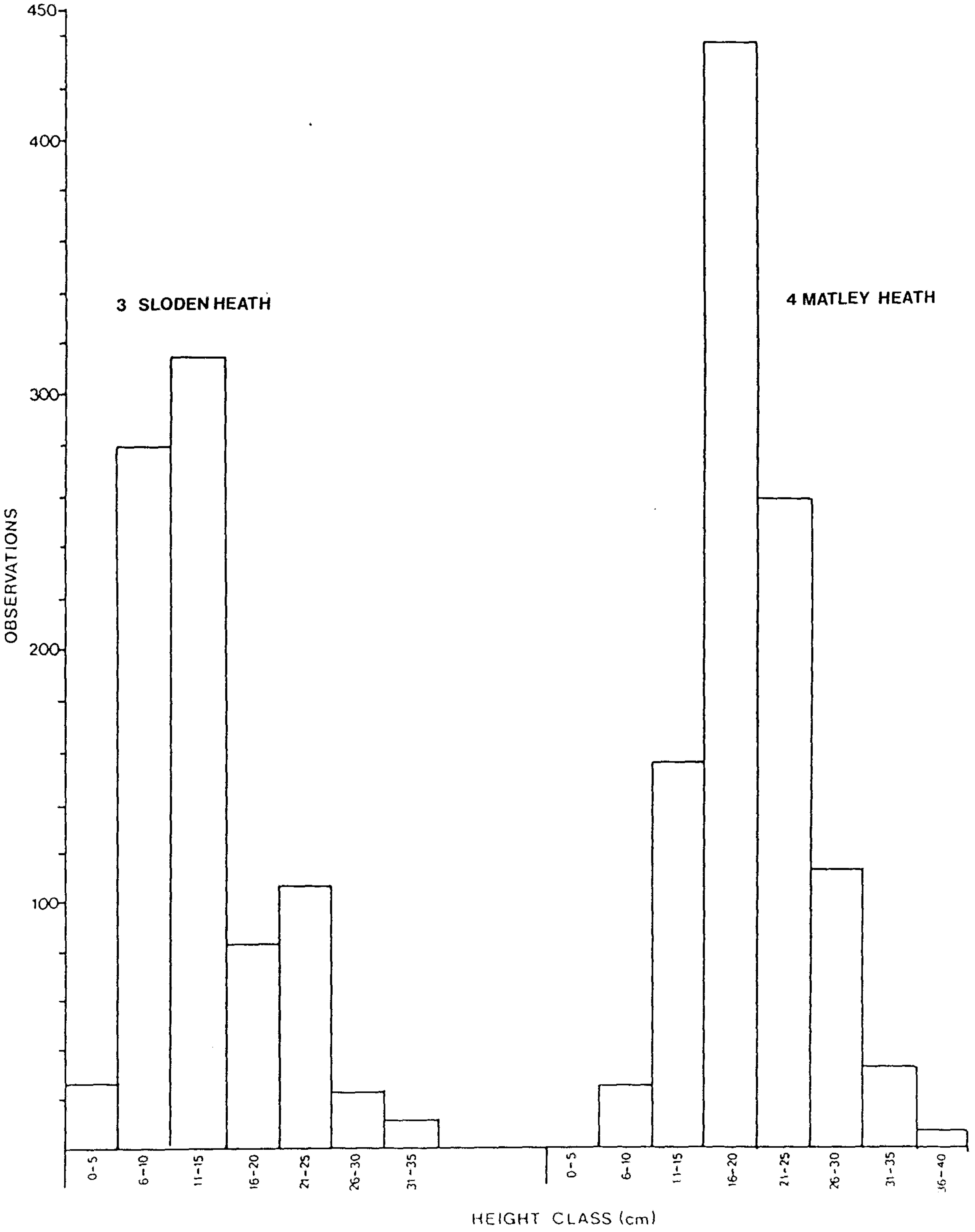
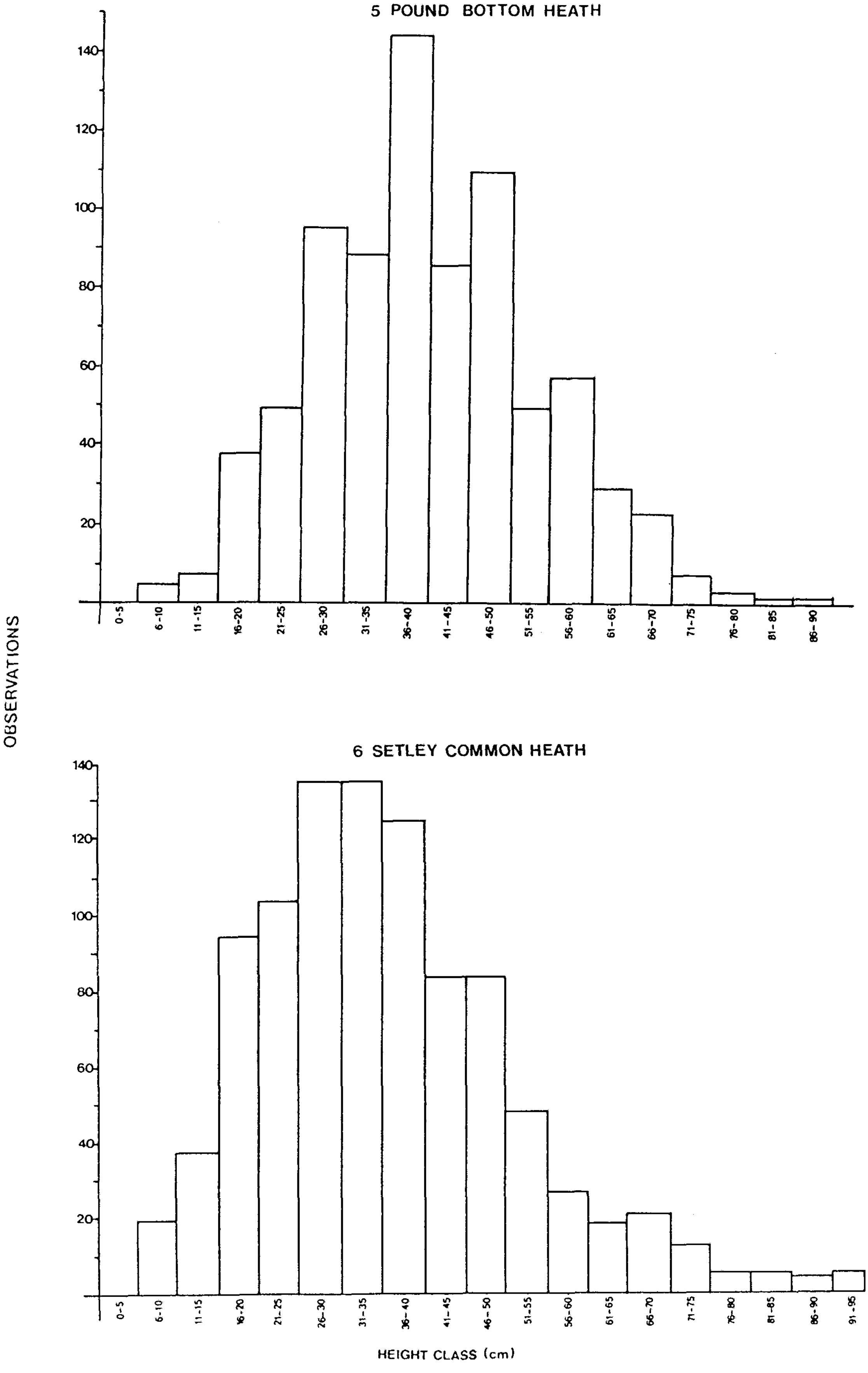


Figure 4.3 Height class distribution of Calluna vulgaris on heathland study sites within the New Forest (sites 1 to 4) and outside (sites 5 & 6). The figure clearly shows the New Forest heathlands to be shorter and less structurally diverse.


450
400
300
200
100
OBSERVATIONS
3 SLODEN HEATH
4 MATLEY HEATH
0-5
6-10
11-15
16-20
21-25
26-30
31-35
0-5
6-10
11-15
16-20
21-25
26-30
31-35
36-40
HEIGHT CLASS (cm)


5 POUND BOTTOM HEATH
6 SETLEY COMMON HEATH
OBSERVATIONS
140
120
100
80
60
40
20
0-5
6-10
11-15
16-20
21-25
26-30
31-35
36-40
41-45
46-50
51-55
56-60
61-65
66-70
71-75
76-80
81-85
86-90
91-95
HEIGHT CLASS (cm)

descriptions (Chapter 2, section 2.2). Although this study concentrated on the dominant species a more diverse flora was found within the ungrazed Denny Pen and at Howse Copse (tables 4.1 and 4.3). As noted previously, grazing reduces the abundance of preferred species in woodland (Adams 1975). The most notable difference between these two sites and the others is the higher bramble cover and greater number of small trees (table 4.1). Bramble is a highly desirable forage species for ponies (Putman *et al.* 1981) and deer (Jackson 1974a) within the Forest woodlands and is taken in high amounts in the autumn and winter months *e.g.* ponies take 60-70% of current years´ shoots (Putman *et al.* 1981). Although differences in soil and canopy characteristics may influence ground flora, absence of bramble from the grazed woodlands is almost certainly due to grazing.

Extensive browsing of tree species occurs within woodlands (Adams 1975) and the New Forest is no exception (Putman *et al.* 1981). Browsing restricts natural regeneration: within the grazed Forest sites very few small trees were found in the 0-2m stratum whereas in the ungrazed Denny Pen and Howse Copse there are many small trees. Regeneration in the ungrazed Denny Pen is greater than at any other site because it has been totally free of grazing for 22 years, and was showing extensive regeneration in Mann´s study in 1977 (Mann 1978).

The TWINSPAN and DECORANA classifications of the woodlands clearly separated Howse Copse and the ungrazed Denny Pen from the other sites (table 4.1 and figure 4.1), this division being based upon the abundance of bramble at these two sites. The remaining sites are all subjected to similar levels of large herbivore use and have similar dominant ground and shrub flora, these being principally grasses and bracken. The second division of the TWINSPAN, and the clustering of the DECORANA classification, divide this group of grazed sites into two, Matley Wood and Sloden Inc forming one group and the remaining four sites the other. This division seems to be due to the number of quadrats in the first group which have bare ground in them, rather than due to the vegetation. Intensive large herbivore grazing can result in the total removal of ground vegetation (e.g. Vogel, Remmert & Lewis-Smith 1984), though no significant differences were observed in the herbivore use in the woodland sites studied (Chapter 3). Reference to the site descriptions (Chapter 2, section 2.2) reveals that these two woodlands are the A & O woodlands with an understorey of holly and yew trees. These two species create extensive shading and little ground vegetation grows underneath them.

An important point to arise from the DECORANA classification (figure 4.3) is the dispersion of quadrats revealing intra-site heterogeneity of the vegetation, especially at Matley Wood and Sloden Inc and slightly less so within the grazed Denny Pen. In the New Forest sites this is thought to be due to the canopy induced variations in ground cover. Within the Denny Pen it is probably related to the small size of the pen. The grid adjoined two edges of the pen so these areas obtained greater light which would also affect ground vegetation.

The grouping of Pound Bottom Wood with the grazed Forest sites is not surprising as the area is a plantation and was found to be used by deer to the same extent as the other sites. With a long history of grazing major vegetational changes are expected to be the same as in the Forest.

Examination of vegetation biomass as another structural measure (table 4.3) endorses the findings of the more subjective cover analysis. At Howse Copse there is a greater biomass of bracken, as well as bramble, affording a high degree of cover whilst within the other sites bracken is the only species that offers any cover above the grasses. this cover is, however, seasonal (plates 4.1 & 4.2) whereas the bramble cover is present all year.

Plates 4.1 and 4.2 Seasonal changes in the cover of bracken (*Pteridium aquilinum*) within a New Forest plantation.

Plate 4.1 Summer bracken cover in a New Forest woodland

Plate 4.2 Winter bracken cover in the woodland in Plate 4.1

4.4.2 Heathlands

As with the ungrazed woodland areas, the ungrazed heathlands have a more diverse dominant flora than the grazed ones, with the indication of advanced succession in the Pound Bottom Heath.

The TWINSPAN classification on the the cover data has not made a clear distinction between the grazed and ungrazed areas. The classification (table 4.2) has separated the quadrats with wet and dry heath characteristics as indicated by the presence of E.cinerea in the former and E.tetralix in the latter. This is probably responsible for the dispersion of quadrats in the DECORANA classification (figure 4.2).

Although grazing can have a dominant effect on the structure of heathlands (Grant *et al.* 1981; Welch 1984), the vegetational differences between areas in this study are more likely to be due to edaphic and management factors as large herbivore occupation of heaths is quite low (Chapter 3; Putman *et al.* 1981; Pratt *et al.* 1985). The cover of heathland vegetation is dominated by ground water content, *i.e.* wet heath or dry heath and so, as areas are not heavily grazed, differences in cover are unlikely. It is more likely that differences between areas will be reflected in the structure of the vegetation, *i.e.* height, burning and cutting leading to younger shorter vegetation in the managed heaths. This difference is seen in the distribution of height classes (figure 4.3), the vegetation in the outside heathlands on average being taller (most being 26 to 50 cm in height at the outside sites and 6 to 15 cm in the Forest) and more varied than the Forest heathlands which is short and quite uniform (figure 4.3).

The DECORANA classification (figure 4.2) has again revealed different degrees of heterogeneity in the vegetation over the trapping grids. The heterogeneity is caused by soil drainage and the age of the vegetation; the older more diverse outside heathlands show greater heterogeneity whilst that of the Forest sites varies from quite wide at Island Thorns Heath to very little at Matley and Sloden Heaths; the latter two sites were most recently burnt and have characteristically short vegetation, whereas the heathland at Island Thorns has not been burnt for over 10 years is much taller and some areas are being invaded by pine.

CHAPTER 5

AUTUMN TREE SEED SUPPLY

5.1 INTRODUCTION

Small rodents have a catholic diet and take advantage of the availability of different foods (Hansson 1985). Deciduous tree seeds have high energetic value (Grodzinski & Sawicka-Kapusta 1970) and production of tree seeds may be very high (Turcek 1966; Shaw 1974; Silvertown 1980; Smal & Fairley 1980a). It is therefore not surprising to find they have been identified as an important food source for most woodland small rodents, for example, Watts (1968) and Smal & Fairley (1980b) found seed accounted for 80% of the diet of wood mice in the autumn months. However, tree seeds are a major autumn food source for other vertebrates too: birds (Perrins 1966; Newton 1967; Shaw 1968a & b), small mammals (Corbet 1974; Moller 1983; Gurnell 1981) and large herbivores (Harlow *et al.* 1974; Jackson 1974a & b; Caldwell, Chapman & Chapman 1983).

The supply of tree seeds can directly affect the demography of small rodents (Chapter 1, section 1.3.2), primarily through increased survival over the winter months (*e.g.* LeLouarn & Schmitt 1972) and increased reproductive capacity of the population (Smyth 1966; Flowerdew 1972). In years following autumns of high seed availability populations entering the new breeding season are large due to the better survival, so the potential for recruitment is greater. When the autumn tree seed crop is small, fecundity of the population ceases early and there is low overwinter survival resulting in a low spring population. This means that the potential for population increase is reduced.

The production of tree seed can vary both annually and regionally (Shaw 1974; Harper 1977; Hansson 1979) and these variations, termed masting, can be a regular occurrence in many species (Davies 1976; Silvertown 1980). This variation in production not only affects small rodent populations but has an adaptive significance for the trees. In years of high production, seed predators are unable to remove significant amounts of seed and there is successful germination and regeneration (Boucher 1981; Jensen 1985; Nilsson 1985 and recent review by Fenner 1985).

The utilisation of tree seed by other vertebrates will also affect the availability to the rodents of this important food source. When seed is abundant the effects upon the rodents are likely to be small, but in years of moderate or low production the effects of reduced food supply will be amplified. This may result in a greater reduction in overwinter survival, and hence population size, in the following breeding season. If production was continually, low rodent population size would be continually supressed.

Within the New Forest, deer (Jackson 1974a,1980; Mann 1983; Parfitt in prep), ponies (Putman et al. 1981) and pigs (Tubbs 1968; Small 1979) all feed upon the autumn seed crop. Deer especially feed upon tree seeds and theoretically offtake can be very high. With a range of large mammals utilising tree seed, the offtake from the Forest is probably quite high and it is apparent that direct competition for tree seeds may exist between large herbivores and small rodents in deciduous woodlands. An attempt was therefore made to assess both tree seed production and large herbivore offtake during 1982 and 1983, so giving information on direct competition between the species and data that may explain some of the demographic aspects of the rodent populations.

5.2 METHODS

5.2.1 Seed production

Sampling of seed production was performed in two parts: visual assessment of production and sampling of seed fall. Accurate assessment of tree seed production poses methodological problems. Adequate sampling using randomly placed seed traps requires many traps covering large areas, and in this study might influence large herbivore use of the area.

Visual assessment

During the late summer of 1982 and 1983, a subjective assessment was made of the visible seed on the trees across most of each woodland using a five point scale:

1) No seed
2) Low
3) Moderate
4) High
5) Very high

Sampling

In November of 1982 and 1983 twentyfour $1m^2$ (0.5m x 0.5m) quadrats were taken over and beyond each trapping grid in two perpendicular transects along the centre row and columns of the grids. Within each quadrat, all identifiable seeds, fragments and cases were collected. These were then dried at $80^{o}c$ for 48 hours and the dry weight of each seed species obtained.

5.2.2 Large herbivore offtake

Autumn 1982

On September 28th 1982 eight $1m^2$ (0.5m x 0.5m) exclosures were placed in a stratified random manner about the trapping grids at Howse Copse, Island Thorns Inc and Matley Wood. Each pen was placed 1.5m from the base of the nearest tree and allowed mast to fall in but denied access to large herbivores and squirrels, whilst small rodents could enter and leave at their leisure. For this study, seed traps were placed at a standard distance, 1.5m, from the base of the tree and used to give an index of seed production. It would have been better to have used randomly placed quadrats to obtain a measure of seed production per unit area, but the wide spacing of trees would have made a very large number of traps necessary. The pens were visited every 30 days after being established and all seed within the pens removed; at the same time all seed from an adjacent $1m^2$ quadrat was removed and dried in the same manner as above. This procedure was repeated 30 and 60 days later.

Autumn 1983

The attempt to measure large herbivore offtake in 1982 was not successful as it was made difficult by a very poor acorn crop and the relatively low sampling intensity; in 1983 the method of collection was altered to exclude all mammals and greatly increase sampling intensity. Due to termination of work at Matley Wood, Backley Inc was included as an alternative New Forest site, and Pound Bottom Wood was also used giving a total of four sites, Island Thorns Inc and Backley Inc within the Forest and Howse Copse and Pound Bottom Wood outside.

In September 1983 twenty circular $1m^2$ collecting cones were established in a stratified random pattern about each of the four woodlands. Each cone was placed 1.5m from the nearest tree. From September 30th the traps were set to hold seed and were then visited every seven days until the first week in January 1984. During each visit, all seed was removed from the cones and from a circular $1m^2$ adjacent quadrat; the seed was then sorted and dried in the above mentioned fashion.

5.3 RESULTS

5.3.1 Visual assessment

The results of the summer visual assessments are presented in table 5.1. These assessments suggested that the acorn crop for both years would be small at most sites, but that there would be a large crop of sweet chestnuts from the localised sweet chestnut trees.

5.3.2 Sampling

The mean weight of all tree seed collected from the November quadrat assessment is presented in table 5.2. The total seed crop was low in 1982 with sweet chestnut accounting for over 90%; no seed was found in the 1983 sampling.

5.3.3 Large herbivore offtake

Autumn 1982

The attempt to assess seed losses was not successful in 1982 (table 5.3) as the seed crop was so poor. No seed was collected inside or outside the exclosures at Howse Copse and very little was collected at Island Thorns Inc. At the Matley Wood site more seed was collected within the pens ($27g/m^2$) than outside ($2g/m^2$). Although the data are very

Table 5.1 Autumn 1982 and 1983 visual assessment of mast crop from within New Forest (sites 1 to 4) and outside (sites 5 & 6) deciduous woodlands.

Site	Species	1982		1983	
		Crop	Distribution	Crop	Distribution
1 Island Thorns Inc	*Q.robur*	Failed	Even	Failed	Even
2 Backley Inc	*Q.robur*	Failed	-	Failed	-
	C.sativa	Good	Even	Good	Even
3 Matley Wood	*Q.robur*	Failed	-		
	C.sativa	Good	Even		
4 Sloden Inc	*Q.robur*	Fair	Patchy	Fair	Patchy
5 Howse Copse	*Q.robur*	Failed	-	Failed	-
6 Pound Bottom Wood	*Q.robur*	Failed	-	Failed	-

Table 5.2 Mean dry weight ($g\ m^{-2}$ +/- S.E.) of tree seed collected from twenty four $1m^2$ quadrats within New Forest (sites 1 to 4) and outside (sites 5 & 6) deciduous woodlands in October 1982 and October 1983.

Site	1982	1983
1 Island Thorns Inc	1·02	0·00
2.Backley Inc	0·25*	0·00
3 Matley Wood	11·77**	0·00
4 Sloden Inc	0·64	0·00
5 Howse Copse	0·00	0·00
6 Pound Bottom Wood	0·00	0·00

* Sweet Chestnuts collected from one quadrat account for 97% of total.

** Sweet Chestnuts collected from two quadrats account for 96% of total.

Table 5.3 Deciduous tree seed (g/m^2) collected from within 8 1m^2 pens and 8 1m^2 quadrats at one month intervals from two New Forest woodlands (sites 1 & 2) and one outside woodland (site 3) in autumn 1982.

	October		November	
	Pens	Outside	Pens	Outside
1. Matley Wood	25.67	1.84	2.27	1.21
2. Island Thorns Inc	0.20	0.66	0.00	0.00
3. Howse Copse	0.00	0.00	0.00	0.00

limited, they suggest that for sweet chestnut the losses of seed are quite high.

Autumn 1983

Unfortunately, as predicted from the visual assessment, the 1983 seed crop was very poor at all study sites and no seed was recorded either within the seed traps nor the quadrat samples.

5.4 DISCUSSION

It was unfortunate that during the two years of study the production of acorns was low; this is probably because they were not mast years. The reasons for masting are complex. Obviously species, age and individual differences exist (Jones 1959; Goodrum, Reid & Boyd 1971; Shaw 1974; Harper 1977) but other factors such as spring weather (Jones 1959; Sharpe & Sprague 1967), leaf defoliators (Shaw 1968a) and size of the previous year's crop all contribute to the variation.

Shaw (1974) shows that observations of acorns on the ground grossly underestimate acorn fall because, before the seed falls, there has been predation on the trees leading to considerable losses. This is why a range of subjective and objective assessments were used in this study. As the amount of seed collected was so small, losses through sampling technique are deemed to be minimal.

Tubbs & Tubbs (1985) made subjective assessments of the tree seed crops in the New Forest for a number of years and show how variable it can be. For 1982 they suggested that seed production was prolific in their study areas, while this study found the opposite. Although they include holly, hawthorn and other fruits in their assessment, they have suggested (pers. comm.) that tree seed supply was large in their study areas in 1982 but low in 1983. The fact that tree seed crop may vary over geographical areas (Harper 1977; Hansson 1979), and the fact that Tubbs & Tubbs (1985) used a subjective method of assessment, could account for the differences assessed by both studies.

Whilst the production of acorns was poor during the study, the production of sweet chestnuts was good in both years. Sweet chestnut trees are present at only two sites, Matley Wood, where there are scattered individuals, and Backley Inc where the northern edge of the plantation is of this species. At Matley Wood these seeds accounted for 96% by weight of the total seed collected in 1982, but this was from just two trees on the grid. At Backley Inc this seed accounted for 97% of the total collected, but was from one tree amongst the oaks; in 1983 however, the chestnut crop at this site was quite reduced in comparison to the previous year.

Although the production of acorns was low at all study sites in both years, the production of sweet chestnuts did present a potential food source to vertebrate seed predators. Due to the 1983 seed traps within Backley Inc being restricted to the oak plantation, no measure of chestnut offtake is possible. As sweet chestnut is not abundant within the Forest it is probable that it represents a rather small and local food source for most species. In contrast, during mast years acorns are abundant in most woodlands so potentially are very important.

In 1982 some seed traps within Matley Wood revealed the offtake of sweet chestnuts to be quite high. However, this cannot be fully attributed to large herbivores. Regular visits to the area did reveal that ponies ate the chestnuts but that squirrels did too. A previously unthought of loss was also discovered. It was found that the crop of chestnuts attracted people into the area who removed large amounts; it is suggested that this was the major source of loss of these seeds.

5.5 DISCUSSION OF LARGE HERBIVORES, VEGETATION AND TREE SEED

Investigations into the interrelationships between commonable animals and the New Forest vegetation (Pickering 1968; Putman et al. 1981; Edwards & Hollis 1982; Hollis 1985) have clarified the effects of these large herbivores upon the Forest ecology. Although less detailed than the previous studies, this investigation has revealed similar patterns of large herbivore habitat use and vegetational differences in grazed and ungrazed areas (Putman et al. 1981).

The differences between grazed and ungrazed heathlands reveal the latter to have greater species diversity and structural complexity. There were also gorse bushes and saplings of birch and pine suggesting that succession was occurring on these areas. Although the numerical classification separates grazed and ungrazed sites, the differences cannot be attributed fully to large herbivore grazing. New Forest heathlands are managed by burning and cutting for the maintenance of grazing (Tubbs 1974). Burning has a dramatic and long lasting effect upon the vegetation: reducing structural complexity and removing invading scrub, the major difference between the grazed and ungrazed heathlands. No records of burning of the heathlands have been found but, as grazing pressure was low on all sites, it is suggested that the major vegetational differences are due more to the effects of management than large herbivore grazing.

Vegetational differences between the woodland sites are more apparent than between the heathland sites and it is less likely that management plays an important role. The total large herbivore habitat use of the New Forest sites and Pound Bottom Wood were found to be quite similar, but significantly less at Howse Copse. The numerical classification separated those sites subjected to low levels of large herbivore use from those of high use (Chapter 4, table 4.1 & figure 4.1). As one would expect, at low or non existent (ungrazed Denny Pen) large herbivore use, those species selected by the grazers, such as brambles, are in abundance and this, allied with reduced trampling, results in greater structural complexity. It is also apparent from the extensive regeneration in the ungrazed Denny Pen that the presence of large herbivores prevents this from occuring elsewhere in the Forest (Chapter 3, table 3.1, Chapter 4, table 4.1 & Mann 1978).

Differences were not found in large herbivore habitat use between grazed New Forest woodlands but some vegetational differences do exist, for example, the greater biomass of grasses at Backley Inc. These differences are probably due less to grazing than to local factors such as soil types and canopy cover. These effects become apparent when one compares the ground vegetation of the two A & O woodlands, Matley Wood and Sloden Inc, with the other New Forest sites which are plantations: the vegetation of the two A & O woods is more heterogenous and more affected by canopy structure.

The classification of the woodland vegetation grouped Pound Bottom Wood with the grazed New Forest plantations (figure 4.1). This site is not subjected to the same type of large herbivore habitat use as the Forest ones but it is, and has been for many years, subjected to high levels of use by deer. This prolonged level of use has resulted in the creation of a similar vegetation community to that found in the Forest plantations and, as total large herbivore faecal accumulation over the period of the study was similar to that in the Forest sites, this woodland cannot be considered as ungrazed.

The effects of large herbivores on the Forest woodland vegetation are now well known (Mann 1978; Putman et al. 1981) and it is apparent that these animals make extensive use of the autumn tree seed supply (Jackson 1974a; Mann 1983; Parfitt in prep.). Due to the low acorn production, this study has been unable to quantify the effects of large herbivores on the supply of tree seeds to small rodents and the apparent failure of the acorn crop during this study means that large herbivores would have been having little effect upon the rodent populations. The poor acorn crop is probably the reason that use of this habitat by deer, the major consumer of this food supply, declined in the autumn months when other studies showed it to increase (Jackson 1974a).

Although one cannot quantify the impact of large herbivores on acorn supply and the resulting affect of competition upon small rodents, one can hypothesise the effects of low seed crops during the study and the effects of the habitat manipulation by grazing on the woodland and heathland rodent populations.

As discussed in Chapter 1 small rodents have preferred levels of vegetative cover, the diversity of rodents being greater in more structurally complex habitats. Large herbivore grazing and management has resulted in reduced complexity and diversity of woodland and heathland vegetation, and it is suggested that examination of the rodent populations in these communities will reveal that rodent species preferring high levels of ground cover will be absent from the grazed areas. It is also likely that the demography of those species present will be altered through reduction in competition and food supply (especially with the acorn crop being so poor) and possibly the alteration of susceptibility to predation. The following chapters now examine the diversity, size and demography of small rodents in the grazed and ungrazed areas.

SMALL RODENT POPULATIONS

In optimal habitats small rodent density can reach very high levels (Petrusewicz & Hansson 1975). Although small rodents are primarily habitat specialists, their success is due to their ability to occupy and survive in sub optimal habitats as and when they become available. The exact mechanisms by which small rodents select their habitats are still unclear (Hansson 1977) but it is obvious they respond to a conglomerate of factors related to their morphology, physiology and social organisation (Chapter 1, section 1.3). Intraspecific competition is reduced by social organisation whilst spatial, temporal and dietary separation and competitive interaction are all responsible for reducing interspecific competition (Chapter 1, section 1.3).

There are, however, data to suggest that small rodent communities can be affected by habitat manipulation, affecting abundance, diversity and population success. The previous chapters (Chapters 3 & 4) have shown the dominating influence large herbivore grazing has upon New Forest habitats. This part of the study aims to investigate the distribution and ecology of small rodent species within various grazed New Forest habitats in relation to populations in areas of reduced grazing.

As noted in Chapter 1 (section 1.4), rodent populations have been investigated in two phases, an initial study of abundance, diversity and distribution between habitats in grazed and ungrazed areas, and a more detailed study of populations within deciduous woodlands.

CHAPTER 6

MATERIALS AND METHODS

6.1 Trapping techniques

Trapping grids

Small rodent populations at each site were studied using Longworth small mammal traps (Chitty & Kempson 1949) arranged in a grid formation. Within each vegetation type at each site, a grid of 7x7 trap stations, at a 15m spacing covering 0.81ha, was established in December 1981. The restricted availability of the heathland habitat at Setley Common heath and Pound Bottom heath necessitated a grid of an 8x6 configuration at the same trap spacing.

The time between trapping periods varied depending upon the part of the study but the actual procedure followed was consistent in each case. Due to public recreational use of the Forest these sites were not trappped at weekends and therefore a five day routine was used.

Two Longworth traps, with treadles set to trip at 6g, were set within 1m radius of each trap station, giving a total of 98 traps per grid (120 traps per ha). Each trap contained a wisp of fresh dry hay and a small amount of whole oats as food. Traps were locked open and prebaited for 24 hours before being set to catch on the morning of the second day. The traps were maintained in this fashion for three nights and visited once a day, in the morning, when all animals caught were marked and released. After each trapping session, the traps were cleaned out and clean dry bedding placed in them. Treadle weights were checked monthly. The trapping routine is summarised in table 6.1.

Table 6.1 Summary of the Longworth small mammal trapping routine used within deciduous woodland, heathland and acid grassland study sites within and outside the New Forest (all trapping grids 7x7 trap stations at 15m spacing (0.81ha), 2 traps per station, unless otherwise stated).

Morning	Day 1	Traps set on prebait
Afternoon	Day 2	Traps set to catch
Morning	Day 3	Traps visited, catch removed
Morning	Day 4	As day 3
Morning	Day 5	As day 3, then traps removed

6.2 Trapping Periods

All vegetation types were trapped four times between January and December 1982 at approximately 90 day intervals. These trapping sessions were designed to coincide with breeding periods and expected periods of population fluctuation.

It was not logistically possible to trap all replicates of the vegetation types simultaneously. Instead, all the different vegetation types at each site were surveyed simultaneously. With this rotation between sites this seasonal survey spanned a 7 week period.

In December 1982 work on the acid grasslands was stopped and work on the heathlands reduced to trapping three heaths (Setley Common, Pound Bottom and Island Thorns) biannually until July 1984. The main reason for this reduction in work on vegetation communities was the small number of animals being caught and to enable greater sampling of the woodland areas.

From January 1983 to July 1984 the seasonal trapping of Sloden Inc and Backley Inc was continued and the two Denny Pens (see Chapter 2) were added to the routine. Trapping within the other woodland sites, Island Thorns Inc and Matley Wood in the Forest and Pound Bottom Wood and Howse Copse outside the Forest, was increased from January 1983 to approximately 35 day intervals. This was continued within Island Thorns Inc and Howse Copse until July 1984 but had to stop at Matley Wood in May 1983 due to public interference and in Pound Bottom Wood in December 1983 due to clearfelling of adjacent woodland up to 200m from the trapping grid. After a very poor mast crop at all sites in autumn 1983 (see Chapter 5), it was decided to transfer the trapping within the Denny Pens to this monthly routine in an attempt to compare overwinter survival in habitats of very different vegetative structure (Chapter 4).

6.3 Animal Techniques

6.3.1 Handling animals

On each trap round, all animals caught were removed from the traps, sexed, aged, their reproductive condition assessed, marked and then weighed to the nearest 0.5g before release.

6.3.2 Ageing animals

Animals were aged on the objective basis of weight and a subjective assessment of pelage (Pucek & Lowe 1975), and placed into one of the following categories which are based on findings of other studies (eg Gibson 1981; Gurnell & Rennolls 1983)

Juveniles	<= 10 grams, pelage grey
Sub adults	> 10 < 16 grams, grey pelage still partially present
Adults	> 16 grams, adult pelage.

The reproductive condition of individuals was subjectively assessed using the following criteria:

Males:

Testes abdominal = not fecund
Testes discernible but small = not fecund
Testes large = fecund

Females:

Imperforate vagina = not fecund
Perforate vagina = fecund
Pregnant = fecund
Lactating = fecund
Finished lactating = fecund

On every occasion of capture each animal was placed into a small polythene bag and weighed to the nearest 0.5g. Large animals were weighed with a 50 gram Pesola balance, while small animals were weighed with a 30 gram Salter balance as this was deemed to give greater accuracy at these lower weights. These balances were regularly calibrated using a range of small weights.

6.3.3 Marking animals

Following the method described by Twigg (1975a) all animals caught were marked by removal of one toe from a fore paw and one from a hind paw giving a total of 649 unique marks for each rodent species at each site. Some animals were also marked with a small monel metal ear tag. A pilot study during 1982 showed these tags to be practical as a method for marking mice and voles, with no adverse effects on the animals' trap response or survival. Full details are presented in Appendix 2.

CHAPTER 7

SPECIES DIVERSITY AND SIZE OF SMALL RODENT POPULATIONS

7.1 INTRODUCTION

Large herbivores directly affect the productivity, heterogeneity and stability of habitats (Chapter 1, section 1.2) and may therefore alter habitat suitability for small rodents (Chapter 1, section 1.3); this may be through a number of routes such as altered food supply, alteration in vegetation cover leading to increased predation pressure or improving habitat suitability for other species so increasing competitive pressure (Chapter 1, section 1.3). The precise effects upon small rodents are complex but it is apparent that alteration through grazing may exclude species that are more specific in their requirements or render the habitat "sub-optimal" to the more generalist species, the rodent species being able to survive within the habitat but its population performance being restricted due to reduced food supply (e.g. Bobek 1969; King 1983) or increased predation (Thompson 1955; Getz 1970; Birney et al. 1976; Hansson 1977). For some species the opposite may occur and suitability is increased (LoBlue & Darnell 1959).

Species diversity is a function of the number of species and their relative abundance (equitability), therefore habitat modification due to grazing will affect small rodent diversity. This is seen clearly in grassland communities (Chapter 1, section 1.1) with both abundance and number of species being altered. Although there is little comparable evidence for the effects of large herbivores within woodlands, other larger mammals, for example pigs (Singer et al. 1984), cause similar changes in species number and abundance. The primary effects of large herbivores are the same as other large mammals and so it is reasonable to suggest that similar changes would result.

This Chapter examines the two factors, diversity and abundance, in an attempt to discover differences between areas with different levels of grazing. Using the information presented in Chapters 3 and 4 the differences are related to the effects of large herbivores.

7.2 METHODS

7.2.1 Species Diversity

As noted above, diversity is a function of the number of species and their equitability; therefore to accurately describe the diversity of a habitat one requires a measure that uses both components. There are a number of measures of diversity based upon these characteristics (see Putman & Wratten 1983, or for more detailed discussions Hill (1973b) and Routledge (1979)). One of the commonly used measures is that of Shannon & Weaver (1949); with this index one is able to calculate equitability too (Lloyd & Ghelardi 1964).

Using the results of trapping data from the woodland and heathland trapping grids the diversity of the small rodent populations in the different study sites was measured using Shannon's diversity index (Shannon & Weaver 1949).

Shannon's diversity Index is:

$$H = - P \log (P_i)$$

where P = relative abundance of the $_i$th species and

H = the observed species diversity

Equitability (E) may be defined as the ratio of the observed diversity (H) to the theoretical maximum diversity (H_{max}) under maximum equitability (Lloyd & Ghelardi, 1964). Therefore equitability is calculated as:

$$E = H / H_{max}$$

Diversity of the animal populations was calculated in two ways:

1) Diversity and equitability of small rodents within each time period.
2) Diversity and equitability of small rodent plus insectivore populations in each time period.

The latter indices were calculated by including the number of shrews (in this case common, Sorex araneus, and pygmy, S.minutus). These two species occupy the same habitats as small rodents (the common shrew preferring woodlands and the pygmy shrew grasslands and heathlands) and so may be interspecific competitors. These insectivores appear to have highest numbers when field cover is greatest (Kirkland 1977; Ferns 1979; Churchfield 1984) so, as large herbivore grazing may affect small rodent diversity, it may also affect shrew diversity; in doing so this may have an additional affect on rodent diversity. It must be stressed that the capture of insectivores might not have been proportionally as high as that of small rodents because no attempt was made to bait for them. However, trap treadle weights were set light enough to catch them if they entered.

7.2.2 Population size

The trapping of small rodents is subject to many variables (see Appendix 2 for a full discussion) and so the actual number of animals caught may be only a small and biased sample of the actual population. In capture-mark -recapture studies (C.M.R.) over a long period of time, one gains information on the presence of animals even if they are not caught on every trapping occasion; although one assumes that animals remain within the study area when they are not trapped. There are many methods for estimating population size from C.M.R. studies (Seber 1973), but the principle limitation of most methods is their inability to accurately estimate population size when data are scarce (Blower, Cook & Bishop 1981) and that they use data from the number of animals caught at any one time which may thus be susceptible to behavioural and climatic influences (see Appendix 2). Use of such estimates for comparing the size of populations would therefore lead to compounding errors.

If one uses C.M.R. data to the full, one can calculate the actual number of animals known to be alive at any one time. This estimation of numbers is the Calendar of Captures estimate (Petruswicz & Andrzewski 1964). As this presents objective values one is able to make statistical comparisons of population size between sites; in this study inter-site comparisons of the rodent populations have been made using these values. Due to the small number of yellow necked mice caught, data comparisons have only been made between the number of mice at each site and the number of voles at outside and ungrazed sites.

7.3 RESULTS

7.3.1 Species diversity

Woodlands

The numbers of each species of small mammal caught in each three day trapping period at each site between 1982 and 1984 in the seasonal and monthly trapping programmes are shown in figures 7.1 & 7.2. These data were used to calculate the diversity and equitability of the populations.

The calculated diversity and equitability for each site are presented in table 7.1 in relation to the number of each species caught in each trapping period. The indices show small mammal diversity to be greater within the ungrazed woodlands, the indices falling in the range 0.18 to 0.70, whilst in the grazed sites the indices are generally 0.31. The exception to this is Sloden Inc where diversity is

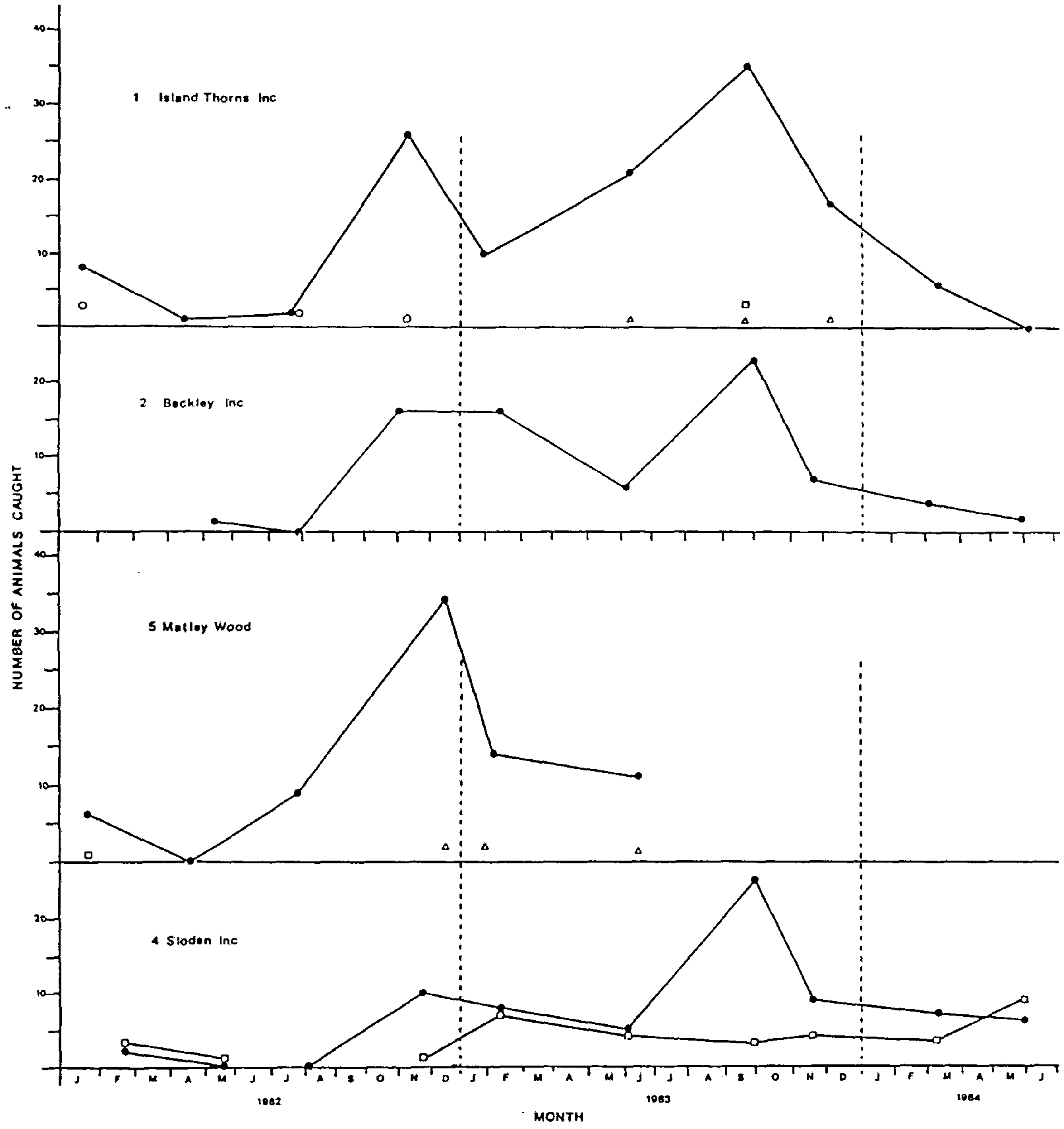


Figure 7.1 Seasonal changes in the numbers of small rodents (● A.sylvaticus, □ A.flavicollis & △ C.glareolus) and small insectivores (○ S.araneus & ■ S.minutus) caught during each three night trapping period within Open New Forest (sites 1 to 4), Enclosed New Forest (sites 5 & 6) and outside (sites 7 & 8) deciduous woodlands between January 1982 and June 1984.

figure 7.1 continued

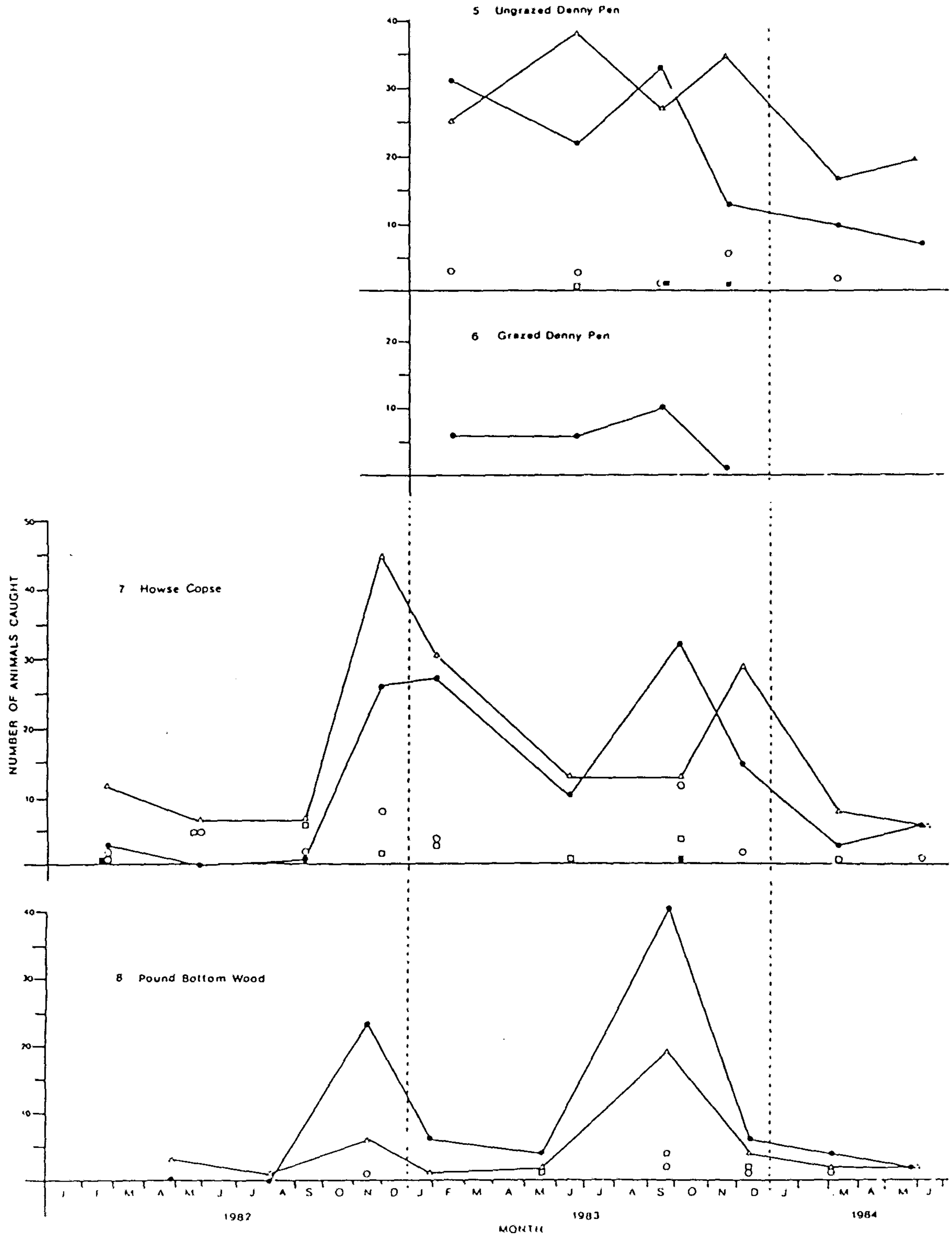


Figure 7.2 Monthly changes in the numbers of small rodents (● *A.sylvaticus*, □ *A.flavicollis* & △ *C.glareolus*) and small insectivores (○ *S.araneus* & ■ *S.minutus*) caught during each three day trapping period within Open (site 1) and Enclosed (site 2) New Forest and outside (sites 3 & 4) deciduous woodlands between November 1982 and June 1984.

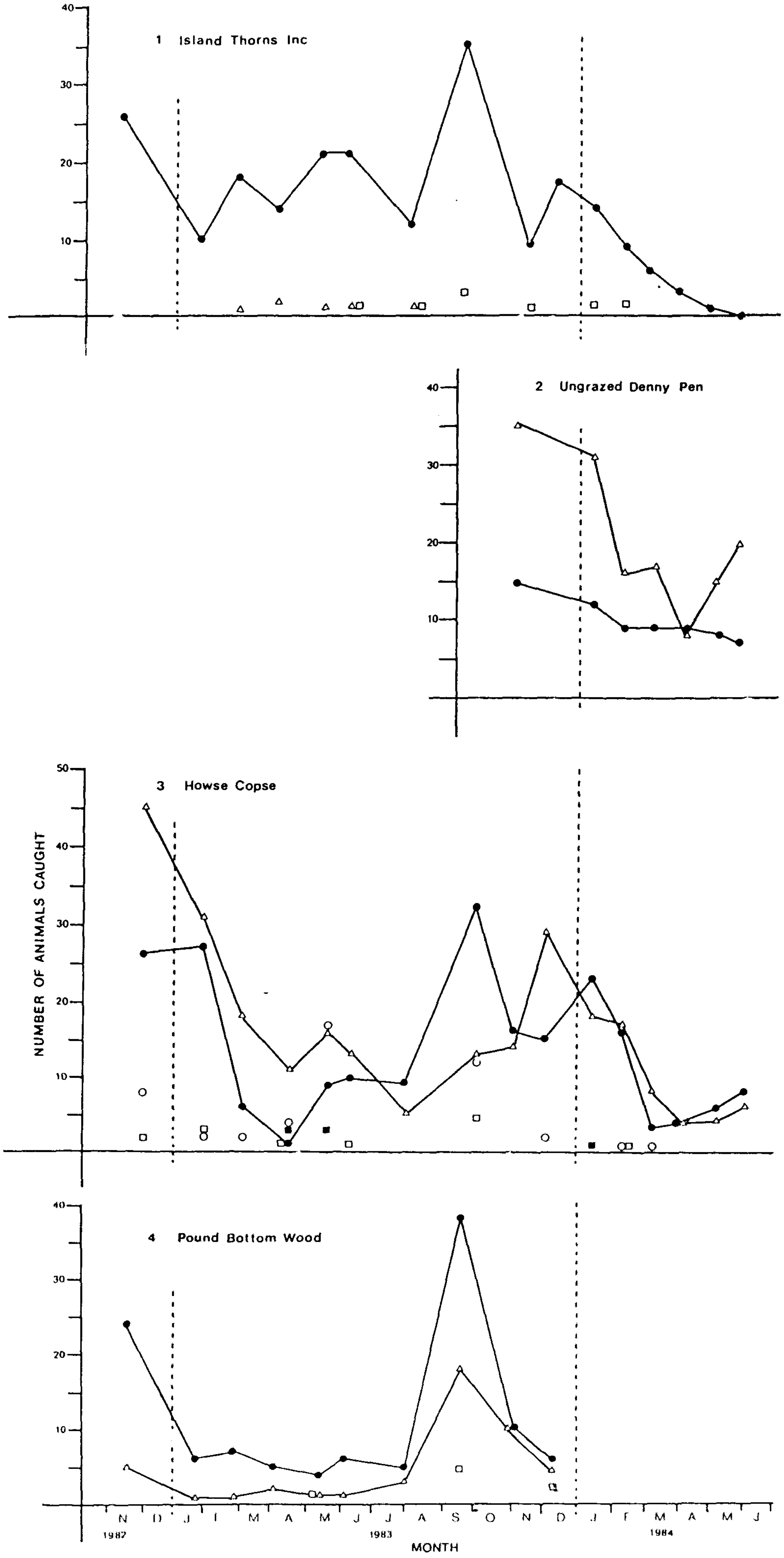

1 Island Thorns Inc
2 Ungrazed Denny Pen
3 Howse Copse
4 Pound Bottom Wood
NUMBER OF ANIMALS CAUGHT
50
40
30
20
10
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1982
1983
1984
MONTH

Table 7.1 Seasonal changes in the calculated diversity (Shannon & Weaver 1949) and equitability (Lloyd & Ghelardi 1964) of small mammals (small rodnts and small insectivores) and small rodents within Open New Forest (sites 1 to 4), outside (sites 5 & 6) and Enclosed New Forest (sites 7 & 8) deciduous woodlands.

Small mammal diversity

Site		1982				1983				1984	
1.Island Thorns Inc	Week	3	16	30	45	3	22	37	49	10	22
	S.I.	0.25	0.00	0.30	0.07	0.00	0.13	0.16	0.28	0.00	0.00
	E	0.85	0.00	1.00	0.24	0.00	0.44	0.35	0.46	0.00	0.00
2.Backley Inc	Week	-	17	31	46	5	21	38	47	9	21
	S.I.	-	0.60	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00
	E	-	0.99	0.00	0.32	0.00	0.00	0.00	0.00	0.00	0.00
3.Matley Wood	Week	4	23	36	49	4	23				
	S.I.	0.18	0.00	0.21	0.00	0.00	0.00				
	E	0.59	0.00	0.68	0.00	0.00	0.00				
4.Sloden Inc	Week	8	18	32	47	5	21	38	47	9	23
	S.I.	0.29	0.00	0.00	0.13	0.29	0.29	0.18	0.25	0.25	0.29
	E	0.97	0.00	0.00	0.44	0.99	0.97	0.59	0.84	0.85	0.97
5.Howse Copse	Week	9	22	37	48	4	23	39	49	10	22
	S.I.	0.54	0.31	0.65	0.44	0.43	0.34	0.70	0.32	0.34	0.37
	E	0.77	0.65	0.93	0.73	0.73	0.72	1.00	0.66	0.72	0.79
6.Pound Bottom Wood	Week	-	18	31	46	3	22	37	49	9	21
	S.I.	-	0.00	0.00	0.28	0.18	0.42	0.41	0.66	0.42	0.30
	E	-	0.00	0.00	0.58	0.59	0.87	0.67	0.85	0.87	1.00
7.Ungrazed Denny Pen	Week	-	-	-	-	6	24	36	46	10	22
	S.I.	-	-	-	-	0.37	0.38	0.36	0.40	0.34	0.23
	E	-	-	-	-	0.78	0.64	0.59	0.66	0.71	0.76
8.Grazed Denny Pen	Week	-	-	-	-	6	24	36	46	10	22
	S.I.	-	-	-	-	0.35	0.22	0.00	0.00	0.00	0.00
	E	-	-	-	-	0.72	0.72	0.00	0.00	0.00	0.00

Small rodent diversity

Site		1982				1983				1984	
1.Island Thorns Inc	Week	3	16	30	45	3	22	37	49	10	22
	S.I.	0.00	0.00	0.00	0.00	0.00	0.13	0.16	0.28	0.00	0.00
	E	0.00	0.00	0.00	0.00	0.00	0.44	0.35	0.46	0.00	0.00
2.Backley Inc	Week	-	17	31	46	5	21	38	47	9	21
	S.I.	-	0.60	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00
	E	-	0.99	0.00	0.32	0.00	0.00	0.00	0.00	0.00	0.00
3.Matley Wood	Week	4	23	36	49	4	23				
	S.I.	0.18	0.00	0.21	0.00	0.21	0.00				
	E	0.59	0.00	0.68	0.00	0.68	0.00				
4.Sloden Inc	Week	8	18	32	47	5	21	38	47	9	23
	S.I.	0.29	0.00	0.00	0.13	0.29	0.29	0.18	0.25	0.25	0.29
	E	0.97	0.00	0.00	0.44	0.99	0.97	0.59	0.84	0.85	0.97
5.Howse Copse	Week	9	22	37	48	4	23	39	49	10	22
	S.I.	0.31	0.00	0.42	0.33	0.37	0.34	0.37	0.28	0.29	0.29
	E	0.47	0.00	0.88	0.69	0.77	0.72	0.77	0.93	0.96	0.96
6.Pound Bottom Wood	Week	-	18	31	46	3	22	37	49	9	21
	S.I.	-	0.00	0.00	0.22	0.18	0.42	0.36	0.59	0.28	0.30
	E	-	0.00	0.00	0.74	0.59	0.87	0.75	0.85	0.92	1.00
7.Ungrazed Denny Pen	Week	-	-	-	-	6	24	36	46	10	22
	S.I.	-	-	-	-	0.29	0.39	0.29	0.23	0.26	0.23
	E	-	-	-	-	0.99	0.66	0.99	0.78	0.86	0.76
8.Grazed Denny Pen	Week	-	-	-	-	6	24	36	46	10	22
	S.I.	-	-	-	-	0.35	0.22	0.00	0.00	0.00	0.00
	E	-	-	-	-	0.72	0.72	0.00	0.00	0.00	0.00

higher, generally 0.29, due to the presence of both wood mice and yellow necked mice. Equitability of species is also greater in the ungrazed sites, being above 0.75. Again the exception is Sloden Inc; here it is close to unity on most occasions and this is due to the almost equal numbers of both mice species (figure 7.1).

If one excludes shrew species from the indices, the diversity in the ungrazed sites is reduced but the equitability of species increases due to near equal numbers of wood mice and bank voles. Calculations such as diversity indices cannot easily be compared statistically because no error term can be calculated (but see Jacknife technique Sokal & Rohlf, 1981, Chapter 18), but these indices do show the rodent populations in the ungrazed and outside areas to be more diverse and not dominated by one species as is seen in the grazed New Forest woodlands where wood mice predominate.

Heathlands

The numbers of each species of small mammal caught in each three day trapping period on each heathland between 1982 and 1984 are presented in table 7.2. As so few animals were caught on the New Forest heaths diversity indices cannot be calculated, but for the two outside heathlands the indices are presented in table 7.3, again in relation to the actual number of individuals caught. These two sites appear to have similar small mammal diversity with indices averaging 0.3, but the calculation of rodent equitability reveals the populations to be dominated by wood mice.

Acid grasslands

As so few animals were caught (see section 7.3.3) on the grasslands, diversity and equitability indices have not been calculated for these areas.

Table 7.2 The number of individuals of small rodents (Harvest mice (*Micromys minutus*) & Wood mice (*Apodemus sylvaticus*)) and small insectivores (Common shrew (*Sorex araneus*) & Pygmy shrew (*Sorex minutus*)) caught during Longworth trapping on *Calluna* heathland within (sites 1 & 2) and outside (sites 3 & 4) the New forest.

Site	Year	Month	Week	*M.minutus*	*A.sylvaticus*	*S.minutus*	*S.araneus*
1.Island Thorns	1982	July	22	0	1	0	0
2.Sloden Inc	1982	Feb	9	0	1	0	0
3.Pound Bottom	1982	Feb	5	12	6	1	0
		May	18	0	4	4	1
		Aug	31	0	6	1	0
		Nov	46	15	22	4	0
	1983	Jun	22	0	7	1	0
		Dec	49	1	25	6	0
4.Howse Copse	1982	Mar	9	11	3	0	0
		Jun	22	0	1	0	0
		Nov	48	15	8	3	0
	1983	Jun	23	0	1	1	1
		Dec	49	11	12	0	1

Table 7.3 Seasonal changes in the calculated diversity (Shannon & Weaver 1949) and equitability (Lloyd & Ghelardi 1969) of small mammals (small rodents and shrews) and small rodents from two Calluna heathlands outside the New Forest.

Site		1982				1983		1984
Setley Common Heath								
	Week	9	22	37	48	23	49	22
Small mammals	S.I.	0.22	0.00	0.00	0.39	0.00	0.36	0.00
	E	0.75	0.00	0.00	0.83	0.00	0.76	0.00
Small rodents	S.I.	0.22	0.00	0.00	0.27	0.00	0.30	0.00
	E	0.75	0.00	0.00	0.92	0.00	0.99	0.00
Pound Bottom Heath								
	Week	5	18	31	46	22	49	21
Small mammals	S.I.	0.34	0.42	0.17	0.47	0.16	0.26	0.00
	E	0.72	0.87	0.57	0.78	0.54	0.55	0.00
Small rodents	S.I.	0.27	0.00	0.00	0.37	0.16	0.26	0.00
	E	0.89	0.00	0.00	0.77	0.54	0.55	0.00

7.3.2 Population size

Deciduous woodlands

Wood mice

a) Seasonal Comparisons

The numbers of wood mice known to be alive at each site over the seasonal periods are presented in figure 7.3. Numbers at the beginning of the study at all sites were low (<5 individuals) but all populations increased in autumn 1982, with numbers at the outside sites being approximately twice those of the grazed sites. The same trend was found in 1983, but, in the winter of 1984, all populations returned to similar levels as those at the start of the study. Population sizes have been compared using a G test of independence (Sokal & Rohlf 1981). All sites have been compared together for the full two and a half years of the study (1982 to 1984) and a significant difference exists in the number of wood mice at each site for the duration of the study ($G = 67.12$, $p<0.001$, 24 d.f.). This comparison excludes the Denny Pens as they were not included in the study until 1983. Comparison of sites in pairs reveals significant differences in the number of wood mice between most pairs of sites (table 7.4), the most significant being found between the mouse population in Pound Bottom Wood and those at Howse Copse and Island Thorns Inc where numbers were greater.

Performing the equivalent test for the 1983-1984 data, but including the two Denny Pens, reveals significantly more mice to have been present in the ungrazed pen than any other site and fewer mice in the ungrazed pen than within Howse Copse or Island Thorns Inc.

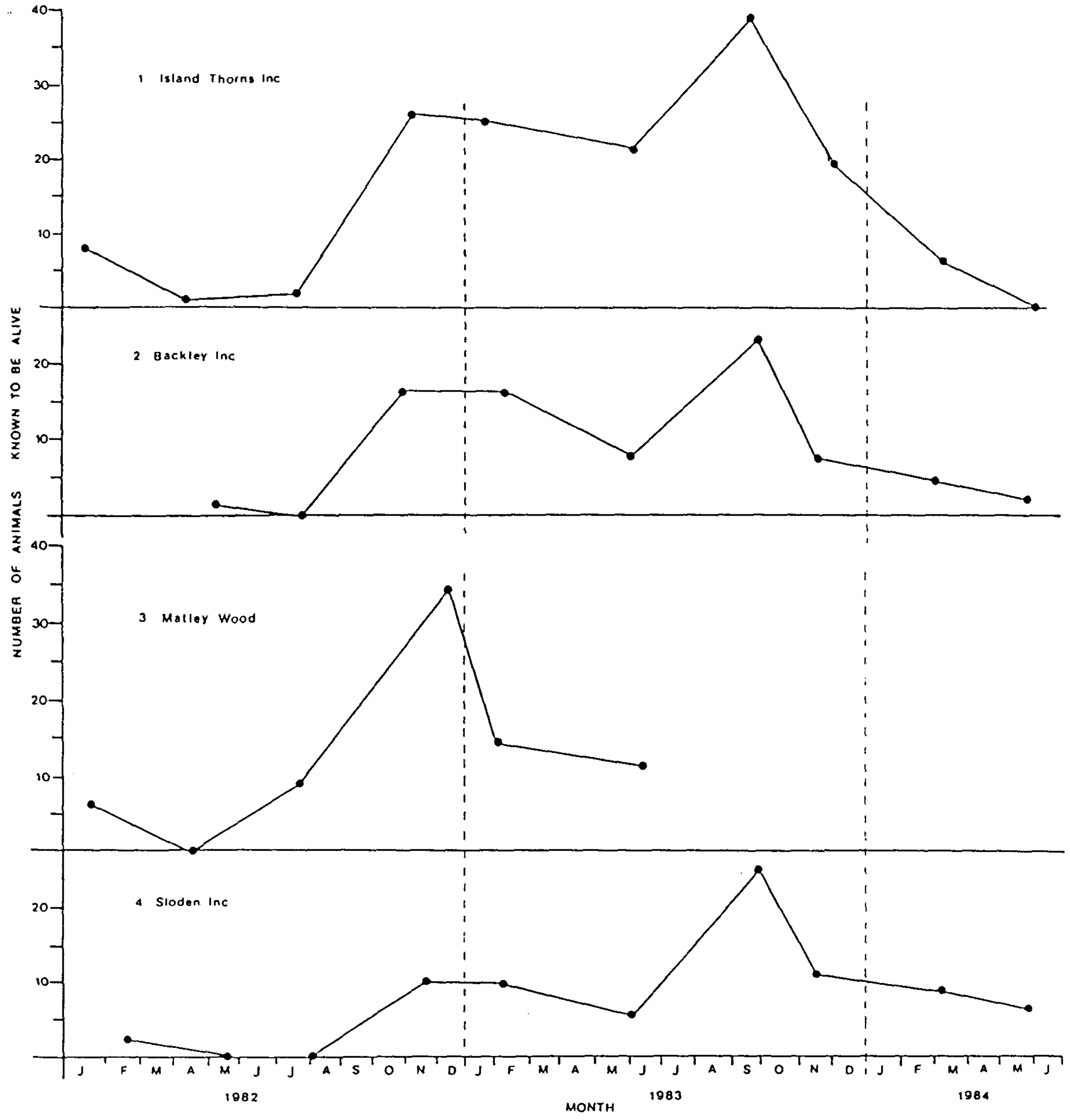


Figure 7.3 Seasonal changes in the numbers of small rodents (A.sylvaticus ●——● and C.glareolus △——△) known to be alive within Open New Forest (sites 1 to 4), Enclosed New Forest (sites 5 & 6) and outside (sites 7 & 8) deciduous woodlands between January 1982 and June 1984.

figure 7.3 continued.

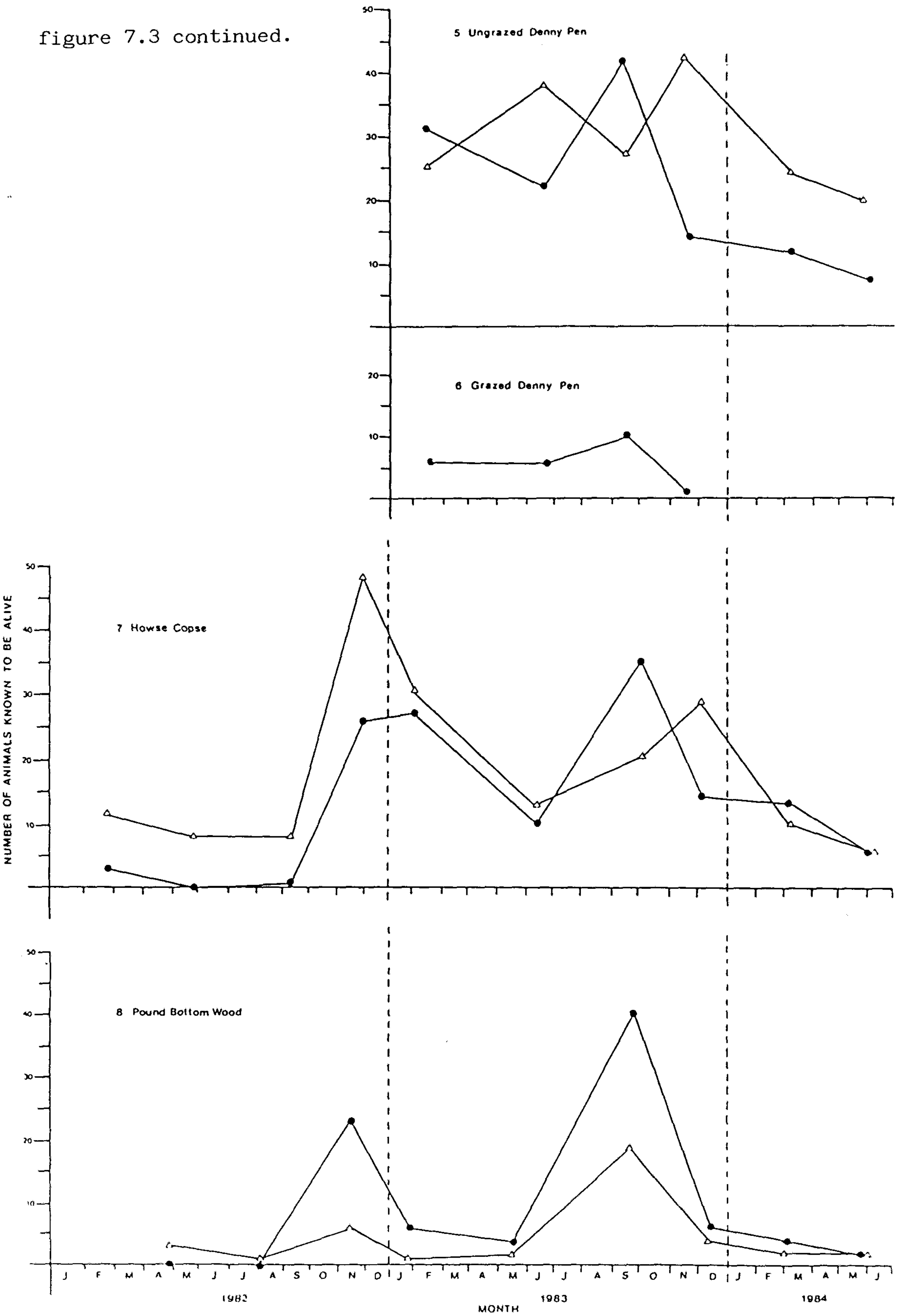


Table 7.4 Summary of the between site comparisons (G test of independence) of the numbers of *A.sylvaticus* known to be alive within New Forest and outside deciduous woodlands (*** $p<0.001$; ** $p<0.01$; * $p<0.05$) during seasonal and monthly trapping routines.

Seasonal Data

	G	df	p	
Island Thorns,Backley,Sloden, Pound Bottom & Howse Copse	67.12	24	<0.001	***
Howse Copse v Backley Inc	5.12	6	>0.500	
Howse Copse v Sloden Inc	3.60	7	>0.800	
Howse Copse v Island Thorns Inc	16.93	7	<0.050	*
Howse Copse v Pound Bottom Wood	32.39	6	<0.001	***
Pound Bottom Wood v Backley Inc	20.59	6	<0.010	**
Pound Bottom Wood v Sloden Inc	27.02	6	<0.001	***
Pound Bottom Wood v Island Thorns	28.93	6	<0.001	***
Island Thorns Inc v Backley Inc	2.94	6	>0.900	
Island Thorns Inc v Sloden Inc	23.41	8	<0.010	**
Backley Inc v Sloden Inc	10.60	6	>0.100	
Ungrazed Denny Pen v Backley Inc	1.46	5	>0.900	
Ungrazed Denny Pen v Sloden Inc	8.90	5	>0.100	
Ungrazed Denny Pen v Island Thor	14.02	5	>0.010	**
Ungrazed Denny Pen v Pound Bott	26.77	5	<0.001	***
Ungrazed Denny Pen v Howse Copse	12.68	5	>0.010	**
Ungrazed v Grazed Denny Pen	13.37	5	>0.010	**

Monthly Data

Howse Copse,Pound Bottom & Island Thorns Inc	53.81	18	<0.001	***
Howse Copse v Pound Bottom Wood	24.01	9	<0.010	**
Howse Copse v Island Thorns Inc	21.39	10	<0.010	**
Howse Copse v Island Thorns Inc	52.12	15	<0.001	***
Pound Bottom Wood v Island Thorns	36.39	9	<0.001	***

Monthly Data from 1984

Ungrazed Denny Pen,Howse Copse & Island Thorns Inc	22.38	10	<0.010	**
Ungrazed Denny Pen v Howse Copse	1.84	5	>0.800	
Ungrazed Denny Pen v Island Tho.	16.59	5	<0.010	**
Howse Copse v Island Thorns Inc	16.54	5	<0.010	**

b) Monthly comparisons

Using the monthly number known to be alive from the three sites (figure 7.4), Island Thorns Inc., Howse Copse and Pound Bottom Wood, the same route of analysis as above was performed. A significant difference was found between data for all sites ($G = 53.81$, $p < 0.001$, 18 d.f.) and between all pairs of sites (table 7.4)). Comparison of the 1984 monthly data replacing Pound Bottom wood with that from the ungrazed Denny Pen also reveals a significant difference in the number of animals at these three sites ($G = 21.62$, $p<0.01$, d.f.=10) and between pairs of sites (table 7.4).

Bank voles

Bank voles were only caught on three occasions at Island Thorns Inc and Matley Wood within the Forest, with generally only one individual caught at any one time and this was too few to allow statistical comparison of numbers with those in outside woodlands and the ungrazed Denny Pen (figures 7.1 & 7.2). The number of voles known to be alive within the outside and ungrazed woodlands was examined in the same manner as used for wood mice above. Both seasonal and monthly data are presented in table 7.5 and it is apparent that significantly fewer voles were present at Pound Bottom Wood than at Howse Copse or the Denny Pen, and that fewer voles were present at Howse Copse than in the Pen.

Fluctuations in numbers

Wood mice

Over the two and one half years of trapping, all wood mouse populations exhibited seasonal fluctuations in numbers (figure 7.3) with autumn peaks approximately ten times the

Figure 7.4 Monthly changes in the numbers of small rodents (*A.sylvaticus* ●—● & *C.glareolus* △—△) known be alive within Enclosed New Forest (site 1), Open New Forest (site 2) and outside (sites 3 & 4) deciduous woodlands between January 1982 and June 1984.

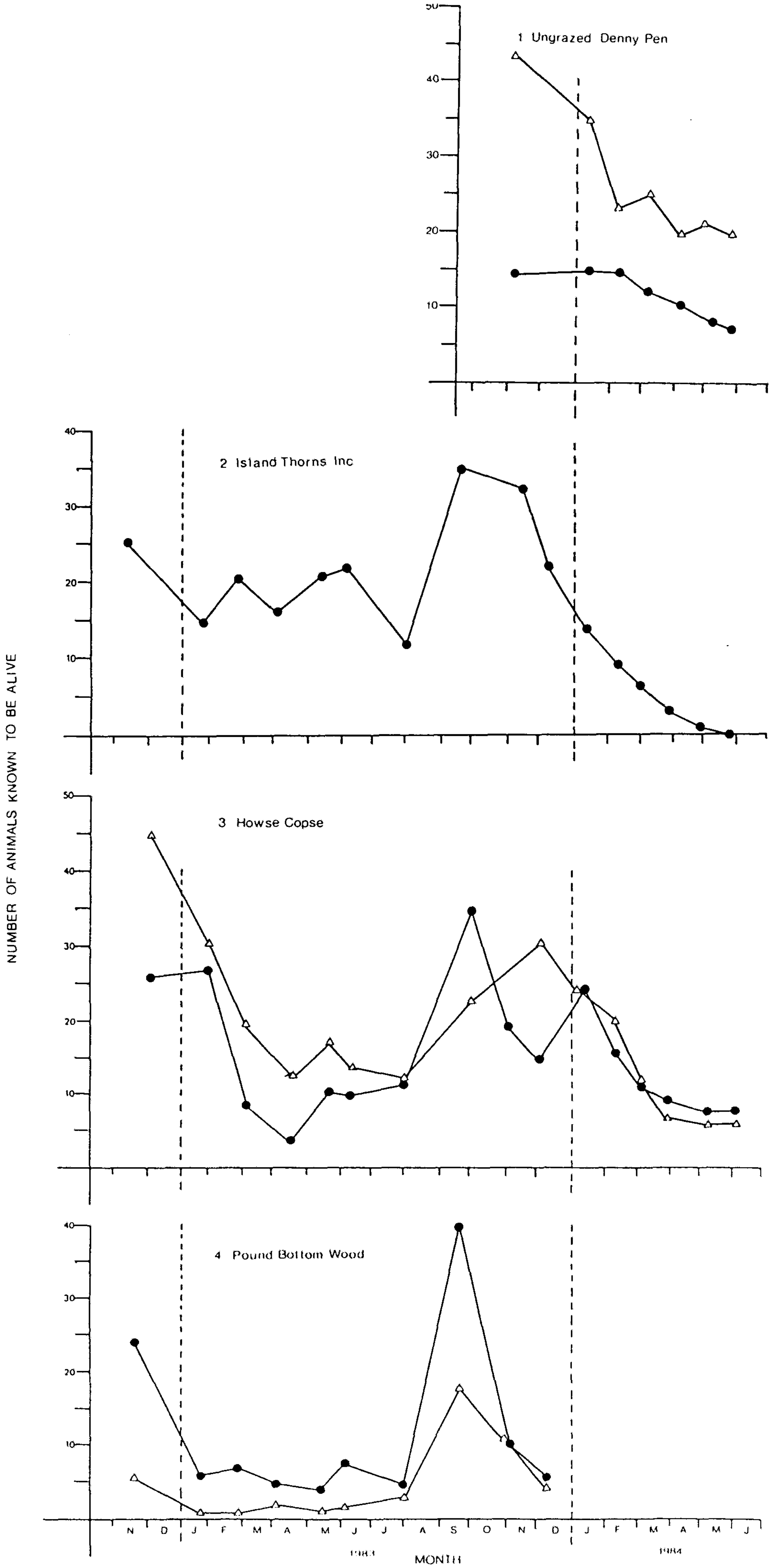

NUMBER OF ANIMALS KNOWN TO BE ALIVE
1 Ungrazed Denny Pen
2 Island Thorns Inc
3 Howse Copse
4 Pound Bottom Wood
50
40
30
20
10
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1983
1984
MONTH

Table 7.5 Summary of the between site comparisons (G test of independence) of the numbers of *C.glareolus* known to be alive within Enclosed New Forest and outside deciduous woodland (*** p<0.001) during seasonal and monthly trapping routines.

Seasonal Data	G	df	p	
Howse Copse v Pound Bottom	33.28	8	<0.001	***
Ungrazed Denny Pen, Howse Copse & Pound Bottom Wood	42.88	10	<0.001	***
Ungrazed Denny Pen v Howse Copse	5.93	5	>0.200	
Ungrazed Denny Pen v Pound Bott	38.06	5	<0.001	***
Howse Copse v Pound Bottom Wood	27.65	5	<0.001	***
Monthly Data				
Howse Copse v Pound Bottom Wood	32.55	9	<0.001	***
Ungrazed Denny Pen v Howse Copse	3.37	6	>0.500	

previous trapping sessions population size at most sites. These gradually declined over the winter to a minimum in the early summer months. These variations are seen more clearly in the 1983 monthly data (figure 7.4) which show the minimum number known to be alive to be in the May/June trapping period where generally less than 10 animals were caught. This was followed by a peak in the October trapping sessions. In Howse Copse and Island Thorns Inc the overwinter decline of 1984 was greater than the previous year and greater in comparison to that seen in the ungrazed Denny Pen. The numbers of wood mice within Pound Bottom Wood during 1983 showed greater seasonal fluctuation than the other sites with very low summer numbers, often less than 5, followed by an October peak eight times greater.

Bank voles

Bank vole populations exhibited similar seasonal changes to those seen in wood mice (figure 7.3). Examination of the monthly data for Howse Copse (figure 7.4) shows the decline to be slower in the voles than the mice: the minimum number known to be alive was later in August 1983, and this was followed by a later peak in numbers in December. Numbers of bank voles were again very varied at Pound Bottom Wood, staying below 5 all year until a marked increase in numbers in October. This was followed by a rapid decline in numbers before the end of the year.

Comparison between the number of voles and mice

Within the grazed New Forest sites, it is apparent that there are far more wood mice than any other small rodent species. In the ungrazed sites this difference is not so apparent and so a comparison of the actual number of voles and mice present at the three ungrazed sites was performed (table 7.4). This reveals significantly more voles than mice within the Denny Pen and more mice than voles at Pound Bottom Wood but no significant differences between the numbers of mice and voles at Howse Copse.

Summary

In summary, it appears that there are significant differences in the number of small rodents present within grazed and ungrazed areas, with more wood mice and bank voles within the ooutside and ungrazed areas. However the data from Pound Bottom Wood indicate fewer mice present over the duration of the study period than within the grazed Forest woodlands and that both mice and vole populations demonstrated wider fluctuations in autumn 1983 than at the other sites.

7.3.3 Heathlands and Acid grasslands

Heathlands

The numbers of rodents known to alive on the *Calluna* heathlands are presented in table 7.2. Only two wood mice were caught on the New Forest heathlands whereas resident populations of wood mice and harvest mice (*Micromys minutus*) were found on the outside heathlands. The wood mouse populations showed seasonal changes in numbers analagous to those found within the woodlands but harvest mouse populations showed distinct peaks, in late autumn and winter, before disappearing from the traps completely in the summer months.

Acid grasslands

The numbers of rodents present on the acid grasslands within the New Forest during 1982 are presented in table 7.6. Few animals were caught in this vegetation, a maximum of 11 being caught in January 1982, and on the grassland at Matley Wood the use of this area was increased in the summer months.

7.4 DISCUSSION

7.4.1 Deciduous woodlands

The diversity and number of woodland small mammals has been shown by a number of workers to vary depending upon habitat structure (Hansson 1978; Grant & Birney 1979). Analysis of species diversity of woodland populations in this study showed diversity to be greater in ungrazed and outside woodlands than the grazed areas and, if one examines small rodent diversity alone, this difference is amplified.

The greater diversity of animals in the ungrazed and outside woodlands can be attributed to the presence of bank voles and of more shrews, with bank voles accounting for approximately 50% of the small rodent populations at most times in these areas (figure 7.3) whereas, in the grazed sites, the populations are dominated by wood mice. Equitability was generally higher within the outside and ungrazed sites where total rodent populations consisted of similar numbers of mice and voles, whereas, in the grazed sites, populations were dominated by wood mice.

These differences in species diversity can be attributed to the differences in vegetative structure of the habitats which arise through large herbivore grazing. It is known that bank voles show a strong preference for ground cover (Newson 1960; Southern & Lowe 1968) and the analysis

Table 7.6 The number of individuals of small rodents caught in three day trapping periods during 1982 on acid grassland at Matley Wood and Sloden Inc within the New Forest.

Site		JAN.	APR.	AUG.	NOV.
Matley Wood	*C.glareolus*	1	0	0	0
	A.sylvaticus	9	0	6	3
	A.flavicollis	1	0	0	0
Sloden Inc	*A.sylvaticus*	1	1	0	0
	M.agrestis	3	2	0	0

of this stratum (Chapter 4) revealed there to be very little cover in the grazed Forest woodlands whilst the two ungrazed sites, Howse Copse and the Denny Pen, have a high degree of cover, principally brambles. Shrews also show a preference for ground cover (Corbet & Southern 1977) It is suggested that one principle reason for the absence of bank voles and shrews from the grazed sites is that the habitat is unsuitable for them. The occassional occurrence of bank voles at Matley Wood is attributed to movement from adjoining habitats where there is quite extensive ground cover.

Although the classification of the vegetation (Chapter 4, table 4.1) did not separate the Pound Bottom Wood site as clearly from the New Forest sites as Howse Copse and the ungrazed Denny Pen, there was a small resident bank vole population at this site. Total large herbivore use of this site was quite high (Chapter 3) and, as with the Forest woodlands, there is little ground cover excepting bracken; however the bracken cover was quite extensive and bracken litter was not broken down by the cattle and ponies as in the Forest. Also, as with the voles at Matley Wood, adjacent habitats may have acted as reservoirs for the voles.

Comparison of the actual numbers of wood mice alive in the grazed, ungrazed and outside sites revealed larger populations in the latter two areas, although this does not mean that the populations in these areas are always larger. At the beginning of the study, all populations of wood mice were at low levels (figure 7.3) and it was only after the greater rise in numbers in autumn 1982 that more mice were in the outside and ungrazed areas. The populations then reached quite high levels in comparison with those in the grazed areas, and significantly greater levels in the ungrazed Denny Pen than the other two outside sites. Unfortunately, details on the size of the wood mouse populations during 1982 within the ungrazed Pen are not known except that during a 10 day trapping period in July only 8 individuals were caught in each pen. It is tentatively suggested that this mouse population was at the same low level as the other sites but that it increased more rapidly in autumn 1982.

Only small numbers of yellow necked mice were caught at most sites and only at Sloden Inc were they caught regularly (figure 7.1); a few animals were recaught in subsequent trapping periods but in small numbers in comparison with the recaptures of wood mice. It is probable that the distribution of this species is localised and numbers are very small in the study areas. The ecology of this species is still not clearly understood (Flowerdew 1985; Gurnell 1985), its distribution and abundance being localised and often variable. In studies with resident populations, they do show a preference for mature woodland but not for any cover characteristics of vegetation (Montgomery 1980b). The occasional occurrence of this species at all sites, except Backley Inc, and the resident population being only within Sloden Inc suggests that distribution is localised throughout the Forest and adjacent areas, and that numbers are generally small.

Differences in the presence and abundance of bank voles between grazed, outside and ungrazed sites areas are very marked (figure 7.3) with only occasional occurrences of voles within the Forest sites. Comparison between the other three sites shows a gradation of numbers, and the differences appear to be similar to those of previous studies (e.g. Newson 1960) where population size was greater in areas of dense vegetative cover. Bank voles show a strong preference for a high degree of cover, and the greatest numbers were caught in the ungrazed Denny Pen which does have dense vegetation. The least number of voles was caught in Pound Bottom Wood where bracken is the only vegetation affording cover. Howse Copse, with its covering of brambles and bracken, had the intermediate number of voles. These sites probably show a gradation in habitat suitability for voles, the ungrazed Denny Pen being the most and Pound Bottom Wood the least suitable.

Comparisons made between sites of bank vole and wood mouse population size for such a short period should be treated with caution because of the marked variability that can occur in localised density (Kikkawa 1964), and one cannot make precise comments on population size without knowledge of population processes such as survival and reproduction. These are examined in detail in Chapters 8 and 9.

Trapping within the two Denny Pens gives the opportunity to comment more directly on the effects of grazing on small rodent distribution and numbers. Obviously these two Pens are quite artificial habitats but they do show that grazing of woodlands can result in a reduction of species and numbers of animals. The number of wood mice caught in the grazed Pen was always much lower than the number in the ungrazed one (figures 7.1 & 7.2). These two Pens are adjacent and it is suggested that animals in the grazed Pen were not resident: on a number of occasions animals caught on one grid would be recaught on the other and there were no recaptures of individuals within the grazed Pen. As no voles were caught in the grazed Pen, one can suggest that both species selected the ungrazed area. From a knowledge of the habitat preferences of these rodents, it is suggested that the more dense vegetation of the ungrazed Pen offered a more suitable habitat.

Therefore the main observations to be drawn from the initial trapping data are the greater diversity of small rodent, and small mammal, populations in the ungrazed woodlands attributable, to the effects of large herbivore grazing, and an indication that population size of wood mouse populations is greater in the ungrazed sites.

Comparisons of woodland populations with other studies

Population size

There have been numerous studies of small rodents within deciduous woodland and as many estimations of density. French *et al.* (1975) reviewed many studies and it can be seen from their work how variable population density for wood mice and bank voles may be: from one study alone within oak woodland they found woodmouse density to vary seasonally from 2.6 to 44.7 ha^{-1} and bank vole densities to range from 0.6 to 44 ha^{-1}, and long term studies have shown marked annual fluctuations in population size (Southern & Lowe 1982). French *et al.* (1975) also showed how population size may vary not only within a habitat but also between them, both seasonally and annually; of course all these conclusions depend upon the method of estimation. Calculated densities from this study are presented in Appendix 3 and these too are very variable, within and between sites.

It is therefore difficult to make objective comparisons between studies from published data, often only general information is given on the habitat which is the important determinant of rodent population size. In 1982 the Mammal Society established the National Small Mammal Survey, with mammalogists around Great Britain using a standard trapping regime bianually, in May/June and November/December, to sample woodland small mammal populations. This regime is almost identical to that used in this study, the only difference being that two traps rounds per day are used in the Survey. This therefore presents the opportunity to directly compare population size and fluctuations found in this study with those elsewhere in Britain between December 1982 and June 1984.

For this comparison, only data from other study sites dominated by oak have been used, and figure 7.5 presents the mean number of wood mice and bank voles caught within these studies in comparison with the mean number caught within the New Forest and outside woodlands. Data from the Denny Pens have been excluded as these are less than 10 ha in area and therefore fail to fulfil a prerequisite of the Survey that woodlands should be greater than 10 ha.

Figure 7.5 shows how the number of wood mice caught nationally in 1982 were low. As one would expect, all the populations show seasonal variation of low summer high winter numbers over the two and a half years. However, from December 1983 the variation in numbers caught increases suggesting that numbers in some areas were increasing faster than others. The numbers of bank voles caught nationally is much more variable than that seen for the wood mice and not so low at the beginning of the survey. Also, comparison with the data from the sites in this study does not reveal similar patterns of population size and fluctuation.

It is accepted that comparisons of this kind must be treated with caution as complete details on habitat, weather and population structure are not available, but it is suggested by Flowerdew (unpublished) that the low numbers of wood mice in 1982, and 1983 in some areas, were due to poor autumn tree seed crops. Those populations seen to increase in 1983 and 1984 were in areas where tree seed crops were good. Accepting the limitations of the comparisons, it is felt that wood mouse numbers in 1982 and 1983 were generally low and that, at that time, the populations in this study were at similar levels to those in similar habitats around Britain.

Population fluctuations

All the small rodent populations exhibited the seasonal changes in numbers seen in most previous studies (see reviews by Alibhai & Gipps (1985) for voles and Flowerdew (1985) for mice). The seasonal number alive data (figure 7.3) only reveal the high winter low summer levels

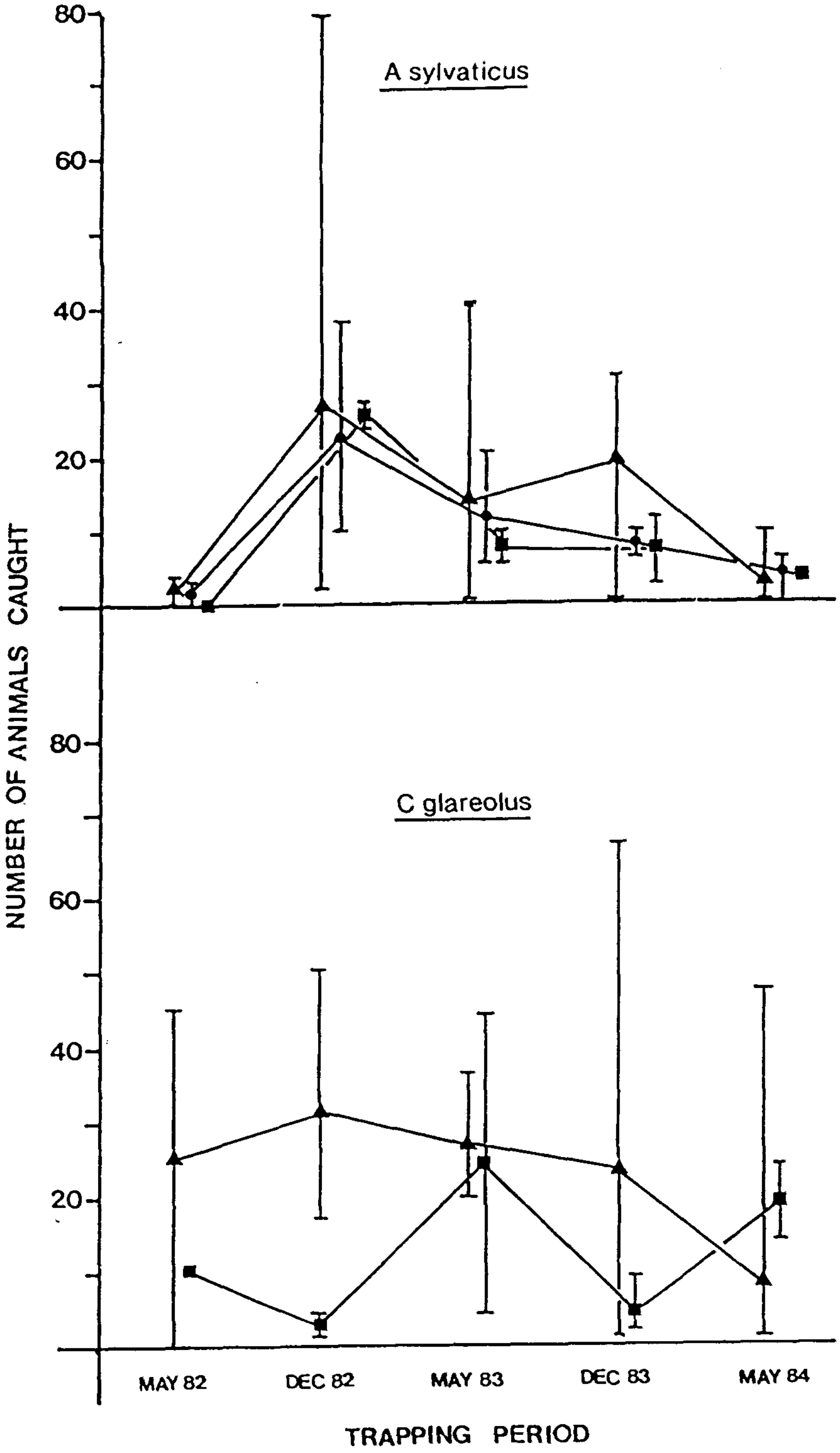


Figure 7.5 Comparison of the seasonal changes in mean numbers (+/- minimum and maximum) of A.sylvaticus and C.glareolus caught during three day trapping periods within Open New Forest (●——●) and outside New Forest (■——■) deciduous woodlands with the mean number (+/- min & max) from ten simultaneous studies in various parts of Great Britain (▲——▲). (Data from the ten studies courtesy of the Mammal Society).

but the monthly woodland data describe these fluctuations in more detail (figure 7.4). Other studies of woodland populations show population peaks in the early winter followed by a slow decline in numbers. The results of this study suggest that the peak in numbers was the same but that the decline in numbers was greater.

7.4.2 Heathlands

The data on species diversity and animal numbers for the grazed and outside heathlands reveal the same basic differences in the small rodent populations seen in the woodlands, *i.e.*, the presence of more species and greater numbers of rodents in the ungrazed areas. Due to so few animals being caught on the grazed heathlands, statistical comparison is felt inappropriate. The change in the presence of harvest mice on the grazed heathlands is interesting but it is probably due to seasonal variation in trap response rather than population fluctuations of animals on the trapping area (Trout pers. comm.).

The same explanation as offered for the differences in woodland populations can be used here to explain the differences between grazed and outside heathland areas. Vegetation analysis of the heathlands reveals the heaths outside the New Forest to be structurally more complex (Chapter 4) this offering habitats more suitable to small rodents. The greater plant diversity of the habitats may offer greater food resources too. Harvest mice show a strong preference for areas of tall dense vegetation and a negative association with livestock (Harris 1979).

7.4.3 Acid grasslands

Very few small rodents were caught on the New Forest acid grasslands. Although four species, wood mice, yellow necked mice, bank voles and field voles, were caught in these areas, only wood mice were caught in any numbers and this was at Matley Wood (table 7.6).

The New Forest acid grasslands are similar in appearance to the Forest lawns, described by Edwards & Hollis (1982), with the grass only reaching a few centimetres in height because of the continual grazing by large herbivores. Hansson (1982) demonstrated that the field vole, a grassland small rodent, prefers thick vegetation and leaf litter with soft soil in which to burrow. The Forest acid grasslands do not offer such a habitat because cover is seasonal with the growth of bracken which disappears in the winter months due to trampling by large herbivores. It is not surprising therefore to find that only three field voles were caught on the grasslands.

The capture of wood mice at the Matley Wood grassland site appears to be seasonal in nature and is possibly linked to the growth of bracken cover. In the summer the grasslands have a high bracken cover, but in the early winter the dead bracken gradually disappears until in the spring there is no vegetative cover above the grass. This may explain the presence of wood mice in the summer and early winter months but not in the spring with the animals being open to a greater risk of predation when cover is low.

The use of the Matley Wood grassland is discussed in more detail in Chapter 10.

CHAPTER 8

STRUCTURE OF THE WOODLAND SMALL RODENT POPULATIONS

8.1 INTRODUCTION

The age and sex structure of small rodent populations varies seasonally with rates of juvenile recruitment, individual survival and behaviour (e.g. for wood mice see Flowerdew 1985). In years of no overwinter breeding, which is normal, a population consists entirely of adults in the spring; after the initial breeding period, juveniles are recruited into the population from July/August (e.g. Gibson & Delany 1984), when adult survival is poor (e.g. Crawley 1970) and so, by the autumn, new animals dominate the population. The age of these animals varies depending upon the time of recruitment, for example, late recruitment will mean the population is dominated by young animals. The autumn population normally attains adult weight quickly and overwinters at this until the following spring when breeding recommences. A number of studies have noted seasonal variations in the sex ratios of trapped wood mouse and bank vole populations, often with more males than females (Tanton 1965; Ashby 1967; Crawley 1970; Montgomery 1980c; Gibson & Delany 1984), and it has recently been suggested that in wood mice this is due to females being less active and also becoming territorial during the breeding season (Wolton & Flowerdew 1985).

Changes in population structure may be affected by physical characteristics of the habitat. Autumn food availability is of extreme importance to small rodents (Chapters 3 & 5, sections 1.3.2 & 5.1), affecting fecundity (Smyth 1966), survival (Bobek 1969) and movement (Flowerdew 1972), all of which result in alteration of population structure. The effects of other factors such as predation pressure (Chapter 3, section 1.3.3) are less clearly understood, but it is suggested that there is differential predation on a population thus further affecting structure (Anderson & Erlinge 1977).

Population structure may also be affected by the population itself. At high density an early cessation to breeding may occur (e.g. Watts 1968), obviously further affecting recruitment. In some species (e.g. M.townsendii (Boonstra & Krebs 1977) and P.maniculatus (Fairbain 1978)) high densities lead to dispersion of younger animals; although the same age classes of bank voles and wood mice disperse, the relationship with density is not so apparent (Wolton & Flowerdew 1985).

A conglomerate of factors therefore affect the structure of small rodent populations, and it should be apparent that habitat modification may influence these factors as the suitability of the environment for the rodents is altered. This has been shown in C.gapperi populations after clear-cutting areas (Martell 1983a), with reduced recruitment and increased juvenile mortality. Many factors may affect habitat suitability and, in this study, it has been found that both diversity and abundance of rodents varies between grazed, low grazed and ungrazed woodlands (Chapter 7). A reduction of diversity and abundance leads to reduced inter and intra-specific competition within the grazed New Forest woodlands which might be favourable to the wood mouse populations present; however, the effects of large herbivores might be unfavourable, for example, reducing cover so increasing vulnerability to predation or reducing food supply. It is therefore suggested that the structure of the wood mouse populations in the grazed Forest woodlands may be different from those in the other areas.

This Chapter therefore compares two aspects, sex ratio and age structure, in relation to reproductive activity, of woodland wood mouse populations between all study areas, and bank vole population structure within the ungrazed Denny Pen and the lightly grazed Howse Copse.

8.2 SEX RATIOS

8.2.1 Wood mice

Sex ratios stayed almost equal and constant at 1:1 within all sites throughout the study; periods where males formed a high or low proportion of the population are related to trapping sessions when the number known to be alive was small (Chapter 7, figures 7.3 & 7.4), mainly in spring and early summer months.

The seasonal and monthly changes in sex ratio at each site were not found to be significantly different (table 8.1) and this result is endorsed by examination of the ratios for each trapping session in which no significant differences in the ratios of males to females were found.

The monthly changes in sex ratios of the woodland wood mouse populations are presented in figure 8.1 as the percentage of the population that were males and are based on the total number of animals known to alive at each period (Chapter 7, figure 7.4).

8.2.2 Bank voles

As with wood mice, the ratios of bank voles stayed equal in most trapping periods and no significant differences were found in the sex ratios over time (table 8.1), but, within each trapping session, some significant differences were found in the ratios of the populations at Howse Copse and the ungrazed Denny Pen. Both these differences were in the winter and spring months when captures were low, but in favour of females in the Denny Pen and males in the Howse Copse site. The monthly changes in sex ratios for the number of bank voles known to be alive are presented in figure 8.2.

Table 8.1 Significance (G test) of seasonal (1982 to 1984) and monthly (1983 to 1984) changes in the sex ratios of A.sylvaticus and C.glareolus populations within Open New Forest (sites 1 to 4), Enclosed New Forest (sites 5 & 6) and outside New Forest (sites 7 & 8) deciduous woodland study sites.

Site	Apodemus sylvaticus			Clethrionomys glareolus		
	G	df	p	G	df	p
Seasonal						
Island Thorns Inc	1.69	9	>0.05	-	-	-
Backley Inc	9.56	8	>0.05	-	-	-
Sloden Inc	5.04	9	>0.05	-	-	-
Matley Wood	1.82	5	>0.05	-	-	-
Ungrazed Denny Pen	1.51	5	>0.05	6.89	5	>0.05
Grazed Denny Pen	3.24	5	>0.05	-	-	-
Howse Copse	8.26	9	>0.05			
Pound Bottom Wood	7.64	8	>0.05			
Monthly						
Island Thorns Inc	8.72	15	>0.05	-	-	-
Ungrazed Denny Pen	1.15	5	>0.05	2.82	5	>0.05
Howse Copse	5.73	15	>0.05	17.63	15	>0.05
Pound Bottom Wood	14.26	9	>0.05	8.96	9	>0.05

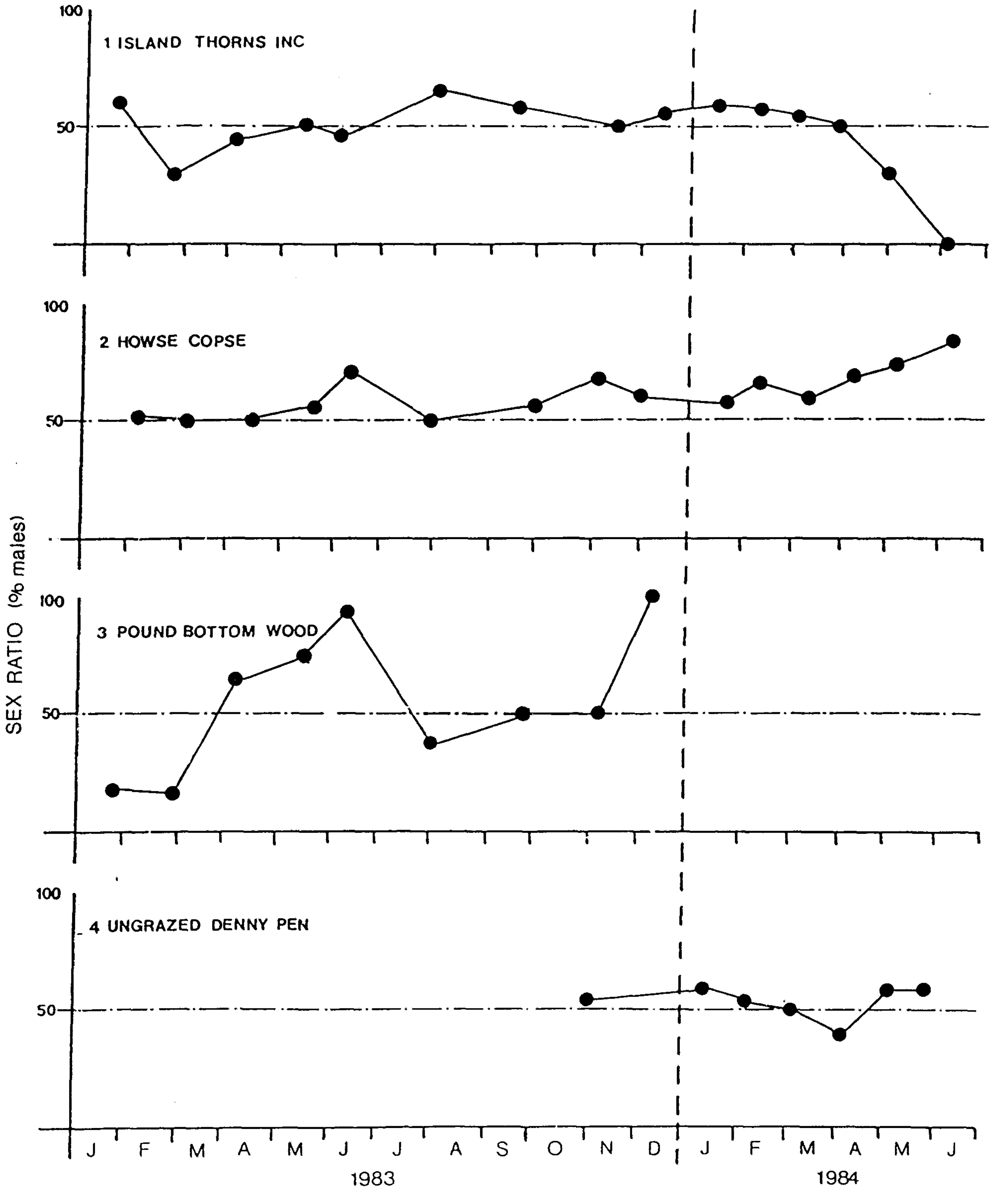


Figure 8.1 Monthly changes in the sex ratios (expressed as % males) of A.sylvaticus populations within Open New Forest (site 1), outside New Forest (sites 2 & 3) and Enclosed New Forest (site 4) between January 1983 and June 1984.

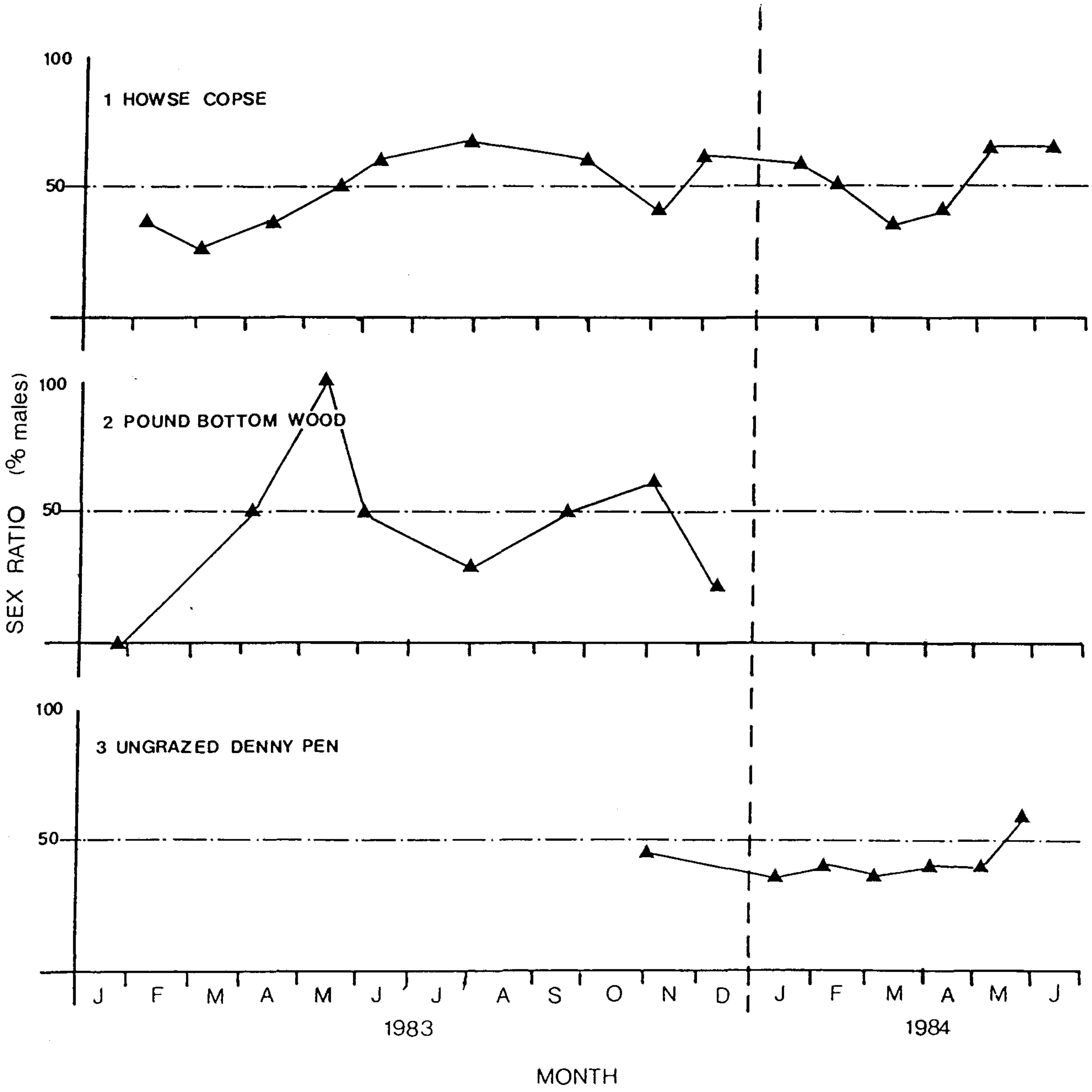


Figure 8.2 Monthly changes in the sex ratios (expressed as % males) of C.glareolus populations within deciduous woodlands outside the New Forest (sites 1 & 2) and an Enclosed New Forest woodland (site 4).

8.3 AGE AND WEIGHT CLASSES, AND REPRODUCTION

8.3.1 Wood mice

Age structure

The seasonal changes in age structure of the wood mouse populations are presented in figure 8.3. In the late summer and autumn juveniles and subadults account for approximately 50% of those caught in the grazed sites. In the other sites, Pound Bottom Wood and Howse Copse, they account for the same in 1982 but only 30% in 1983. In the two Denny Pens during 1983 this age class accounted for 30% of the population in the autumn in the ungrazed pen but 75% of animals caught in the grazed one. From the seasonal trapping data it is not possible to identify the start of recruitment, however, the monthly changes in age structure at the four sites trapped under this routine (figure 8.4) reveal that, within the two sites outside the New Forest, juveniles and sub-adults appeared in the population in June and July 1983, and were most abundant in the trapped population in September of that year. The age structure of the populations at Island Thorns Inc in the Forest shows sub-adults to be present in the population all year, recruitment of new juveniles and sub-adults occurring from late June to a peak in September. At this time they formed the major part of the trapped population (figure 8.4).

Mean weight

Comparison of mean weight for all age classes between sites (comparing seasonal data within all sites and monthly data within Island Thorns Inc, Howse Copse and Pound Bottom Wood) reveals no significant differences between sites but does reveal significant differences over time (2 way ANOVA: $p<0.01$). The monthly changes in mean weight of sex classes

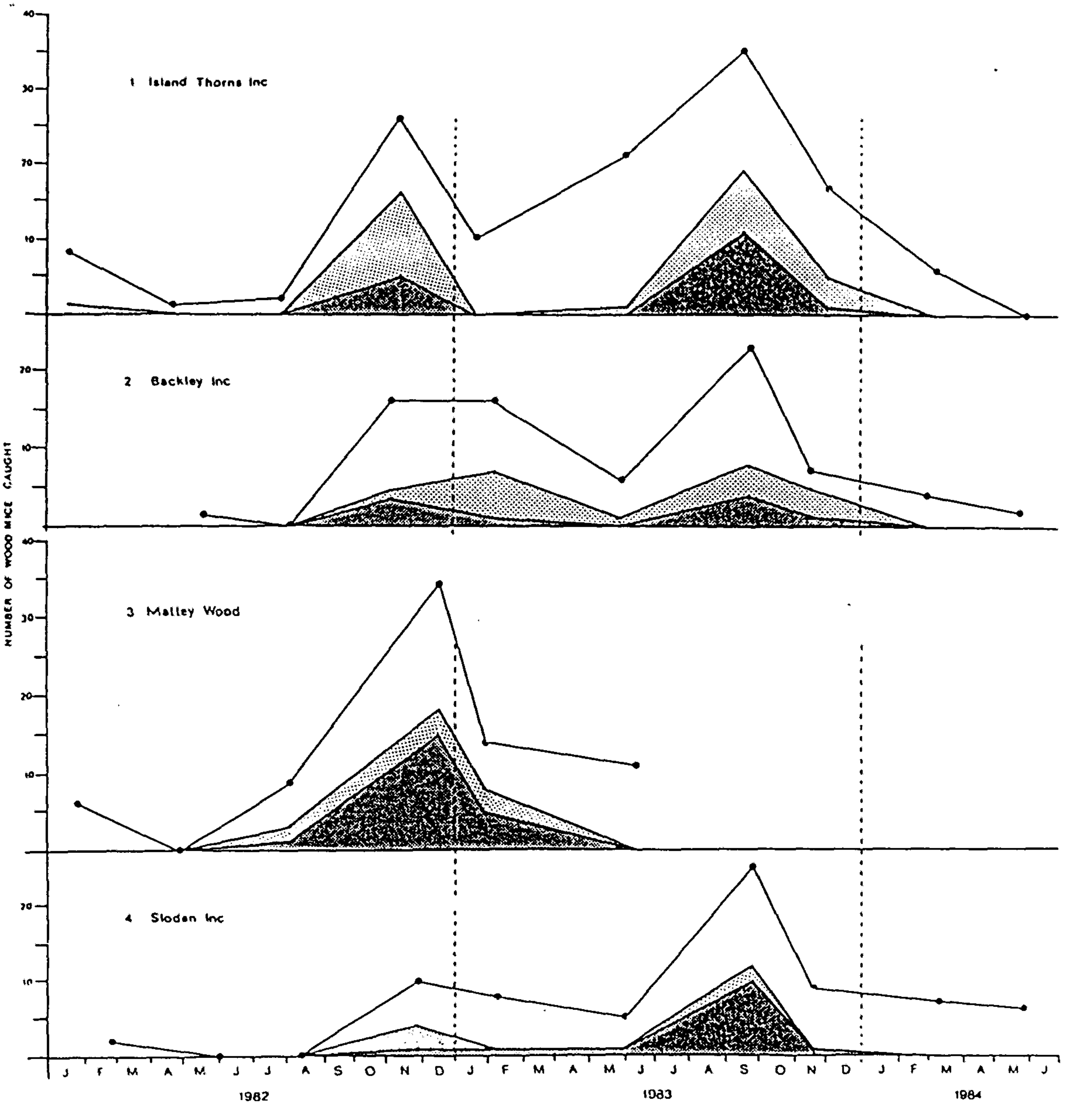


Figure 8.3 Seasonal changes in the age structure (☐=Adults, ▒ =Sub-adults & ▓=Juveniles) of A.sylvaticus populations caught during 3 night trapping periods within Open New Forest (sites 1 to 4), Enclosed New Forest (sites 5 & 6) and outside (sites 7 & 8) deciduous woodlands between January 1982 and June 1984.

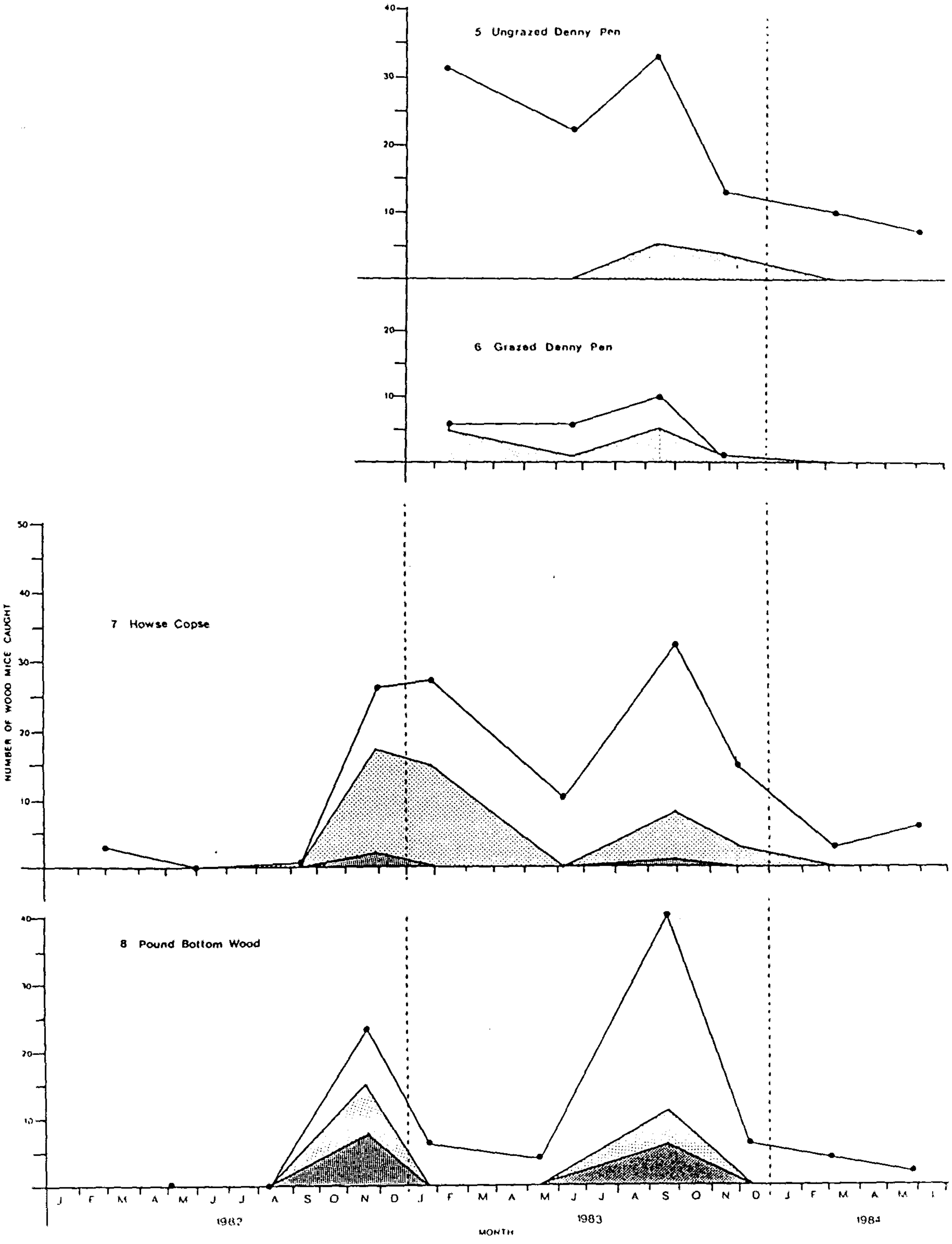
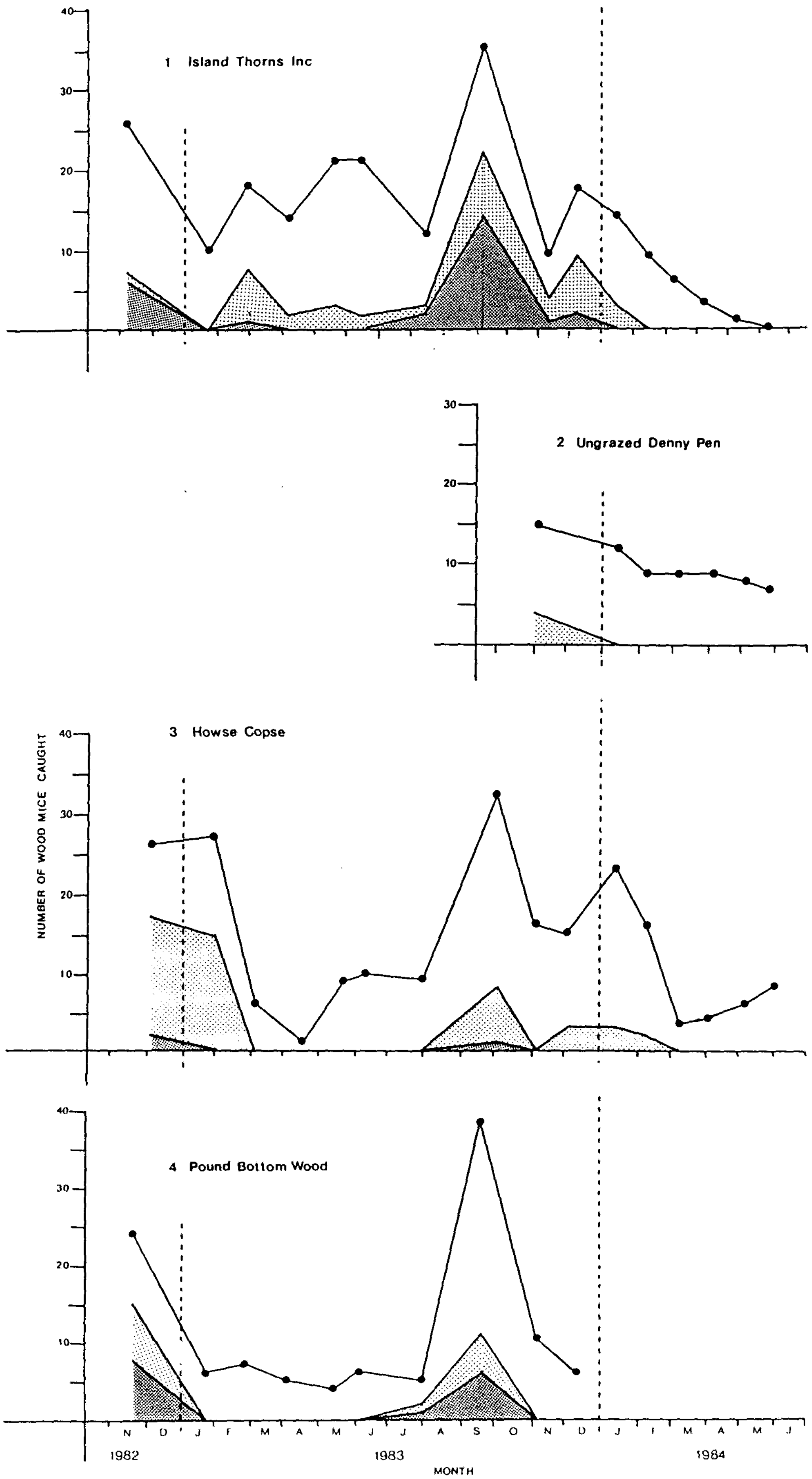


figure 8.3 continued

Figure 8.4 Monthly changes in the age structure (□=Adults, ░=Sub-adults, ▓=Juveniles) of *A.sylvaticus* populations caught during 3 night trapping periods within Open New Forest (site 1), Enclosed New Forest (site 2) and outside New Forest (sites 3 & 4) deciduous woodlands between November 1982 and June 1984.


1 Island Thorns Inc
2 Ungrazed Denny Pen
3 Howse Copse
4 Pound Bottom Wood
NUMBER OF WOOD MICE CAUGHT
40
30
20
10
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1982
1983
1984
MONTH

and the two age groups are presented in figure 8.5. The monthly changes in adult mean weight are related to periods of fecundity: adult males becoming fecund (see below) and increasing in weight before females. Juvenile and sub-adult weights increased during the autumn coming close to adult weights by the winter.

Fecundity

Periods of fecundity are shown in figure 8.6 for the four sites trapped under the monthly routine: males became fecund approximately one month before females, in late March 1983, and remained approximately so one month longer, into October 1983. In 1984 fecund males also appeared by March but fecund females did not appear until late June, approximately one month later than the previous year.

Comparison of fecundity between sites in 1983 suggests no differences in the proportion of fecund adults except that female fecundity at Island Thorns Inc began to subside earlier than at the two outside sites. Fecund males were caught at Island Thorns Inc and Howse Copse in March 1984 but, within the ungrazed Denny Pen, fecund males first appeared in February of that year and constituted 30% of the population by March. No fecund females were caught at Island Thorns Inc or Howse Copse by the end of the study but appeared in the ungrazed Denny Pen in June 1984.

8.3.2 Bank voles

Age structure

Seasonal changes in bank vole population structure are shown in figure 8.7. Recruitment occurred within the ungrazed Denny Pen, Howse Copse and Pound Bottom Wood from late summer in both years, reaching a peak in late autumn/early winter at Howse Copse. This was not seen in

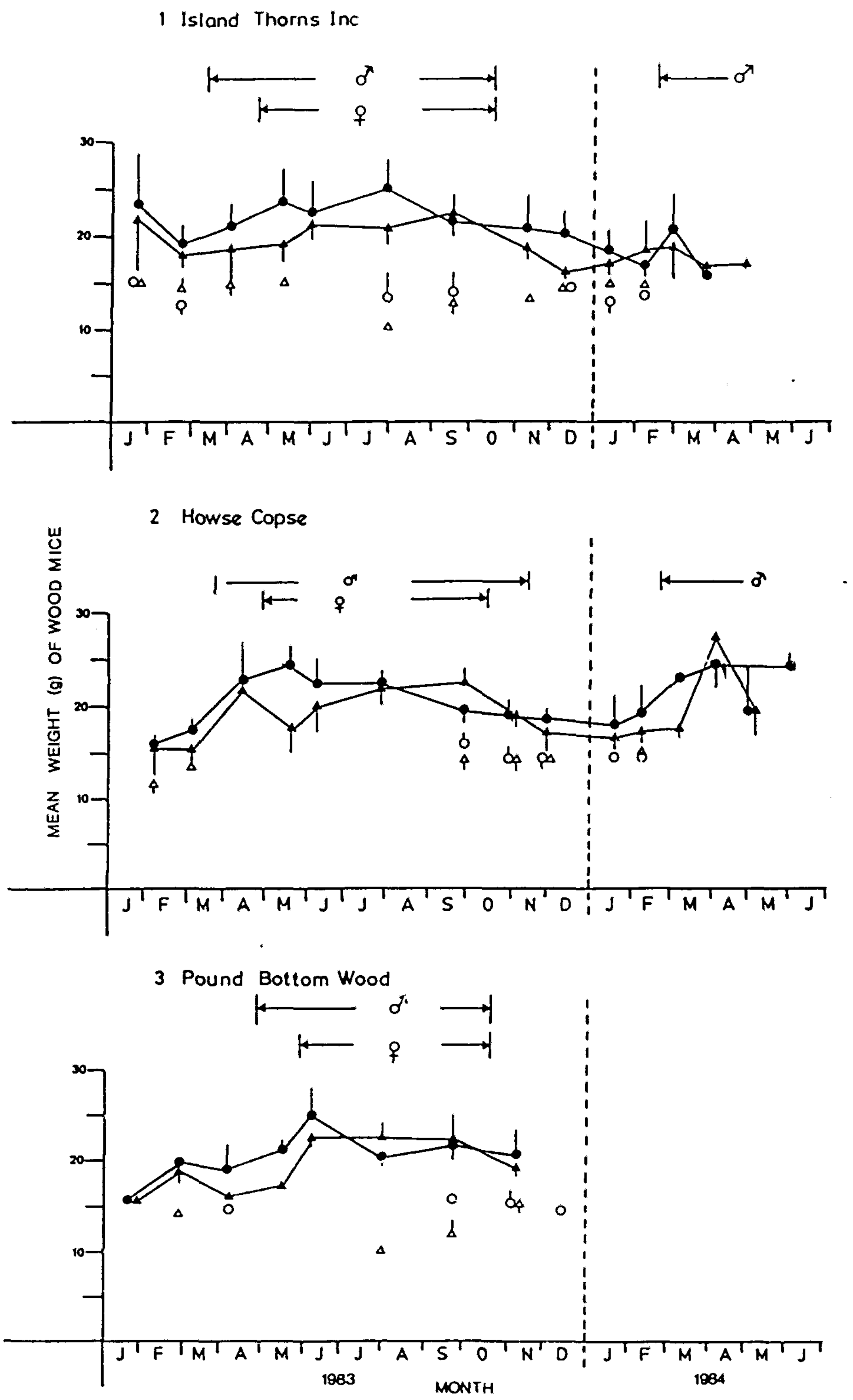
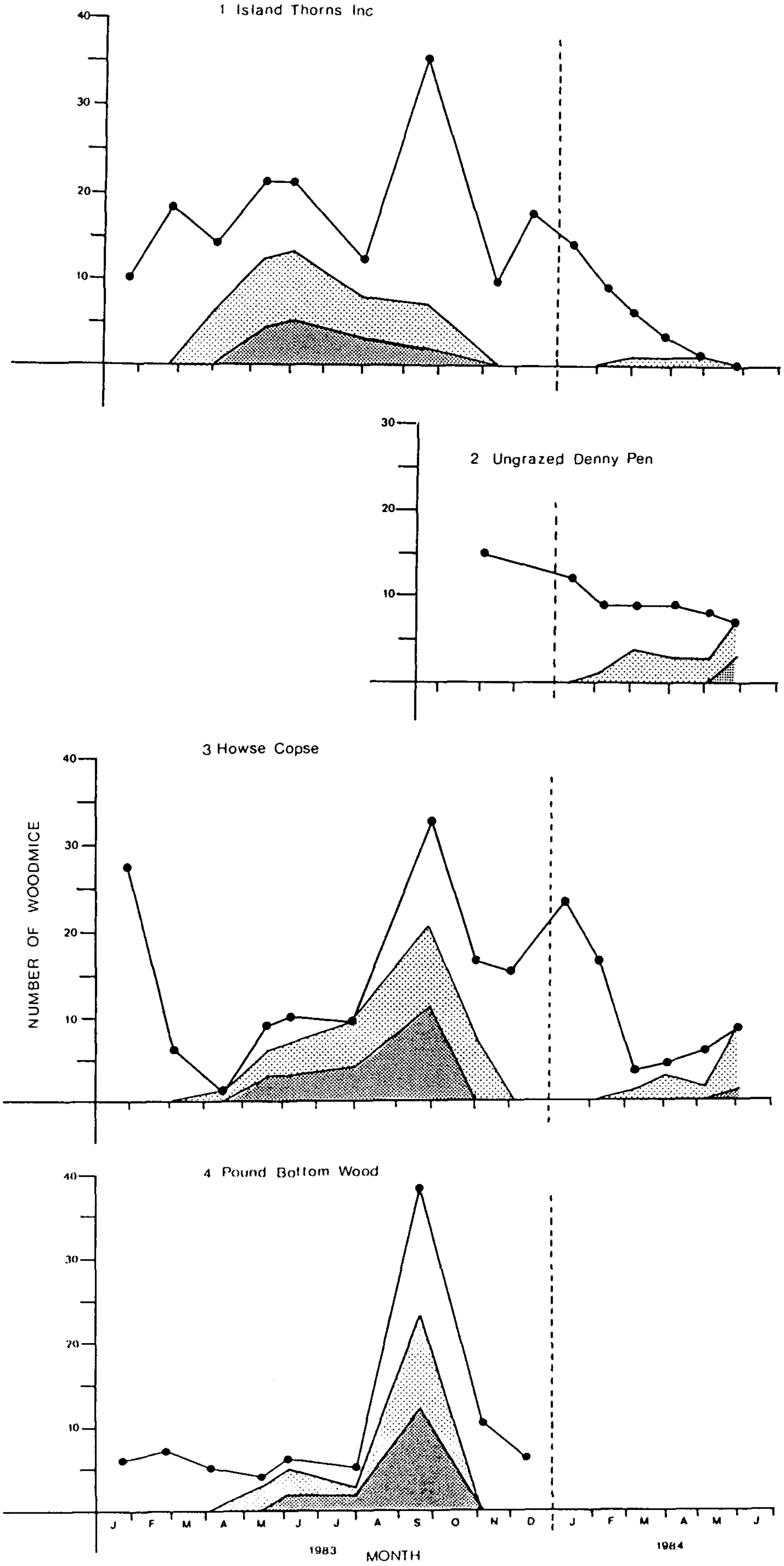


Figure 8.5 Monthly changes in the mean weight (g +/- one S.E.) of adult (♂ ●—●; ♀ ▲—▲) and juvenile/sub-adult (♂ o ; ♀ △) A.sylvaticus caught during 3 night trapping periods within Open New Forest (site 1) and outside New Forest deciduous woodlands (Periods of male and female fecundity are marked).

Figure 8.6 Monthly changes in the numbers of fecund male (░) and female (▒) A.sylvaticus caught during 3 night trapping periods within Open New Forest (site 1), Enclosed New Forest (site 2) and outside New Forest (sites 3 & 4) deciduous woodlands between January 1983 and June 1984.


1 Island Thorns Inc
2 Ungrazed Denny Pen
3 Howse Copse
4 Pound Bottom Wood
NUMBER OF WOODMICE
10
20
30
40
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1983
MONTH
1984

Pound Bottom Wood as the numbers caught were so small (<5). Population structure during 1983 is seen more clearly from the monthly data (figure 8.8). Recruitment into the trapped population occurred from July, with new animals forming 50% of the population in the winter of 1984 at Howse Copse.

Mean weight

The seasonal and monthly changes in adult mean weight were not found to be significantly different between sites but were found to vary over time (2 way ANOVA: $p<0.01$). These variations are related to periods of fecundity, marked on figure 8.9, adult weight increasing as the animals became fecund. Monthly changes in mean weight of animals (figure 8.9) show male and female weights to be more variable when juveniles are present in the population than when adults dominate.

Fecundity

In 1983 fecund males and females appeared in April within the Howse Copse and Pound Bottom Wood populations, reaching 100% of the trapped population by May/June, but reproductive activity subsided in September of that year (figure 8.10). In 1984 fecund males within Howse Copse appeared in May but fecund females did not appear until June. Within the Denny Pen, fecund males first appeared in March and females in April, and by June of that year nearly 100% of animals caught at this site were fecund.

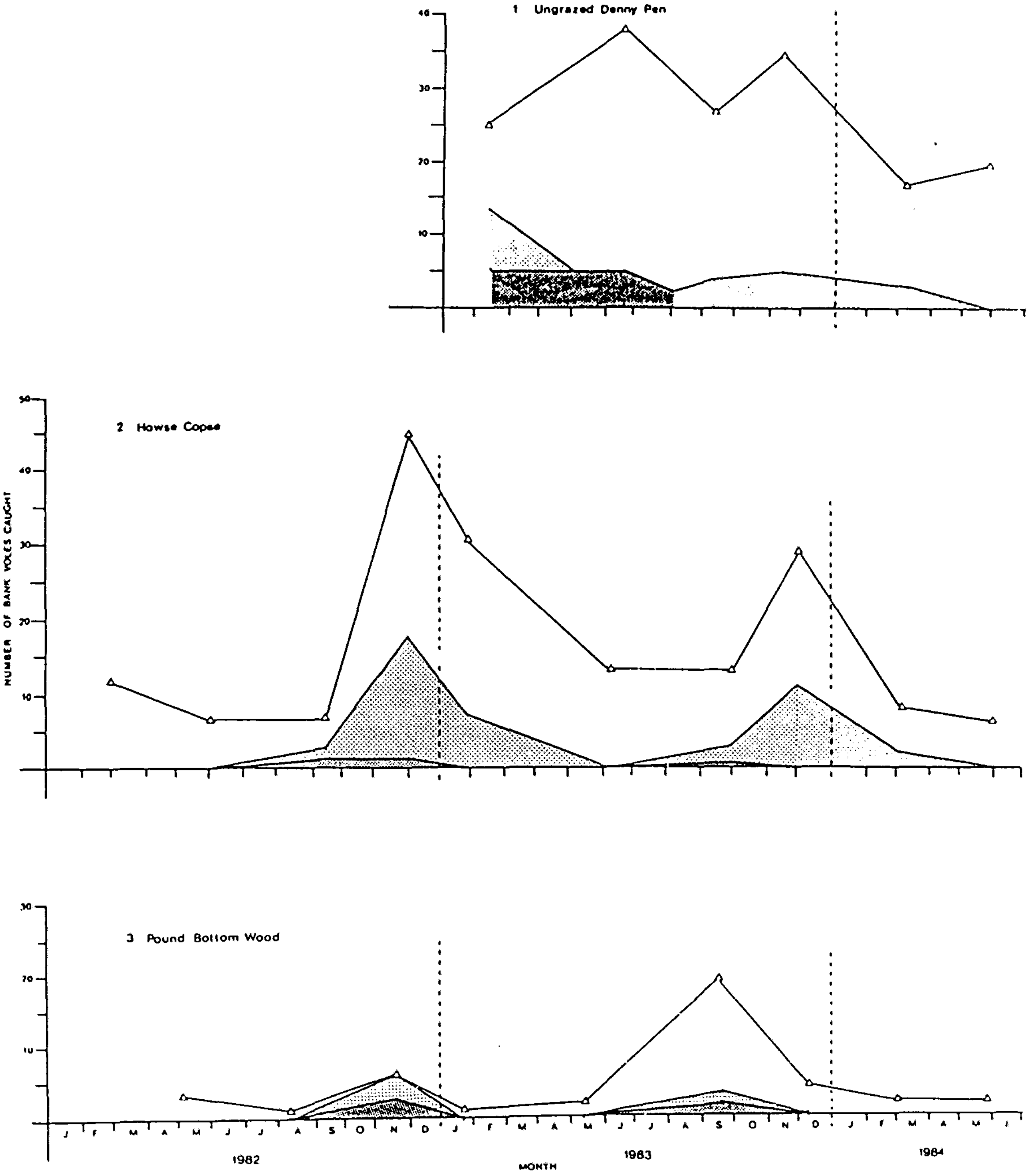


Figure 8.7 Seasonal changes in the age structure (☐ =Adults, ▨ =Sub-adults & ▩ =Juveniles) of C.glareolus populations caught during 3 night trapping periods within Enclosed New Forest (site 1) and outside New Forest (sites 2 & 3) deciduous woodlands between January 1982 and June 1984.

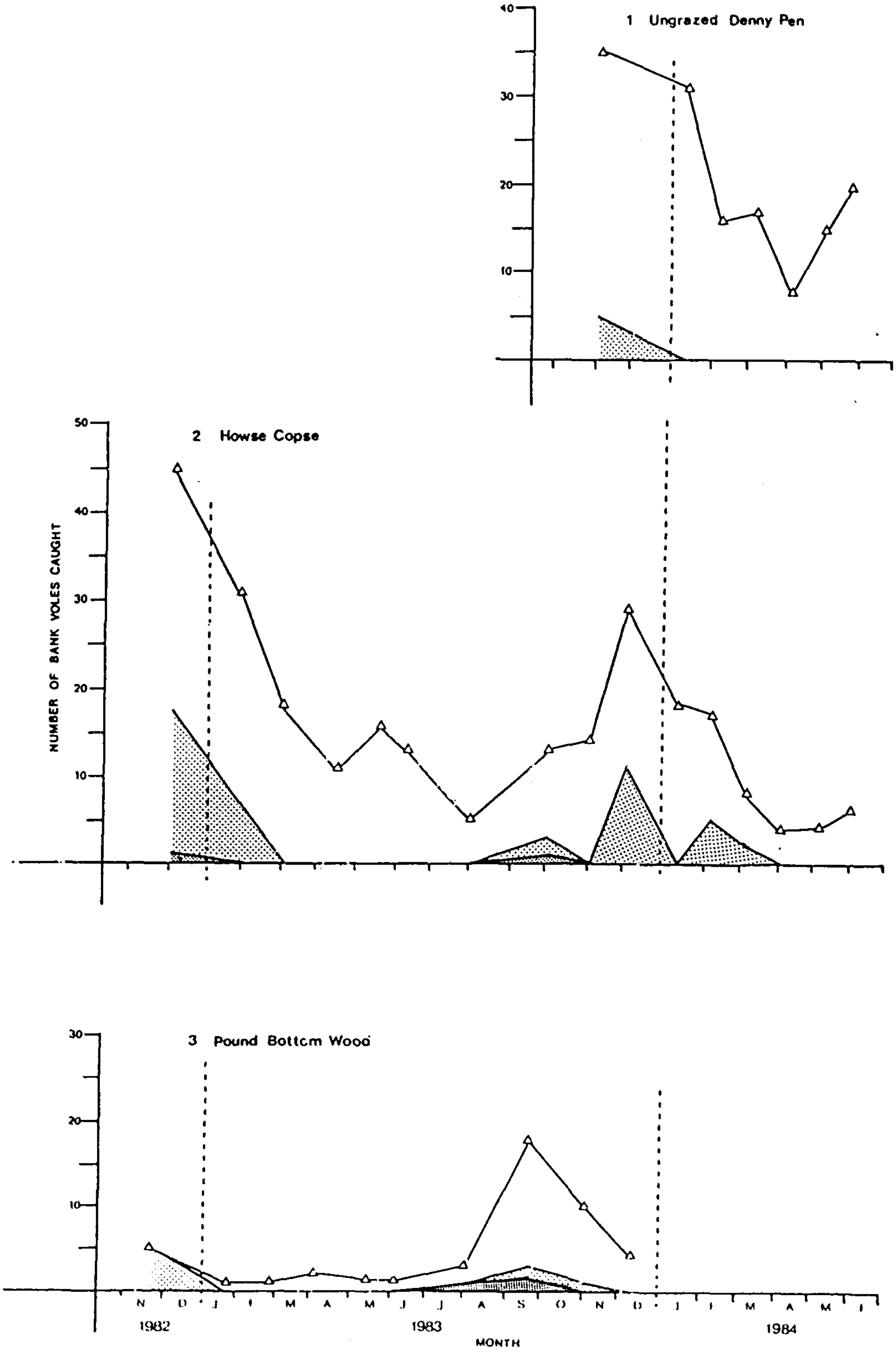


Figure 8.8 Monthly changes in the age structure (□=Adults, ░=Sub-adults, ▒=Juveniles) of <u>C.glareolus</u> populations caught during 3 night trapping periods within Enclosed New Forest (site 1) and outside New Forest (sites 2 & 3) deciduous woodlands between November 1982 and June 1984.

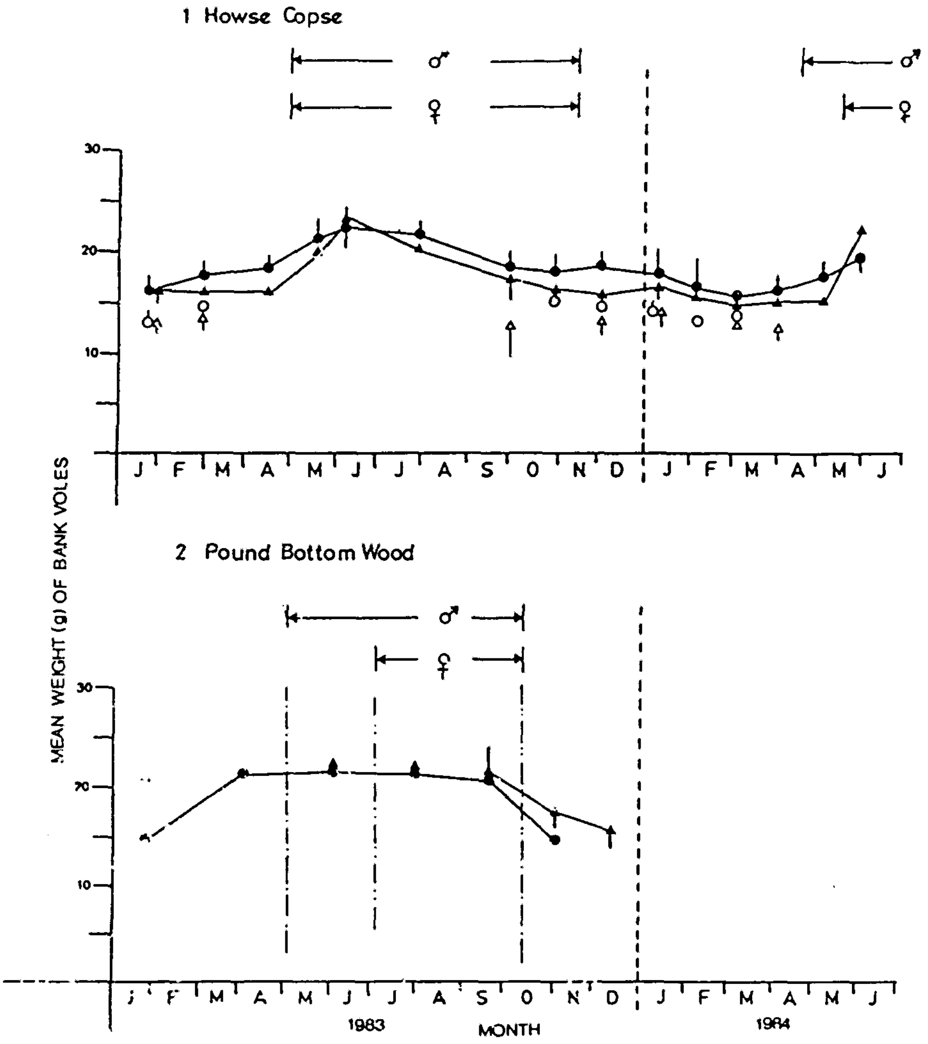


Figure 8.9 Monthly changes in mean weight (g +/- one S.E.) of adult (♂ ●—● ; ♀ ▲—▲) and juvenile/sub-adult (♂ o ; ♀ △) *C.glareolus* caught during 3 night trapping periods within deciduous woodlands outside the New Forest (Periods of male and female fecundity are marked).

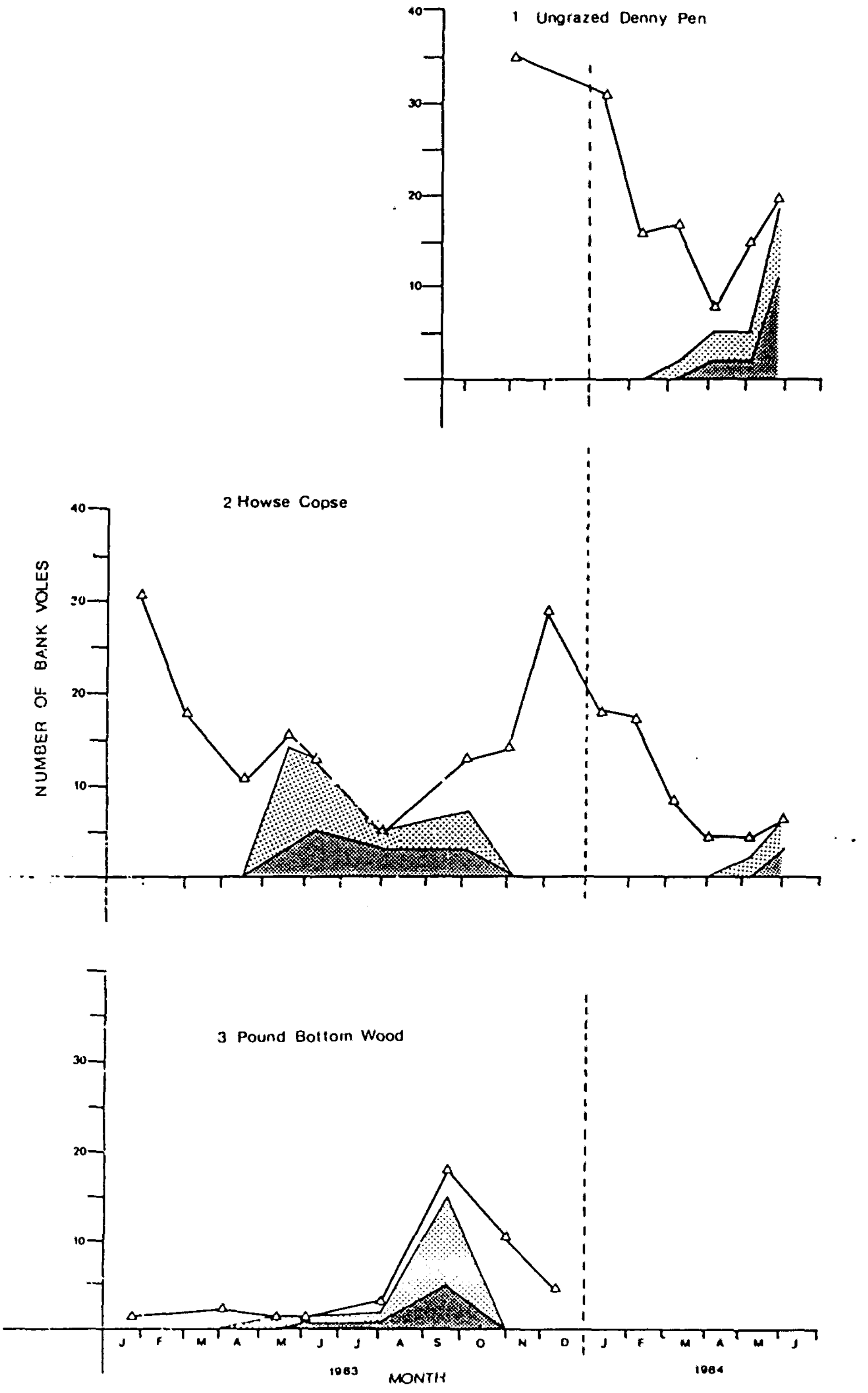


Figure 8.10 Monthly changes in the numbers of fecund male (░) and female (▓) C.glareolus caught during 3 night trapping periods within Enclosed New Forest (site 1) and outside New Forest (sites 2 & 3) deciduous woodlands between January 1983 and June 1984.

8.4 DISCUSSION

8.4.1 Wood mice

A number of previous studies have noted seasonal variations in the sex ratios of trapped wood mouse populations often finding a higher proportion of males than females (Tanton 1965; Ashby 1967; Crawley 1970; Montgomery 1980c; Gibson & Delany 1984). In this study none of the seasonal or monthly catches differed significantly from a 1:1 ratio. It has been suggested that males dominate the catch during the breeding season, when they are more active and more likely to be caught whilst the females become territorial and less active (Wolton & Flowerdew 1985). The data from this study do not support this hypothesis but the number of animals caught at all sites was low in comparison with many other studies and, as noted in section 8.1, population size can also affect movement behaviour (Wolton & Flowerdew 1985).

The seasonal changes in age structure of the wood mouse populations are similar to those shown by most other workers (Montgomery 1980c; Smal & Fairley 1982; Gibson & Delany 1984), with juveniles and sub-adults being recruited into the population in the late summer after the spring breeding season. In this study the breeding season in 1983 at all sites was shorter than those recorded in some other studies (Bergstedt 1965; Crawley 1970); fecund individuals of both sexes were caught from May to September whereas other studies show fecund animals to be present from March to October and, in periods of high food abundance, through the winter too (Smyth 1966; Watts 1968). As expected, seasonal variations were found in adult mean weight, periods of high weight being related to periods of fecundity, with the fecund adults being heavier. The variations during 1983/1984 are seen in the monthly data (figure 8.5) and are quite similar to those reported elsewhere (Bergstedt 1965;

Crawley 1970; Flowerdew 1985). With the period of female fecundity being shorter than that of the males, it is the females which dictated the actual breeding season and, as shown in figure 8.6, fecund females were not caught after September/October 1983. In all years of this study the autumn tree seed crop was poor (Chapter 5). This would explain the early cessation of breeding and the lack of overwinter breeding amongst the mouse populations.

Comparison of the 1984 wood mouse populations at Island Thorns Inc, Howse Copse and the ungrazed Denny Pen revealed that fecund males were first caught one month earlier at the latter site. No fecund females were caught at Howse Copse and Island Thorns Inc by the end of the study but were caught in June in the Denny Pen. This was no earlier than at other sites the previous year and again shows that breeding at all sites was later than recorded in many other studies and that it was female fecundity that governed the length of the breeding season.

The seasonal data of changes in age structure (figure 8.3) show that, in both years, the autumn months are the period of juvenile recruitment. The population at Matley Wood stands out because the first juveniles were caught in the August trapping session. This would suggest that breeding occurred earlier at this site. Analysis of the mean adult weights (figure 8.5) does not suggest that the adults in this woodland increased weight and bred earlier than in the other sites. With the 7 week trapping routine of 1982 it is possible that, as this site was one of the last to be trapped in the routine, young of the year were just entering the trappable part of the population and so give the impression of early recruitment. This shows a limitation of the 1982 data when one is comparing population structure; the 1983 seasonal and monthly trapping routine was not as dispersed and so enables one to examine inter-site differences in more detail.

Recruitment of new animals into the summer trapped population relates to the spring breeding period: animals born in the late spring entering the population in the late summer (figure 8.4). Young animals increase in weight rapidly (Flowerdew 1972; Gurnell & Rennolls 1983) but are generally not caught until they are a few months old and often over 10 grams in weight (figure 8.5). From Gurnell & Rennolls´ (1983) growth data , it is seen that animals born in June will attain this weight approximately three months later, i.e. September. The September populations at Howse Copse and Pound Bottom Wood outside the Forest show an increase in adult animals in the trapped population at this time too, suggesting that population increase is due to adult, as well juvenile/sub-adult, recruitment. In October 1983 69% and 72% of the catch at Howse Copse and Pound Bottom wood respectively were classed as adults whereas at Island Thorns Inc only 26% of the catch were in this age group. There are two possible explanations for this.

One explanation may be the method of age determination. Age is based on weight and a subjective assessment of pelage. In September 1983 the mean weight of animals at both sites in the >16g category was very widespread (figure 8.5) and it is suggested that some animals which were recruited into the population at the "adult" weight class in fact may have been animals born that year. At Howse Copse fecund females were first caught in May 1983 meaning that, following pregnancy, their young would have been born in May/June. Again, using data from Flowerdew (1972) and Gurnell & Rennolls (1983), these animals could have atttained weights >16g by the following September. Comparison of the December 1982 and December 1983 population structures at these sites confirms this since by this time, in both years, new adults accounted for the majority of the population (figures 8.3 & 8.4). As fecund females in Island Thorns Inc were not caught until June 1983, it is likely that births, and thus recruitment, took place at a later date than the the Howse Copse site.

At Pound Bottom Wood the first fecund females were not caught until June either, so the explanation forwarded for the large number of new adults at Howse Copse cannot hold for this site. The second explanation relates to the fact that a block of woodland adjacent to this site was clear-felled between August and October 1983: it is possible that the increase in numbers was due to an influx of animals from that area since small rodents are known to move from areas that become unsuitable (Wolton and Flowerdew 1985). This theory is supported by the result of analysing the number of new animals in each catch (table 8.2). At this time new adults account for 71% of the trapped population whereas, at the other sites, new juveniles and sub-adults account for the large proportion of the catch. This would also explain the large increase in the number of animals caught at this time (table 8.2 and Chapter 7, figure 7.2).

Some of the increase in adults at Howse Copse can also be attributed to movement. The trapping grid at this site was quite close to a cereal field and it has been shown by other workers (Miller 1958; Kikkawa 1964; Corke 1977) that rodents resident in fields may move back into woodland areas in the autumn months. It is suggested that the increases in adults seen at the outside sites are due to a combination of movement and early recruitment.

The monthly age structure of the wood mouse population within the grazed Island Thorns Inc is opposite to that of the two outside sites. There appears to be a proportion of sub-adults all year, with recruitment of juveniles and new sub-adults being from late spring to September 1983 when they formed the major part of the population. The apparent presence of sub-adults in the winter and spring populations is probably related to the method of age determination. Mean weight of the population was slightly lower than at the other two sites (figure 8.5). During the winter and spring months, few new animals are caught (table 8.2) and the presence of young animals is not due to recruitment. It is

Table 8.2 The number of new individuals of *A.sylvaticus* and *C.glareolus* caught, in each 3 night trapping period between 1982 and 1983, from within Open New Forest (sites 1 to 4), Enclosed New Forest (sites 5 & 6) and outside New Forest (sites 7 & 8) deciduous woodlands.

1.Backley Inc <u>A.sylvaticus</u>

	Number of animals caught				
Week	Total	New	%	J/SA	%
1982					
-	-	-	-	-	-
17	1	1	100.0	0	0.0
31	0	0	0.0	0	0.0
46	16	16	100.0	8	50.0
1983					
5	16	7	43.8	3	18.8
21	5	2	40.0	2	40.0
38	16	16	100.0	12	75.0
47	7	4	57.1	4	57.1
1984					
9	4	2	50.0	0	0.0
21	2	2	100.0	0	0.0

2.Sloden Inc <u>A.sylvaticus</u>

	Number of animals caught				
Week	Total	New	%	J/SA	%
8	2	2	100.0	1	50.0
18	0	0	0.0	0	0.0
32	0	0	0.0	0	0.0
47	10	10	100.0	4	40.0
5	8	6	75.5	0	0.0
21	5	3	60.0	0	0.0
38	25	23	92.0	16	64.0
47	9	5	55.5	3	33.3
9	7	4	57.4	1	14.3
23	6	5	83.3	0	0.0

5.Ungrazed Denny Pen <u>A.sylvaticus</u> <u>C.glareolus</u>

	Number of animals caught					Number of animals caught				
Week	Total	New	%	J/SA	%	Total	New	%	J/SA	%
1983										
6	31	31	100.0	10	32.3	24	12	100.0	12	50.0
24	21	7	33.3	0	0.0	37	21	56.7	0	0.0
36	33	25	75.8	8	24.3	18	10	55.5	0	0.0
46	15	7	46.6	3	20.0	35	26	74.3	12	34.3
1984										
2	12	10	83.3	4	33.3	31	10	32.3	1	3.2
6	9	2	22.2	0	0.0	16	0	0.0	0	0.0
10	9	2	22.2	0	0.0	17	1	5.9	0	0.0
14	9	0	0.0	0	0.0	8	0	0.0	0	0.0
18	8	1	12.5	0	0.0	15	3	20.0	0	0.0
22	7	2	28.6	0	0.0	20	3	15.0	0	0.0

6.Grazed Denny Pen <u>A.sylvaticus</u>

1983					
6	6	6	100.0	5	83.3
24	6	6	100.0	1	16.6
36	10	9	90.0	3	30.0
46	1	1	100.0	1	100.0
1984					
2	5	3	60.0	0	0.0
6	2	2	100.0	0	0.0
10	0	0	0.0	0	0.0
14	0	0	0.0	0	0.0
18	0	0	0.0	0	0.0
22	0	0	0.0	0	0.0

3.Island Thorns Inc <u>A.sylvaticus</u>

	Number of animals caught				
Week	Total	New	%	J/SA	%
1982					
3	8	4	100.0	3	37.5
16	1	0	0.0	0	0.0
30	2	2	100.0	0	0.0
45	26	24	92.3	7	26.9
1983					
3	10	6	60.0	5	50.0
8	18	5	27.7	3	16.6
13	14	1	7.1	1	7.1
19	21	5	23.8	0	0.0
22	21	4	19.0	0	0.0
30	12	6	50.0	3	25.0
37	35	27	77.1	8	51.4
44	9	2	22.1	2	22.2
49	17	10	58.8	8	47.0
1984					
2	14	2	14.3	0	0.0
6	9	3	33.3	0	0.0
10	6	3	50.0	1	16.6
14	3	0	0.0	0	0.0
18	1	0	0.0	0	0.0
22	0	0	0.0	0	0.0

4.Matley Wood <u>A.sylvaticus</u>

	Number of animals caught				
Week	Total	New	%	J/SA	%
4	6	6	100.0	0	0.0
23	0	0	0.0	0	0.0
36	9	9	100.0	6	66.6
49	34	11	32.4	5	14.7
4	6	4	66.6	3	50.0
23	11	10	90.4	0	0.0

7.Howse Copse <u>A.sylvaticus</u> <u>C.glareolus</u>

	A.sylvaticus					C.glareolus				
	Number of animals caught					Number of animals caught				
Week	Total	New	%	J/SA	%	Total	New	%	J/SA	%
1982										
9	3	3	100.0	0	0.0	12	12	100.0	0	0.0
22	0	0	0.0	0	0.0	6	6	100.0	0	0.0
37	1	1	100.0	0	0.0	7	6	85.7	2	28.0
48	26	25	96.2	0	0.0	45	38	84.4	18	40.0
1983										
4	27	17	62.9	0	0.0	31	14	45.2	6	19.4
9	6	0	0.0	0	0.0	18	2	11.1	0	0.0
15	1	0	0.0	0	0.0	11	2	18.2	0	0.0
20	9	6	66.6	0	0.0	16	8	50.0	0	0.0
23	10	6	60.0	0	0.0	13	1	7.7	0	0.0
30	9	3	33.3	0	0.0	5	0	0.0	0	0.0
39	32	29	90.6	7	21.9	13	11	84.6	2	15.4
44	16	0	0.0	0	0.0	14	0	0.0	0	0.0
48	15	8	53.3	5	33.3	29	19	65.5	9	31.0
1984										
2	24	14	58.3	2	8.3	18	6	33.3	2	11.1
6	16	3	18.7	0	0.0	17	4	23.5	2	11.1
10	3	0	0.0	0	0.0	8	0	0.0	0	0.0
14	4	0	0.0	0	0.0	4	1	25.0	1	25.0
18	4	0	0.0	0	0.0	6	0	0.0	0	0.0
22	6	1	16.6	0	0.0	9	3	33.3	1	11.1

Pound Bottom Wood <u>A.sylvaticus</u> <u>C.glareolus</u>

	A.sylvaticus					C.glareolus				
	Number of animals caught					Number of animals caught				
Week	Total	New	%	J/SA	%	Total	New	%	J/SA	%
1982										
18	0	0	0.0	0	0.0	3	3	100.0	0	0.0
31	0	0	0.0	0	0.0	0	0	0.0	0	0.0
46	24	24	100.0	13	54.2	1	1	100.0	0	0.0
1983										
3	2	0	0.0	0	0.0	5	5	83.3	5	100.0
8	7	2	28.6	0	0.0	1	1	100.0	0	0.0
13	5	2	40.0	0	0.0	2	2	100.0	0	0.0
19	4	2	50.0	0	0.0	1	1	100.0	0	0.0
22	6	6	100.0	0	0.0	2	2	100.0	0	0.0
30	5	3	60.0	1	20.0	3	2	66.6	1	33.3
37	39	38	97.4	10	25.6	18	16	88.8	3	16.6
44	10	2	20.0	2	20.0	11	0	0.0	0	0.0
49	2	2	100.0	2	100.0	4	3	75.0	0	0.0
1984										
9	1	1	100.0	0	0.0	2	2	100.0	0	0.0
21	2	1	50.0	0	0.0	2	1	50.0	0	0.0

more likely that mean weight was low and this could be due to a number of factors, for example, juveniles being recruited into the trapped population at slightly lower weights or reduced autumn food supply. The latter is the most likely. In both autumns of 1982 and 1983, the mast crop at Island Thorns Inc was very poor, and as this major food supply was scarce, the animals were unable to attain adult weights at which to overwinter (Flowerdew, 1972). At the other two sites the mast crop was poor, but it is probable that other foodstuffs were available: invertebrate fauna is greater in woodlands with greater ground vegetation and other plant species also act as a food supply. Therefore animals were able to attain and overwinter at adult weights. The age stucture of the wood mice within the two Denny Pens shows young animals to dominate the population in the grazed area. As noted in Chapter 7, there was interchange between these two adjacent areas and it is suggested that the juveniles and sub-adults exhibited movement into the grazed area during the period of population increase in the ungrazed pen.

8.4.2 Bank voles

Similar patterns of population structure seen in the wood mouse populations were found in the bank voles. The sex ratio of the voles at Howse Copse and the ungrazed Denny Pen generally did not differ significantly from the 1:1 ratio; the actual periods when it did (winter and spring 1983) were periods when few voles were caught and it is suggested that this is an artifact of the data. This is similar to the findings of other studies (Ashby 1967; Crawley 1970) where the ratios were quite similar throughout the year.

Seasonal changes in age structure of the vole populations follow the same patterns as seen for wood mice and found in other studies (Crawley 1970): adults becoming fecund in the spring and new recruits dominating the late summer autumn populations. Recruitment of voles took place approximately one month later than wood mice, in December, and this appears to be related to the first fecund individuals being caught in May, slightly later than mice (figure 8.10). This again is similar to the findings of other studies (Ashby 1967; Crawley 1970; Gurnell 1981). Unlike the wood mice, fecund males and females were caught at the same time, reproductive activity also ceasing in the same months. It is not possible therefore to identify one sex as dictating the breeding season.

Seasonal changes in mean weight of voles are related to periods of fecundity (figure 8.9) and are similar to other studies (Crawley 1970): adult weight increasing when fecund animals appeared in the trapped populations. In 1983 fecund individuals of both sexes appeared in the Pound Bottom Wood and Howse Copse populations in April, but in 1984 fecund males did not appear until May and females not until June at Howse Copse. As with the wood mice, this was slightly later than found in previous studies (Crawley 1970). However, within the ungrazed Denny Pen in 1984 fecund males appeared in March and females in April. This indicates that breeding took place earlier in the Pen than at the other sites.

Recruitment of young voles coincided with an increase in the number of new adults, although this is not as great as seen in the mice. This is shown in figures 8.7 and 8.8 where the young age classes made up 31% of the trapped population in autumn 1983, a similar situation to that of the previous year. The explanation offered previously is again suggested: recruited animals attaining adult weight before being trapped. Within Pound Bottom Wood, the number of adult voles in the autumn population did increase at the time when the adjacent area was being clear-felled (table 8.2) but the increase was not as marked as that of the wood mice. This is probably because the size of the vole populations was generally lower (Chapter 7, figure 7.4).

8.5 Summary

It would appear from these data that the structure and breeding of wood mouse and bank vole populations within the New Forest and outside sites are similar to each other and to the findings of most other studies (see Alibhai & Gipps 1985; Flowerdew 1985).

Although the usual annual cycle of breeding and recruitment was seen in all populations, there is some indication that breeding, and hence recruitment, within the grazed Island Thorns Inc was later during 1983 than the outside sites (figures 8.4 & 8.6), and that the breeding season started later in 1983 than 1984 at both Island Thorns Inc and Howse Copse. These variations may be related to overwinter food supply. In the spring, overwintered animals have to attain adult weights to enable breeding to occur; this is reliant to some extent on food availability, but other factors, such as day length and climate, are also important (Clarke 1985). In periods of low autumn tree seed crop, animals overwinter at low weights and so have to gain proportionally more weight than in years of good food supply. This takes time and so obviously delays breeding.

In this study, autumn tree seed crop was poor in all years at all sites (Chapter 5), and it is suggested that the mice at Island Thorns Inc overwintered at lower weights than at the other sites because of this and because of later recruitment. It is therefore suggested that both mouse and vole breeding seasons were delayed partly because of reduced autumn food supply.

In the spring of 1984, breeding of both species started earlier in the Denny Pen than in Howse Copse and Island Thorns Inc. The 1983 tree seed crop was poor at all sites and this suggests that other factors within the Denny Pen must have been more favourable. No assessment was made of other foodstuffs but one possible explanation of an earlier start to the breeding season is greater plant and animal food availability within this Pen, resulting from the lack of large herbivore grazing.

Wood mouse breeding began approximately one month earlier at all sites than bank vole breeding and recruitment of individuals was subsequently earlier. This explains the earlier peak in wood mouse numbers found in the 1983 populations at Howse Copse and Pound Bottom Wood and is analagous to the findings of other studies.

CHAPTER 9

SURVIVAL OF THE WOODLAND SMALL RODENT POPULATIONS

9.1 INTRODUCTION

The survival of individuals and cohorts is an important factor in the demography of small rodents and exerts a dominating effect on population size: high survival rates lead to a greater recruitment, increasing population size and the potential for high numbers of reproductively active animals which in turn may lead to greater recruitment.

Survival varies seasonally (e.g. Montgomery 1980c) and with age of the individuals (e.g. Gibson & Delany 1984). Trapping studies measure the length of time an animal is known to be alive and resident within the trapped population, the losses from the population being due to both mortality and dispersal. Although one is unable to determine which factor is responsible for the loss of an individual, previous studies have identified habitat factors which affect trap defined survival, and, with this knowledge, one is able to hypothesise as to the cause.

Food supply, especially autumn tree seed crop, has been identified as a major factor (e.g. Flowerdew & Gardner 1977), with survival being positively correlated to food availability; in abundance, food not only reduces mortality but also restricts movement. Other losses from a population may be due to predation (e.g. Abramsky & Tracy 1979) or social (Wolton & Flowerdew 1985) or competitive pressures (Gliwicz 1981). These factors affect sections of the populations in different ways (Chapter 3, section 1.3.3, Chapter 8, section 8.1), for example dispersing animals may be subjected to greater predation (Ambrose 1972).

Habitat modification by large herbivores may therefore influence survival of small rodents, and alteration of habitat suitability is likely to affect both individual and cohort survival through a number of routes already identified, being the reduction or alteration of food supply or increased predation.

The preceding Chapters have identified habitat differences between grazed and ungrazed woodlands in small rodent abundance and also diversity within these habitats and some differences in population structure, such as earlier juvenile recruitment within low and ungrazed sites. Survival is an important factor in small rodent demography, and the above shows that it is altered by a number of habitat characteristics; modification of these by large herbivore grazing may therefore alter survival, and may be responsible for differences in abundance and structure of the rodent populations, for example the reduction in ground cover may increase vulnerability to predation, but it also reduces competitive pressure by reducing diversity; the effects may therefore reduce or increase survival. Although it is difficult to separate dispersal from mortality within the population, it may be possible to relate differences between sites to the effects of large herbivore grazing. Therefore this Chapter examines the trap defined survival of small rodent populations in the grazed and ungrazed woodland sites.

9.2 METHODS

One may examine survival in a number of ways: by studying the survival of groups over a given time period, giving information on changes in survival over time, or by studying the survival of individuals, this being a measure of the minimum length of time an animal is known to be alive. The latter is often referred to as the ´duration of residence´ and can be extended to groups of animals to give information on cohort survival. Therefore, one may examine short-term survival, looking for periods of poor or good survival, or one may examine long-term survival of cohorts.

9.2.1 Duration of residence

Duration of residence is measured as the time interval between first and last capture. Obviously an animal does not have to be caught on each sampling occasion and so one cannot guarantee permanent residence in the area. Variations in sampling intensity will alter the probability of capturing animals and hence calculation of duration of residence. As retrapping between seasons was low (this is seen in Chapter 8, table 8.2 where the number of new animals in each catch is presented) and as the low intensity of seasonal trapping greatly reduces the probability of recapture at any one time, duration of residence is examined here using only the data obtained for residence of each individual caught in the monthly trapping session at Island Thorns Inc, Howse Copse and Pound Bottom Wood.

The duration of residence of each individual has been calculated from these retrapping data pooled on the basis of cohorts from each trapping session and analysed in the following way:

1) For each cohort the difference in duration of residence of each sex of the three age groups, juveniles, sub-adults and adults, has been compared using a Mann Whitney U test (Seigel 1956).

2) If differences in residence for each sex class were not significantly different, they were pooled and age class in each cohort compared in the same fashion as 1). Again if no significant differences between age classes was found they too were combined.

3) The difference in duration of residence between cohorts and between sites could then be tested using a 2 way ANOVA.

9.2.2 RESULTS

Wood mice

Duration of residence of cohorts and age classes are presented in figure 9.1. Intra-site comparisons between sex, and then age classes resulted in no significant differences in residence of different groups within a cohort at any of the three sites. Intra-site comparisons were performed on two sets of data: the data from Island Thorns Inc and Howse Copse from January 1983 to July 1984 and then on these data modified to stop after the last trapping session of 1983 to allow direct comparison with the shorter period of trapping (January to December 1983) performed at Pound Bottom Wood.

Data for each cohort from each site were pooled and compared using a 2 way ANOVA. This resulted in a significant interaction between site and time (table 9.1) and so data were split into two age classes, adults and juveniles with sub-adults, and re-tested in the same manner. This analysis revealed no significant differences in residence of adults between sites or cohorts, but did reveal significant interaction between site and time for residence of the juvenile/sub-adult class (table 9.1). Data were further split into pairs and a significant difference in residence between each pair of sites for both groups was located.

In an attempt to locate the inter-site differences, Mann Whitney U tests were performed on pairs of cohorts for the two age groups. This comparison found no differences between pairs of cohorts for the data from 1983, however using the data up to 1984 revealed a significant difference in residence in the group of subadults caught at Island Thorns Inc and Howse Copse in February 1983, with survival being greater in the latter site ($p=0.0017$).

Table 9.1 Comparison of A.sylvaticus survival (2 way ANOVA) from deciduous woodlands: Island Thorns Inc (Open New Forest), Howse Copse and Pound Bottom Wood (outside New Forest).

A) All three sites for 10 time preiods: All ages

	F-ratio	df	p
Site	7.884	2	0.000
Time	1.024	9	0.421
Interaction	1.856	18	0.020

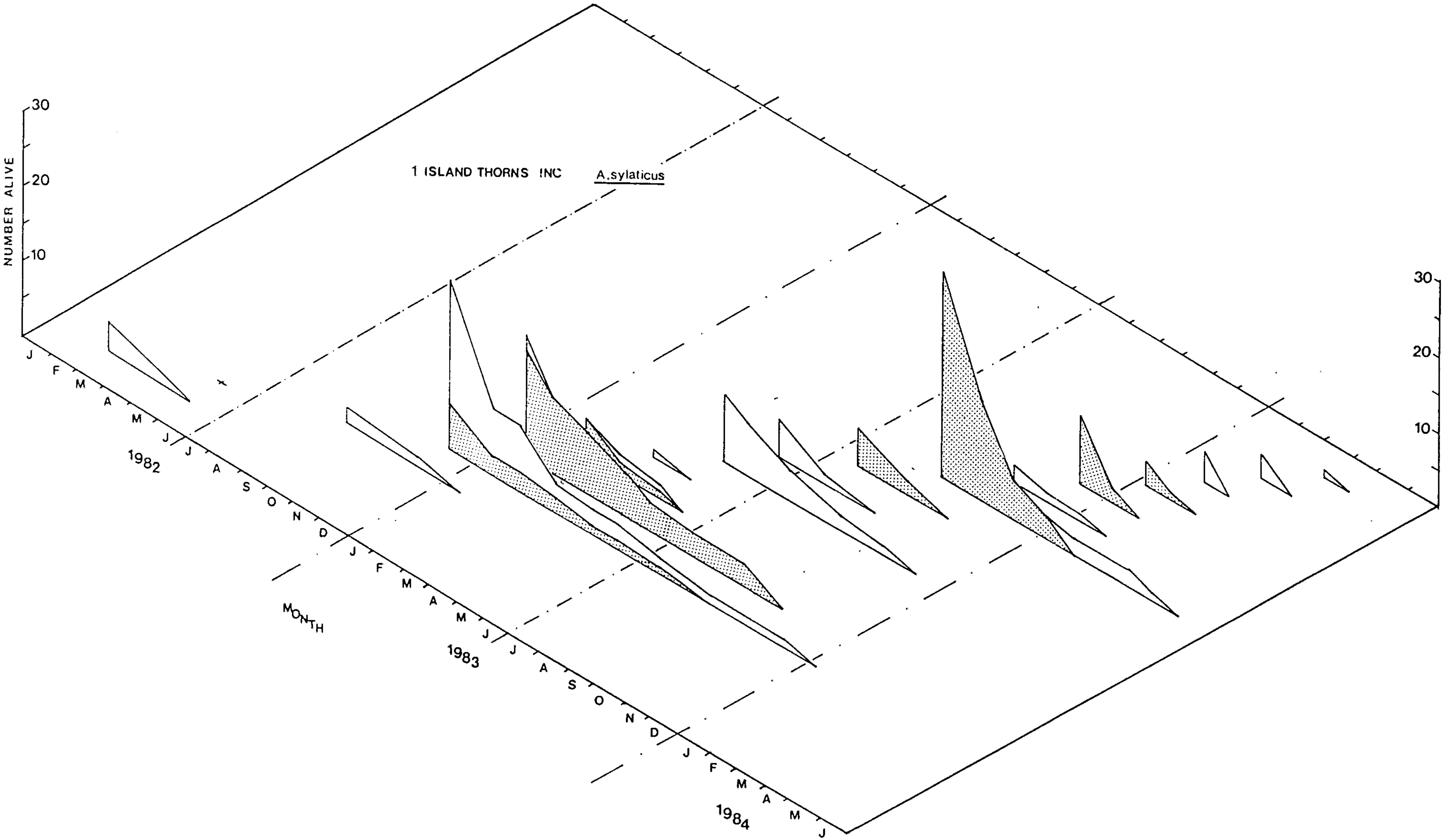
B) All three sites for 10 time periods: Adults

Site	2.963	2	0.056
Time	0.928	8	0.496

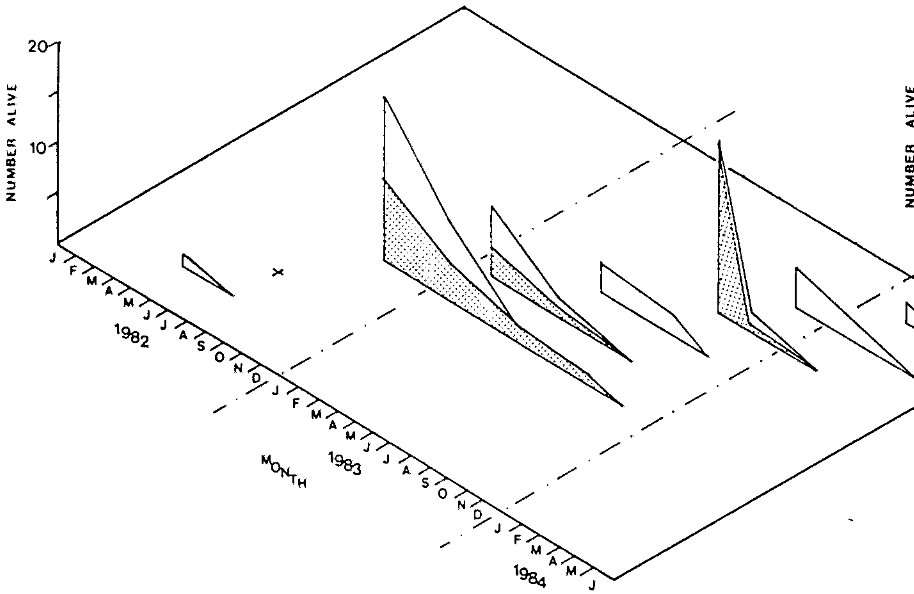
C) All three sites for 10 time periods: Juveniles/Sub-Adults

Site	6.730	2	0.002
Time	2.315	9	0.019
Interaction	2.842	16	0.001

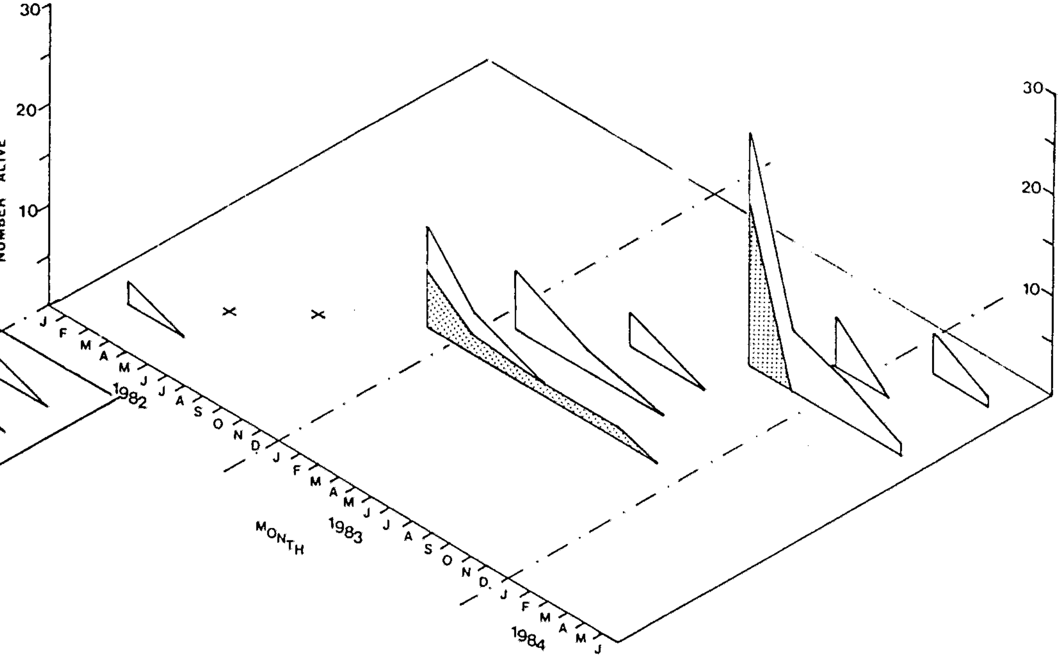
Figure 9.1 Duration of residence of different age classes (□ =Adults; ░ =juvenile/sub-adults) of *A.sylvaticus* and *C.glareolus* within Open New Forest (sites 1 to 3), Enclosed New Forest (site 4) and outside New Forest (sites 5 & 6) deciduous woodlands.


1 ISLAND THORNS INC
A.sylaticus
NUMBER ALIVE
30
20
10
30
20
10
J
F
M
A
M
J
1982
J
A
S
O
N
D
J
F
M
A
M
J
1983
J
A
S
O
N
D
J
F
M
A
M
J
1984
MONTH

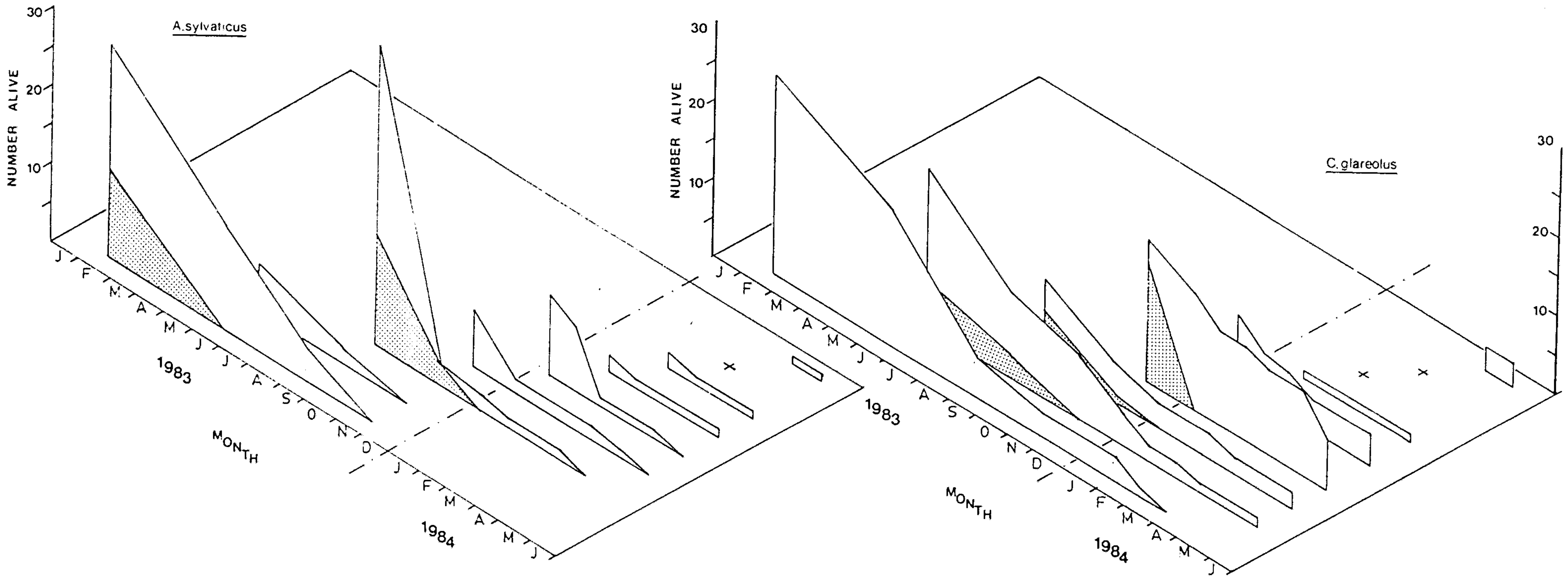
2 BACKLEY INC *A.sylvaticus*

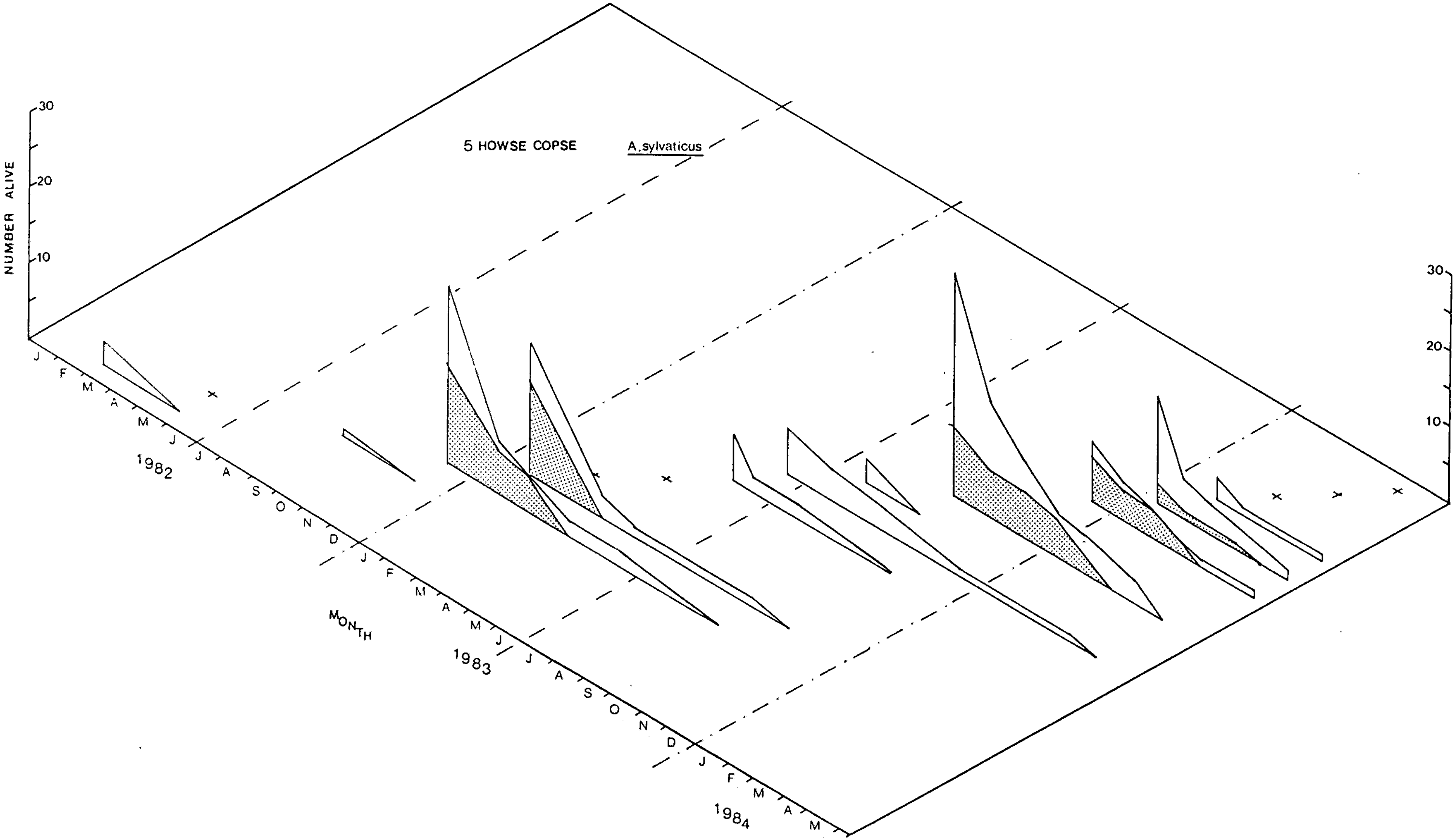


3 SLODEN INC *A.sylvaticus*

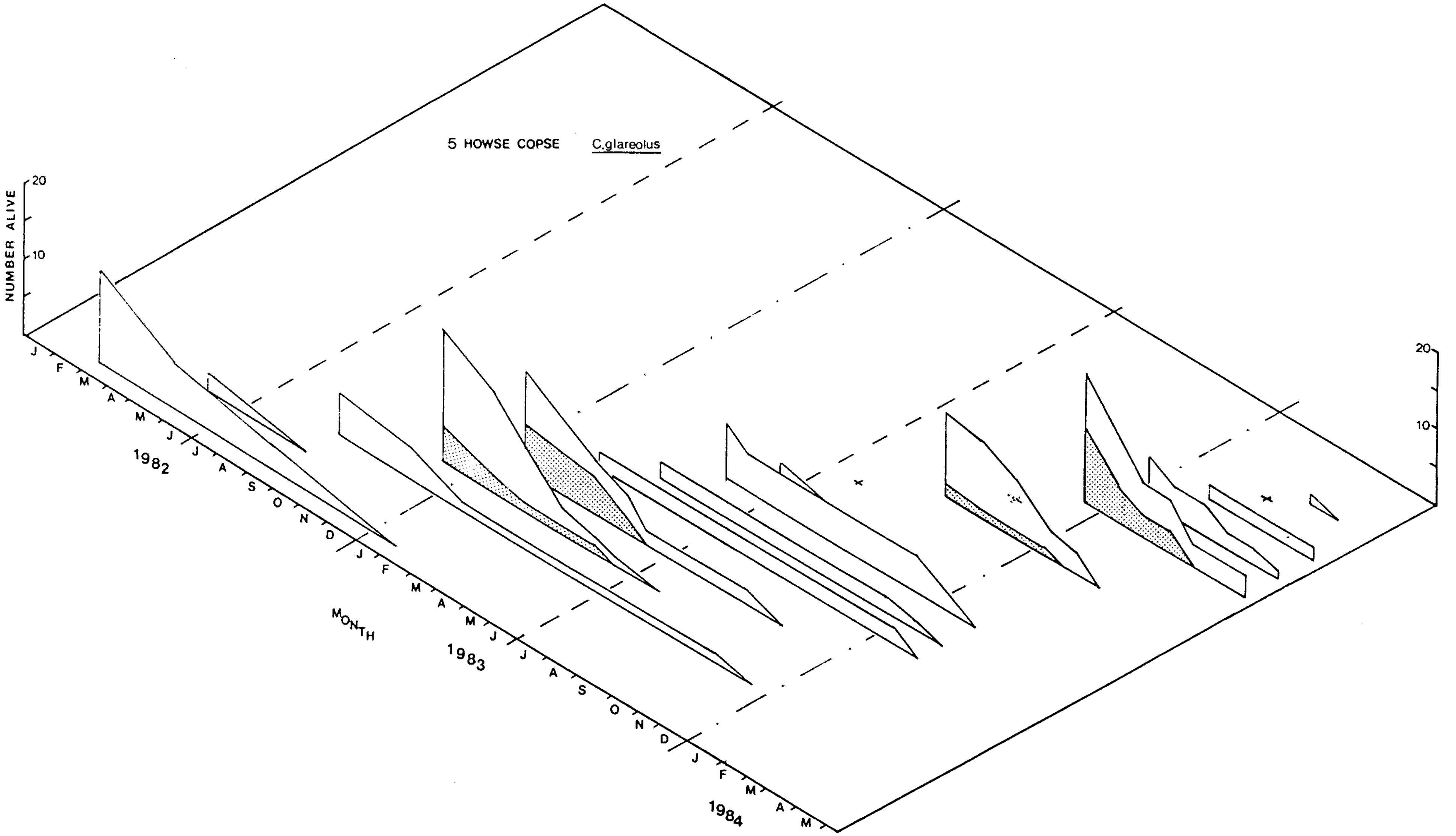


4 UNGRAZED DENNY PEN

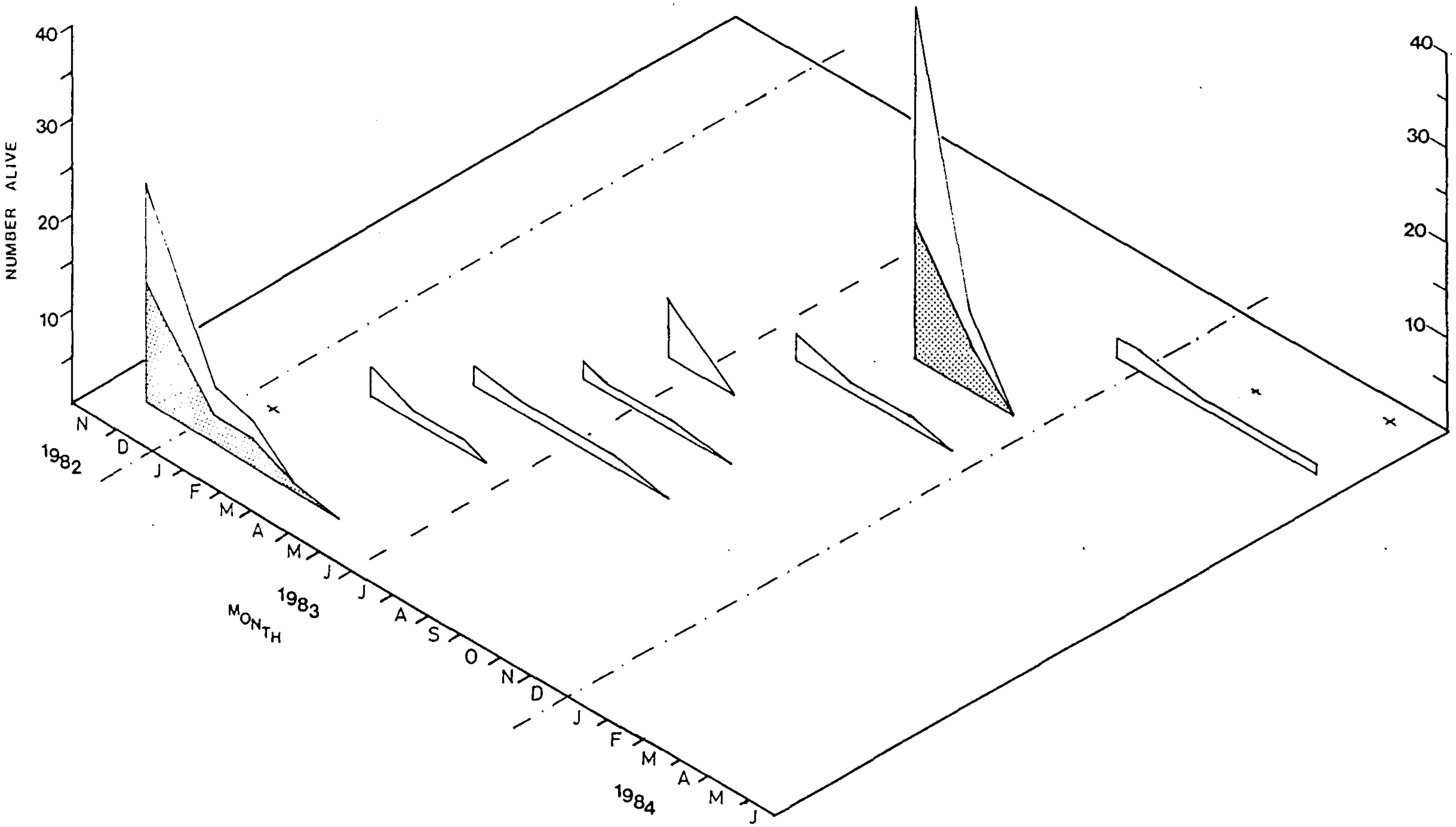




5 HOWSE COPSE *A.sylvaticus*


5 HOWSE COPSE
C.glareolus
NUMBER ALIVE
20
10
20
10
J
F
M
A
M
J
J
A
S
O
N
D
1982
J
F
M
A
M
J
J
A
S
O
N
D
1983
J
F
M
A
M
1984
MONTH
x
x
x

6 POUND BOTTOM WOOD *A.sylvaticus*



Bank voles

The same route of intra-site analysis of cohorts of voles at the Howse Copse site was used on the residence data for bank voles; very few recaptures of voles at the Pound Bottom wood (Chapter 8, table 8.2) meant the data would not support this analysis. There were no significant differences in duration of residence between age groups or sex classes so these were pooled for each cohort. These data were then tested against the equivalent data for wood mice which resulted in neither significant differences between the cohorts nor between the two species.

9.2.3 Minimum monthly survival

The calculation of a monthly survival statistic gives information on the short term survival of groups of animals, and this may be examined with respect to age or sex classes. From this statistic one can locate variations in survival between months, and with knowledge of the species, possibly identify the causes.

Minimum survival (P_{min}) is calculated following Leslie, Chitty & Chitty (1953), as:

$$\log P_{min} = \frac{\log P \times min}{T}$$

where T = the time interval between trapping sessions
and min = the time interval required, in this case 30 days.

This statistic was calculated for both sex and age classes (juveniles/sub-adults and adults) using information from the calendar of captures data and not the number caught. The number of recaptures in each trapping session was often low (Chapter 8, table 8.2 & table 9.2), and although the number of animals surviving but not caught was also low (table 9.2), it was felt that these data gave a more accurate picture of the number surviving and made full use of available data.

Wood mice

The calculated 30 day survival for the wood mouse populations are presented in figures 9.2a & b. Minimum monthly survival at all sites was quite erratic throughout the year, but, as one would expect, in the late autumn/early winter months juvenile/sub-adult survival was greater than that of the adults. A Wilcoxon's matched-pairs test (Seigel 1956) on each set of data revealed no significant differences between sex or age class survival for each time period and so they were pooled to enable inter-site comparisons (see below). Although no significant differences were found between age and sex classes, a Spearman Rank correlation (Seigel 1956) comparing age classes, and comparing sex classes only revealed correlations in P_{min} between the two age classes at Pound Bottom wood ($R = 0.0733$, $p,0.05$) and the two sex classes at Island Thorns Inc ($r = 0.49685$, $p<0.05$)(figure 9.2b), although survival of the two sex classes at all sites follow similar patterns. The data do indicate some seasonal variation in survival at all sites, with poor survival in the winter and spring of 1983, when it was below 50%, improving in the summer and remaining at approximately 50% for the rest of the year.

Bank voles

The monthly P_{min} statistics for voles from Howse Copse are presented in figure 9.3. The same route of analysis as

Table 9.2 The number of new individuals of *A.sylvaticus* and *C.glareolus* caught, in each 3 night trapping period between 1982 and 1984, within Open New Forest (sites 1 to 4), outside New Forest (sites 5 & 6) and Enclosed New Forest (sites 7 & 8), in comparison to the actual number known to be alive.

1 Backley Inc *A.sylvaticus*

	Number	Number of new animals			
Week	Alive	Total	%	J/SA	%
1982					
-	-	-	-	-	-
17	1	1	100.0	0	0.0
31	0	0	0.0	0	0.0
46	16	16	100.0	8	50.0
1983					
5	16	7	43.8	3	18.7
21	7	2	28.6	2	28.5
38	18	16	88.8	12	13.6
47	6	4	66.6	4	66.6
1984					
9	4	2	50.0	0	0.0
21	2	2	100.0	0	0.0

2 Sloden Inc *A.sylvaticus*

	Number	Number of new animals			
Week	Alive	Total	%	J/SA	%
8	2	2	100.0	1	50.0
18	0	0	0.0	0	0.0
32	0	0	0.0	0	0.0
47	9	9	100.0	4	44.4
5	9	6	66.6	0	0.0
21	5	3	60.0	1	20.0
38	24	23	95.8	16	66.6
47	11	5	45.5	3	27.3
9	8	4	50.0	1	12.5
23	6	5	83.3	0	0.0

3 Island Thorns Inc *A.sylvaticus*

	Number	Number of new animals			
Week	Alive	Total	%	J/SA	%
1982					
3	8	4	50.0	3	37.5
16	1	0	0.0	0	0.0
30	2	2	100.0	0	0.0
45	26	24	92.3	7	29.2
1983					
3	15	6	40.0	5	33.3
8	21	5	23.8	3	14.3
13	16	1	6.3	1	6.3
19	20	5	25.0	0	0.0
22	21	4	19.0	0	0.0
30	12	6	50.0	3	25.0
37	35	27	77.1	18	51.4
44	31	2	6.5	2	6.5
49	22	10	45.5	8	36.4
1984					
2	14	2	14.3	0	0.0
6	9	3	33.3	0	0.0
10	6	3	50.0	1	16.6
14	3	0	0.0	0	0.0
18	1	0	0.0	0	0.0
22	0	0	0.0	0	0.0

4 Matley Wood *A.sylvaticus*

	Number	Number of new animals			
Week	Alive	Total	%	J/SA	%
4	6	6	100.0	0	0.0
23	0	0	0.0	0	0.0
36	9	9	100.0	6	66.6
49	34	11	32.3	5	14.7
4	13	4	30.7	3	23.0
23	11	10	90.9	0	0.0

5.Howse Copse *A.sylvaticus* *C.glareolus*

	A.sylvaticus					*C.glareolus*				
	Number	Number of new animals				Number	Number of new animals			
Week	Alive	Total	%	J/SA	%	Alive	Total	%	J/SA	%
1982										
9	12	12	100.0	0	0.0	3	3	100.0	0	0.0
22	8	2	25.0	0	0.0	0	0	0.0	0	0.0
37	8	5	62.5	0	0.0	1	1	100.0	0	0.0
48	43	38	88.4	18	41.8	26	25	96.2	20	80.0
1983										
4	29	14	48.3	6	20.7	27	17	62.9	12	44.4
9	20	2	10.0	0	0.0	8	0	0.0	0	0.0
15	13	2	15.4	0	0.0	4	0	0.0	0	0.0
20	17	8	47.0	0	0.0	11	6	54.5	0	0.0
23	14	1	7.1	0	0.0	10	6	60.0	0	0.0
30	12	0	0.0	0	0.0	12	3	25.0	0	0.0
39	22	11	50.0	2	9.1	34	29	85.3	7	20.6
44	30	0	0.0	0	0.0	19	0	0.0	0	0.0
48	33	19	57.6	9	27.3	15	8	53.3	5	33.3
1984										
2	24	6	25.0	2	8.3	24	14	58.3	2	8.3
6	19	4	21.0	2	10.5	15	3	20.0	0	0.0
10	17	0	0.0	0	0.0	12	0	0.0	0	0.0
14	8	1	12.5	1	12.5	9	0	0.0	0	0.0
18	7	0	0.0	0	0.0	7	0	0.0	0	0.0
22	9	1	11.1	1	11.1	7	1	14.3	0	0.0

Pond Bottom Wood *A.sylvaticus* *C.glareolus*

	A.sylvaticus					*C.glareolus*				
	Number	Number of new animals				Number	Number of new animals			
Week	Alive	Total	%	J/SA	%	Alive	Total	%	J/SA	%
1982										
18	0	0	0.0	0	0.0	1	1	100.0	0	0.0
31	0	0	0.0	0	0.0	0	0	0.0	0	0.0
46	24	23	95.8	13	54.2	1	1	100.0	0	0.0
1983										
3	6	0	0.0	0	0.0	6	5	83.0	5	83.3
8	7	2	28.6	0	0.0	1	1	100.0	0	0.0
13	3	2	66.6	0	0.0	2	2	100.0	0	0.0
19	4	2	50.0	0	0.0	1	1	100.0	0	0.0
22	8	6	75.0	0	0.0	2	2	100.0	0	0.0
30	5	3	60.0	1	20.0	3	2	66.6	1	33.3
37	40	38	95.0	10	25.0	18	16	88.8	3	16.6
44	10	2	20.0	2	20.0	11	0	0.0	0	0.0
49	2	2	100.0	2	100.0	4	3	75.0	0	0.0
1984										
9	1	1	100.0	0	0.0	2	0	0.0	0	0.0
21	1	1	100.0	0	0.0	2	1	50.0	0	0.0

7.Ungrazed Denny Pen *A.sylvaticus* *C.glareolus*

	A.sylvaticus					*C.glareolus*				
	Number	Number of new animals				Number	Number of new animals			
Week	Alive	Total	%	J/SA	%	Alive	Total	%	J/SA	%
1983										
6	32	32	100.0	1	3.1	24	24	100.0	12	50.0
24	22	7	31.8	0	0.0	39	21	53.8	0	0.0
36	42	25	59.5	8	19.0	27	10	37.0	0	0.0
46	14	7	50.0	3	21.4	43	26	60.5	12	27.9
1984										
2	15	10	66.6	4	26.6	35	10	28.5	1	2.8
6	15	2	13.3	0	0.0	23	0	0.0	0	0.0
10	12	2	16.6	0	0.0	25	1	4.0	0	0.0
14	10	0	0.0	0	0.0	20	0	0.0	0	0.0
18	7	1	14.3	0	0.0	21	3	14.3	0	0.0
22	7	2	28.6	0	0.0	22	3	13.6	0	0.0

8.Grazed Denny Pen *A.sylvaticus*

1983					
6	5	5	100.0	0	0.0
24	6	6	100.0	1	16.6
36	10	9	90.0	1	10.0
46	1	1	100.0	0	0.0
1984					
2	5	3	60.0	0	0.0
6	0	0	0.0	0	0.0
10	0	0	0.0	0	0.0
14	0	0	0.0	0	0.0
18	0	0	0.0	0	0.0
22	0	0	0.0	0	0.0

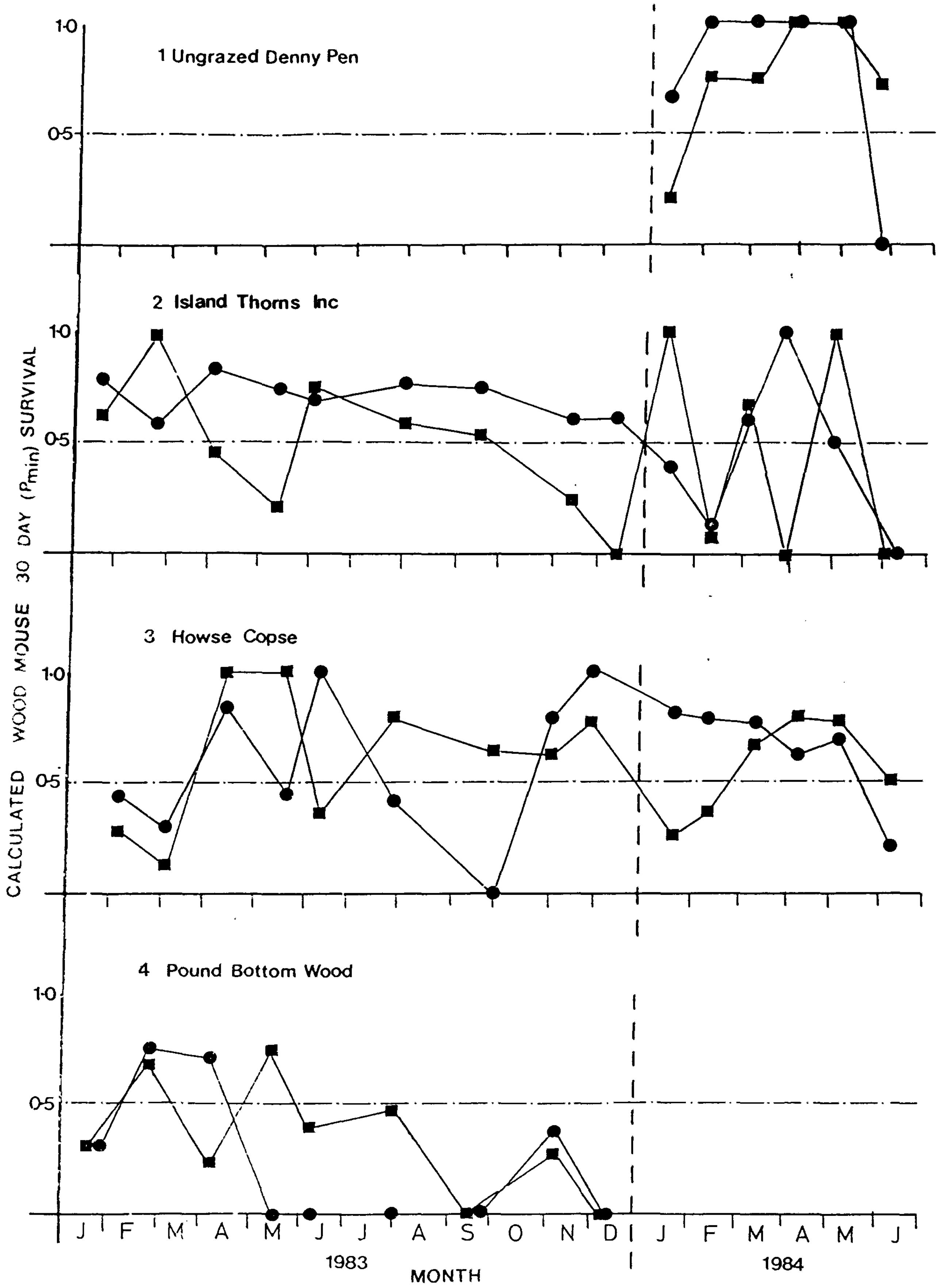


Figure 9.2 a. Minimum 30 day survival of age (adults ■—■ ; juvenile/ sub-adults ●—●) classes of <u>A.sylvaticus</u> within Enclosed New Forest (site 1), Open New Forest (site 2) and outside New Forest (sites 3 & 4) deciduous woodland.

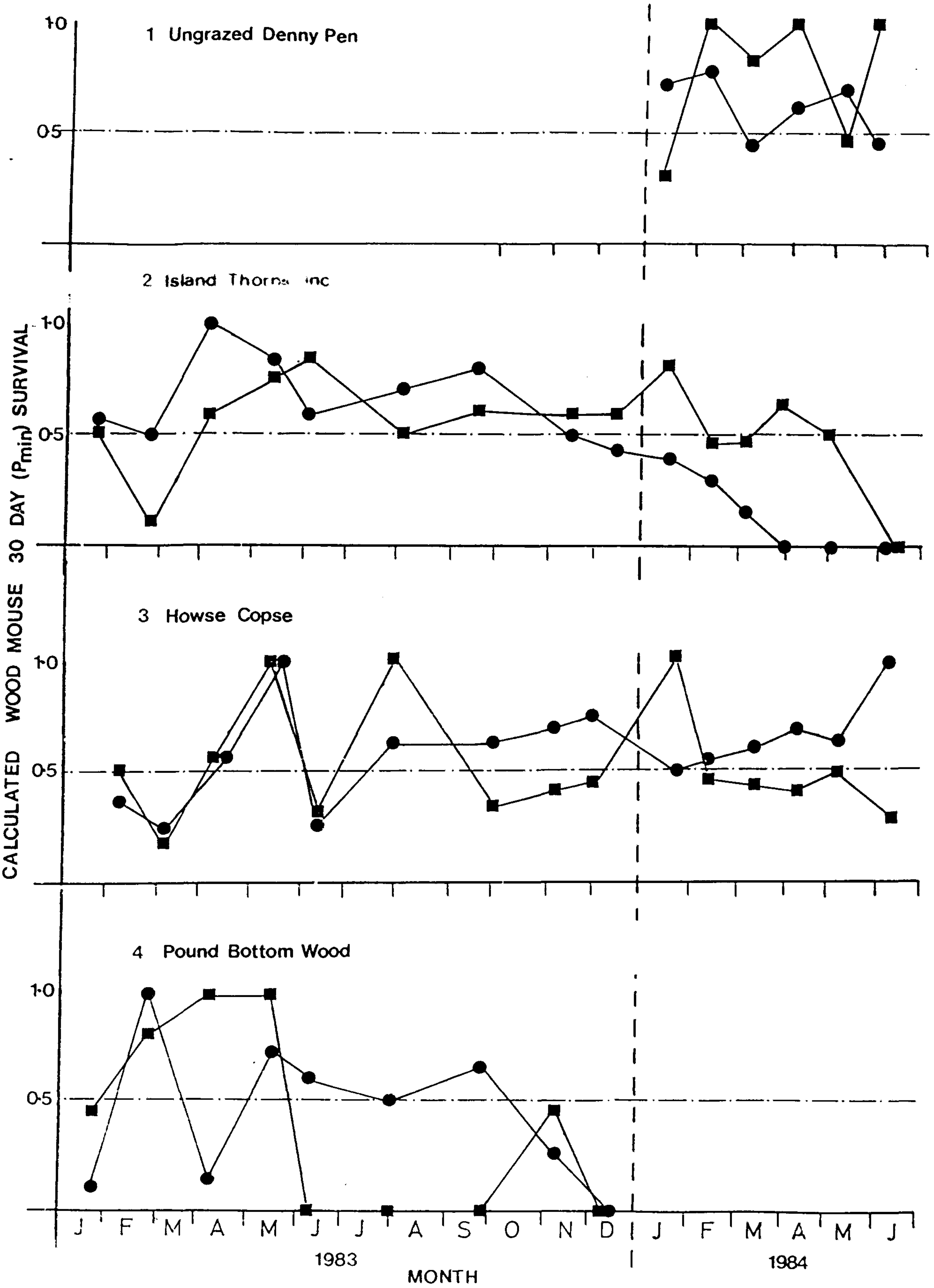


Figure 9.2 b. Minimum 30 day survival of sex (males ●—● ; females ■—■) classes of A.sylvaticus within Enclosed New Forest (site 1), Open New Forest (site 2) and outside New Forest (sites 3 & 4) deciduous woodland.

above revealed no significant differences between age classes or sex classes. Again, although no significant differences between the age and sex groups was found, survival was not correlated.

Inter-site comparison of P_{min}

Wood mice

Minimum monthly survival between sites was compared using a Wilcoxon´s matched-pairs test on the combined classes for pairs of sites, and resulted in a significant difference being found between the survival of wood mice at Pound Bottom Wood and Island Thorns Inc ($T=3$, $N=9$, $p=0.02$) indicating better survival at the latter grazed New Forest site. The data from these sites were split into two age classes and a significant difference in P_{min} was found between the juvenile/sub-adult age class at the two sites ($T=3$, $N=9$, $p=0.02$), again with better survival at Island Thorns Inc.

Although no significant difference was found between age classes at Pound Bottom Wood and Howse Copse, in the light of the above differences the age classes at these sites were also compared and a slight difference was again found between the juvenile/sub-adult groups ($T=4$, $N=8$, $p=0.05$) with greater survival at Howse Copse. No significant difference was found in P_{min} between populations at Howse Copse and Island Thorns Inc.

Comparison of P_{min} between wood mice and bank voles

There are insufficient data available on the survival of voles at Pound Bottom Wood to enable comparison with survival of voles at Howse Copse, but the survival of this species at the latter site, and for the six months of 1984 within the ungrazed Denny Pen, have been compared to that of

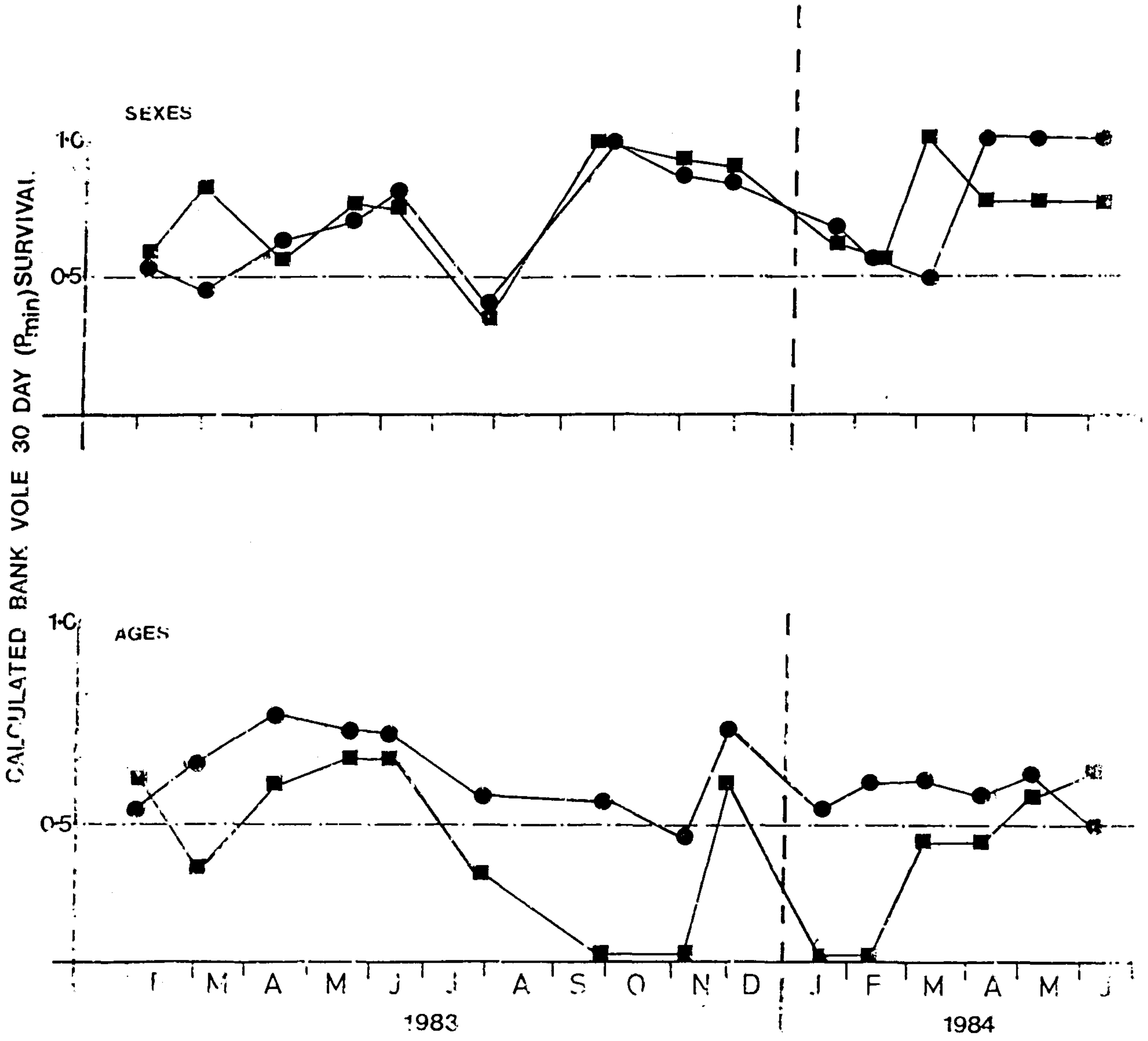


Figure 9.3 Minimum 30 day survival of sex (males ●—● ; females ■—■) and age (adults ■—■ ; juveniles/sub-adults ●—●)classes of C.glareolus within Howse Copse deciduous woodland.

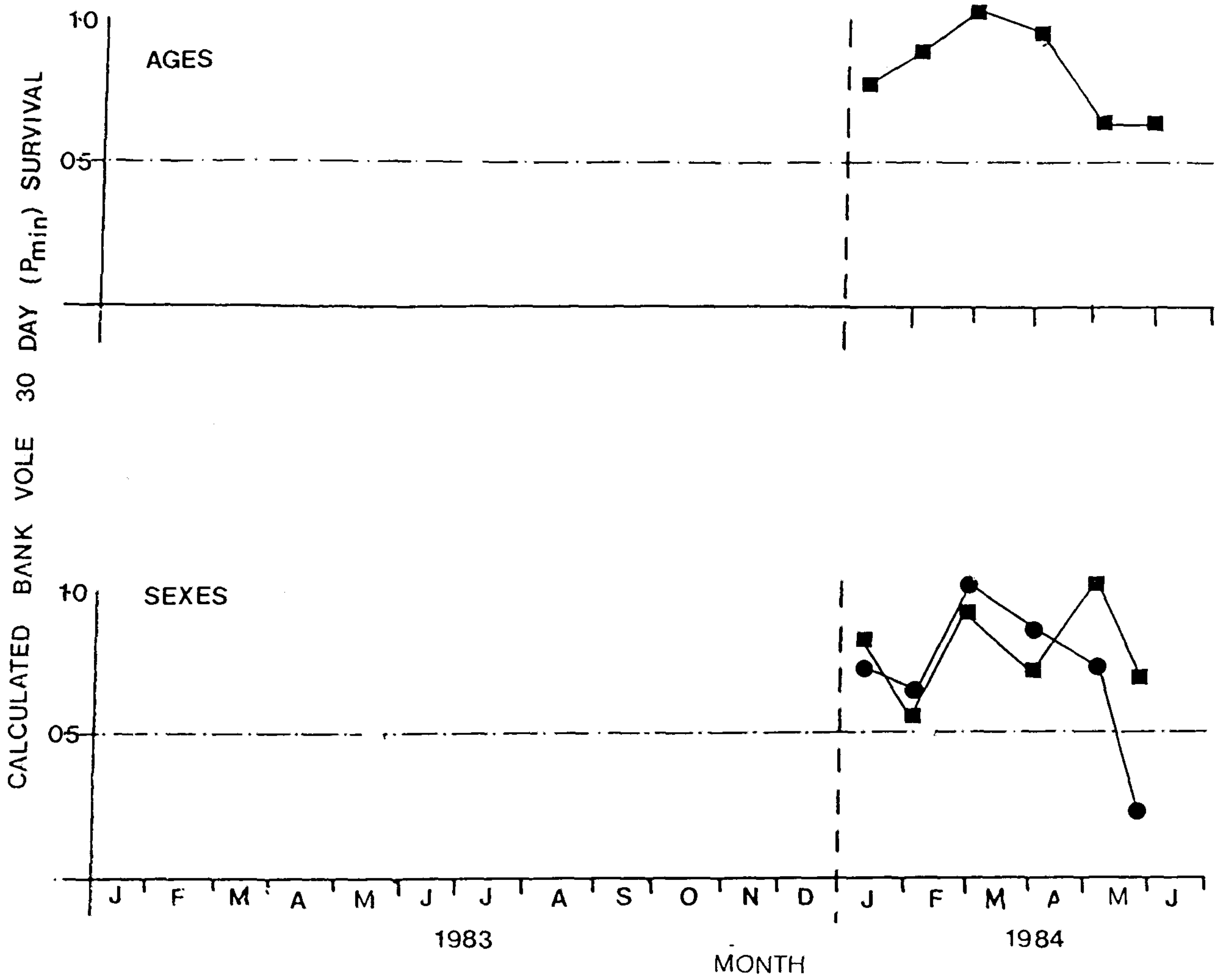


figure 9.3 continued....

Minimum 30 day survival of age (adults ■—■) and sex (males ●—● ; females ■—■) classes of C.glareolus within the Ungrazed Denny Pen in the New Forest.

the wood mice. Analysis has been performed in the same way as above and no significant differences have been found between the survival of the wood mice and bank voles at either site.

9.2.4 Overwinter survival

The overwinter survival of rodent populations is important to their success in the following year since individuals who survive this period are potentially capable of breeding in the spring. The greater the overwinter survival, the greater the potential for production of young.

Overwinter survival is measured as the proportion of animals in the population that are present in the late spring that were also present in the previous autumn. To correct for differences in time periods between trapping sessions, this value can be standardised using the equation for P_{min}.

Wood mice

The calculated survival statistics for wood mice from the two years, 1982/1983 and 1983/1984, are presented in table 9.3 and it is apparent that overwinter survival at all sites was poor in both, the maximum overall survival being 12.5% at Island Thorns Inc and Backley Inc within the Forest. As would be expected adult overwinter survival was generally poorer than amongst the younger age classes. Comparison of survival between age classes for both years revealed no significant differences at any site, after pooling age classes the same test revealed no significant difference in overall survival.

The overwinter survival has also been examined for Island Thorns Inc, Howse Copse and the ungrazed Denny Pen using data for the duration of residence of animals caught in November 1983. These three sites were trapped monthly and

Table 9.3 Calculated overwinter survival (Nov/Dec to May/June) of different age classes of *Apodemus sylvaticus* and *Clethrionomys glareolus* within Open New Forest (sites 1 to 4), outside New Forest (sites 5 & 6) and Enclosed New Forest (site 7) deciduous woodland (see also figure 9.1 Duration of residence)

	1982/83			1983/84		
	Adult	J/SA	Overall	Adult	J/SA	Overall
Apodemus sylvaticus						
1. Island Thorns Inc	0.00	0.00	0.00	0.00	0.00	0.00
2. Backley Inc	0.00	0.25	0.13	0.00	0.00	0.00
3. Matley Inc	0.15	0.05	0.08			
4. Sloden Inc	0.00	0.17	0.10	0.11	0.00	0.09
5. Howse Copse	0.00	0.15	0.09	0.08	0.00	0.04
6. Pound Bottom Wood	0.00	0.00	0.00	0.00	0.50	0.50
7. Ungrazed Denny Pen				0.00	0.00	0.00
Clethrionomys glareolus						
5. Howse Copse	0.00	0.25	0.25	0.09	0.09	0.09
7. Ungrazed Denny Pen				0.00	0.33	0.33

so these data are available. No significant differences in these residences have been found between these wood mouse populations.

Bank voles

The overwinter survival statistics of the bank vole populations are presented in table 9.3. Again, overwinter survival was examined for the two sites trapped monthly on the basis of duration of residence, and no significant differences in residence were found between the two sites.

9.2.5 Summary

Survival of woodland wood mouse and bank vole populations has been examined in three ways, cohort duration of residence, minimum monthly survival and minimum overwinter survival. The results of this analysis indicate no significant differences between age and sex classes within each site, and only a few differences between survival in grazed and ungrazed areas. The data available for each analysis is small and so statistical comparisons must be viewed with caution. As expected, juvenile/sub-adult survival is slightly better than that of the adult age group, especially during the late autumn/early winter months and as measured for the ovewinter, December to May, period.

9.3 DISCUSSION

Previous studies of the survival of wood mice and bank voles have revealed it to vary seasonally and with age (Watts 1969; Crawley 1970; Montgomery 1980c; Smal & Fairley 1982). Analysis of cohort duration of residence revealed no significant differences between age groups of wood mice or voles within each site, and comparison between sites also revealed no significant differences. Due to the short duration of the monthly trapping (18 months) it is not possible to compare cohort survival between or within years, but there is some indication of better survival in the summer of 1983 than the previous spring (figures 9.1 & 9.2). Analysis of minimum monthly survival also revealed no significant differences between age groups, but figure 9.2 reveals that, at all three sites, adult survival was generally lower than juvenile/sub-adult survival; this would be expected from older animals.

Overwinter survival (table 9.3) of both species was poor and there is little difference between the sites, but there is some indication in support of the monthly survival data that juveniles/sub-adults survived better over this period; again, due to age, this would be expected.

Survival may be affected by a number of factors previously described (section 9.1). It is important to note that as data are collected by trapping animals, trap response and emigration from the study area will account for some losses which is why the measures of survival are ´minimum´ values and why data from calendar of captures were used instead of trapping data. Movement may occur through social interactions (Wolton & Flowerdew 1985) or in response to food supply (Flowerdew 1972). When moving, rodents may make themselves more susceptible to predation (Boonstra 1977; Abramsky & Tracy 1979) which means that re-immigration will not occur. Predation rates may vary amongst different parts of the population (Metzgar 1967) and may vary with habitat type (Southern & Lowe 1968), the degree of cover being especially significant.

A number of studies have shown the importance of the autumn tree seed crop to overwinter survival (Smyth 1966; Vincent 1977; Flowerdew & Gardner 1978) with a positive correlation between survival and seed production. In this study, the tree seed crop was poor in both years and is almost certainly a contributing factor to the poor overwinter survival seen in all populations. Small rodent diet also changes seasonally (Watts 1969) and survival may also be related to other food supplies, although other foods are not thought as important as tree seeds in the autumn/winter months (Flowerdew 1985). The effects of other factors, such as climate, are still poorly understood (Flowerdew 1985).

Variations in survival rate found in this study do not show the same trends as found by some previous workers, except that overwinter survival was poor and probably related to the poor autumn tree seed crops. Survival of wood mice during autumn and winter months has been shown to be good during winter months (Watts 1969; Montgomery 1980c; Smal & Fairley 1982) with a decrease in the spring and summer months (Crawley 1970) as overwintered adults disappear from the population. Monthly survival rates were more erratic than in these previous studies and did not follow these seasonal trends. This may be related to the poor tree seed crop reducing overwinter survival to less than in previous studies; spring and summer survival might therefore have been similar and so the differences in survival are not obvious. This is suggested because food supply is not thought to be as important to the spring and summer survival.

Of course other factors such as predation may be important. It has already been noted that dispersion and habitat type affect susceptibility to predation. One major effect of large herbivore grazing is to alter vegetative cover on the woodland shrub layer and this may increase the risk to predation. If social interactions cause dispersion of juveniles (Wolton & Flowerdew 1985), the increased activity of this age class and their movement to unfamiliar habitats may mean there is increased predation upon this age group. However, no significant differences were found in survival of the two age groups, although, in the winter survival of the younger animals was slightly better. If predation were greater on the younger age class it would explain why juvenile/sub-adult survival was not found to differ significantly from that of the adults. As cover is greater in the ungrazed Denny Pen and the two outside sites, one would expect the risks of predation to be less, and thus survival to be greater, than in the grazed New Forest woodlands but this was not found to be the case. Only in the winter of 1984 was the survival of wood mice within Island Thorns Inc within the Forest noticeably different to that within the ungrazed Denny Pen and Howse Copse.

In the first six months of 1984, monthly survival of the wood mouse and vole populations within the ungrazed Denny Pen, Howse Copse and Island Thorns Inc are quite different (figures 9.2 & 9.3), with a continual decline in survival of the mouse populations within the grazed Island Thorns Inc which was not seen in the populations at the other site. This may be due to the smaller number of animals caught within the Forest site (losses would therefore amplify the reduction in survival), or it may be related to the fact that tree seed crop was poor at all sites in autumn 1983, which would be a contributing factor to poor survival over the winter months. However, this does not explain the difference in P_{min} between sites. Habitat structure is known to be important to survival and it is suggested that this is a contributing factor to the increased losses at Island Thorns Inc, there large herbivore grazing has totally removed the shrub layer vegetation and so the animals may be more susceptible to predation or may move to other areas.

It therefore appears that survival of both wood mice and bank voles, in grazed and ungrazed woodlands, was not significantly different during the study. The importance of tree seed crop to overwinter survival identified by previous workers (*e.g.* Flowerdew & Gardner 1977) has been confirmed here, the poor overwinter survival of all the populations being attributed to the poor seed crop each year. This poor survival explains the wide fluctuations in population size (Chapter 7, figure 7.4) at all sites. Although recruitment

(Chapter 7, figure 7.4) at all sites. Although recruitment increases population size, poor survival led to low spring numbers. As tree seed crop was so poor, differences that may be attributable to large herbivores are not apparent, apart from the better survival of wood mice in the ungrazed Denny Pen in the winter of 1984.

CHAPTER 10

WOODLAND SMALL RODENT MICRODISTRIBUTION AND HABITAT USE

10.1 INTRODUCTION

Previous studies on the microdistribution and habitat use of woodland small rodents suggest that their local distribution is related to their selection for a number of biotic habitat characteristics (Miller et al. 1976; Dueser & Shugart 1978): vegetative cover (Newson 1960; Kikkawa 1964; Southern & Lowe 1968; Montgomery 1980c); food supply (Hansson 1968,1979; Getz 1970; Flowerdew 1972) and predator avoidance (Southern & Lowe 1968; Price 1984).

The three Northern European woodland species of small rodent have all been found to exhibit variation in numbers and occurrence depending upon the available vegetation cover. Bank voles prefer dense cover whilst wood mice appear to have no preference (Newson 1960; Kikkawa 1964), although it has been suggested that wood mice select areas of dense cover in the absence of their potential competitors, the bank vole (Fairley & Comerton 1972; Montgomery & Bell 1981; Abramsky 1981). The yellow necked mouse too displays no apparent preference for ground cover (Hoffmeyer 1973; Corke 1974), but it is found predominantly in mature woodland areas whereas the other two species often occupy other habitats (Corke 1971; Corbett & Southern 1977). The preference for habitats with a degree of cover may be to reduce predation which can play an important role in rodent population dynamics (Southern & Lowe 1968; Andersson & Erlinge 1977; Taitt & Krebs 1983). For example, Southern & Lowe (1968) demonstrated that tawny owls caught more voles successfully from areas of intermediate cover and wood mice from open areas.

Habitat selection in multi-species communities would appear to be complex. Current theory (Pianka 1981) suggests that microhabitat segregation occurs with some overlap for common resources so competition may be one controlling factor. As wood mice, bank voles and yellow necked mice all occur within the same habitat they are all potential competitors. Montgomery (1980a & b) suggests that there is horizontal and vertical spatial separation (a view supported by some short-term studies: Brown 1981; Ward 1982; Cusworth 1983), as well as temporal (Brown 1956) and dietary (Watts 1968; Hansson 1971,1975) segregation. Although small rodents are habitat specialists, in the absence of potential competitors it has been shown that a species will make greater use of the available habitat, but not change its microhabitat associations (Montgomery 1981), and that the population may perform better (Gliwicz 1981; Chapter 1, section 1.3.4).

Increased use of different habitats requires individuals of the population to move. Small rodents have complicated social organisations but it is apparent that interspecific competition is averted or reduced by different habitat use both seasonally within age and sex classes and between different age classes (e.g. Van Horne 1982a). Home range studies have revealed that some of these changes are related to periods of reproduction (Randolph 1977) and recruitment (Kikkawa 1964). During periods of population increase, it is the recruits that move (Wolton & Flowerdew 1985) and that are more likely to occupy sub-optimal habitats. Movement between habitats may also occur in response to resource availability, such as food (Flowerdew 1972; Abramsky 1978), or availability of a preferred habitat (Corke 1974; Montgomery 1981).

The distribution of woodland small rodents may be affected by the availability of suitable vegetation, the species attempts at predator avoidance, food supply and by the fact that these species may alter their occupation of habitats in response to the availability of these resources.

It is therefore apparent that the distribution of woodland small rodents is not only affected by availability of preferred habitats but by other habitat characteristics such as competition and food supply. Alteration of these characteristics and resources thus leads to differential occupation of habitats. Chapters 4 and 7 have revealed that large herbivore grazing alters the physical nature of the habitat and, through this, the level of intra-specific competition by the exclusion of bank voles which show a strong preference of vegetation cover. This Chapter examines two aspects of rodent microdistribution which may be affected by the results of large herbivore grazing.

1) Microhabitat use

The primary difference in habitat characteristics between grazed and ungrazed areas in this study is the absence of dense ground cover in the New Forest woodlands, and it has been suggested (Chapter 7) that this is the reason for the absence of bank voles from these areas. This enables one to examine microhabitat selection of wood mice in the absence of one potential competitor and in the presence of only a few of another, the yellow necked mouse. One is also able to examine preferences for dense ground cover when wood mice and voles are together and when voles are absent.

2) Use of different habitats

The New Forest consists of many different vegetation communities, and the Matley Wood site was chosen specifically for the close proximity of the three communities used most extensively by the large herbivores: deciduous woodland; heathland and acid grassland. In the course of the initial study of rodents on the grasslands (Chapter 7), it became apparent that there were seasonal changes in occupation of the vegetation, with no animals being caught in the spring months but animals being caught on the sections of the grids closest to the woodland areas in the summer months; this coincided with the growth of bracken over the grassland.

As this area contains a variety of habitats, the movement of rodents about them was investigated with respect to vegetative cover and seasonal changes.

10.1.2 A Caveat

Attention is drawn to the note of caution (Chapter 1, section 1.3.5) regarding the use of trapping data to describe habitat occupation. It was noted that the behaviour of small rodents and trap efficacy can bias trapping results. Also the small rodent populations in this study were all at relatively low levels and so the amount of data available is quite small; this has meant that some pooling of data has had to be employed to enable statistical analysis. Therefore, seasonal changes in microhabitat selection are not examined.

10.2 METHODS

10.2.1 Microhabitat use

The examination of microhabitat use employs the data obtained from trapping sessions on the woodland grids at Howse Copse and Pound Bottom Wood outside the Forest, and the grazed Island Thorns Inc, Sloden Inc, Backley Inc and the ungrazed Denny Pen from within the Forest. For the Howse Copse, Pound Bottom Wood, Island Thorns Inc and Denny Pen sites, all seasonal and monthly trapping data were pooled for each site, and from Sloden Inc and Backley Inc all seasonal data were pooled to give the total number of captures in each grid square at each site.

Distribution about trapping grids

Before proceding with the analysis of preference for cover types, the distribution of captures about the trapping grids has to be analysed: if captures are random or regularly distributed, one need not proceed with analysis attempting to correlate captures with variations in vegetation cover.

Individuals of a population can follow three basic types of spatial distribution (Elliott 1977):

1) random.
2) regular (= under distribution, uniform or even distribution)
3) contagious (= over distribution, clumped or aggregated distribution)

and the distribution of a population determines the relationship between the variance and arithmetic mean:

1) random: variance = mean
2) regular: variance < mean
3) contagious: variance > mean

A provisional examination of distribution was performed by examining the variance mean ratio.

There are a number of models available for examining the spatial distribution of a population, these all being derived from the Binomial family (Elliott 1977). One of the most commonly used methods is the Poisson series, however, the use of this has a number of requirements (Elliott 1977, page 22), one being that the presence of an individual at a given point may not increase or decrease the probability of another individual occurring nearby, i.e. each catch is independent. Longworth traps are single capture traps and, although two traps were at each point and even at the maximum daily catch only 40.8% of traps were filled (site:

Ungrazed Denny Pen, June 1983) the data fail to fulfil this requirement.

Another member of the Binomial family is the Negative binomial. This model is not subject to the restrictions of the Poisson series and agreement with it indicates a contagious distribution, which is being examined for here. Therefore the frequency of capture of wood mice and bank voles from each site was compared to the Negative binomial.

Distribution in relation to ground vegetation

Comparison of capture distribution with the Negative binomial revealed that animals were neither uniformly nor randomly distributed about the trapping grids (see 10.3.1 Results). Therefore, the distribution of captures was compared with the degree of cover of the dominant ground vegetation in the shrub layer, the vegetation strata found by previous workers to be the most important (Newson 1960; Southern & Lowe 1968; Montgomery 1980b). Using the data from the study of vegetative stucture (Chapter 4), the abundance of the dominant vegetation in each grid square ($225m^2$) was put into one of the following categories:

0) absent
1) 1-5%
2) 6-25%
3) 26-50%
4) 51-75%
5) 76-100%

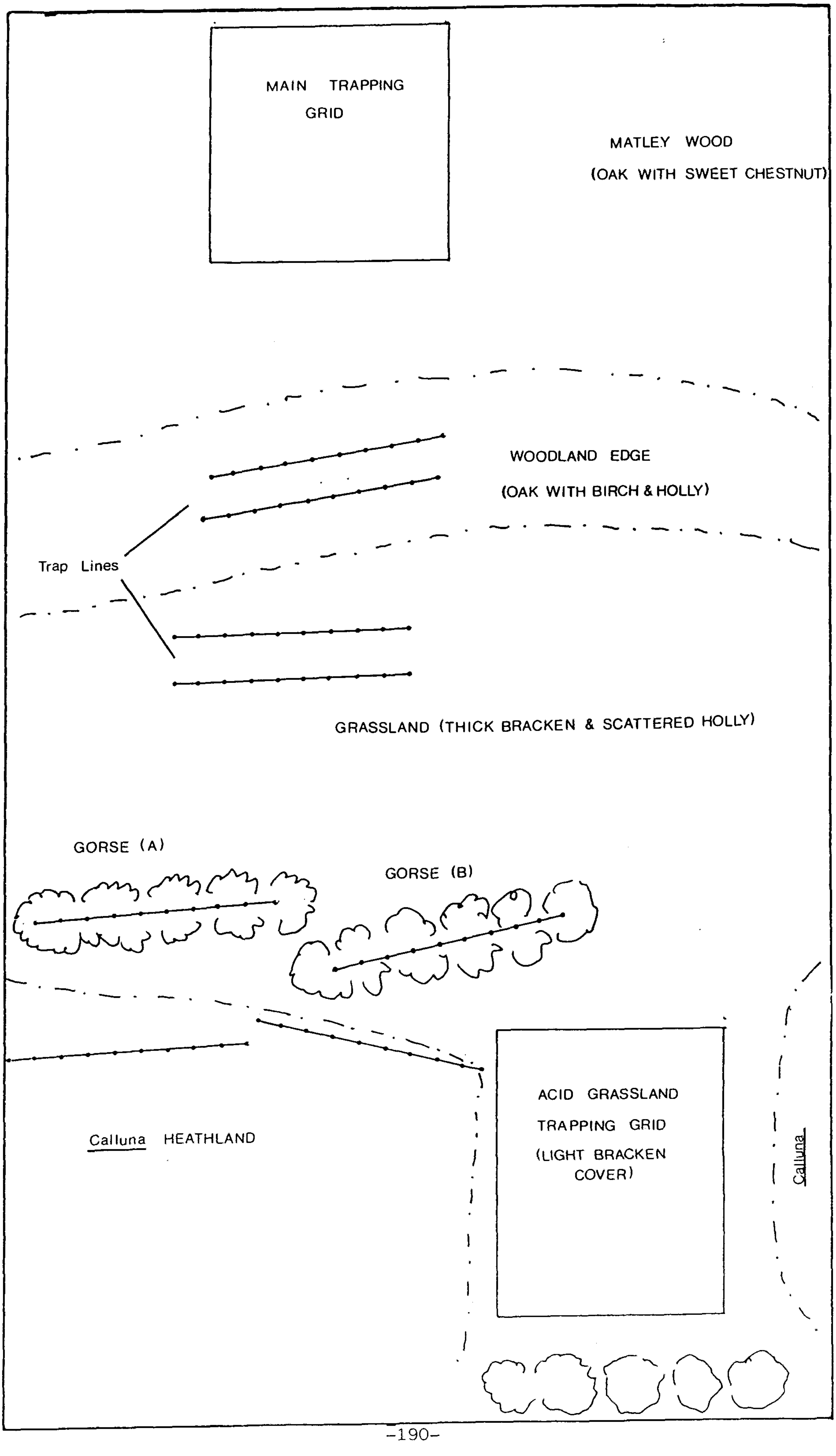
Analysis of the distribution of animals was based on the total number of wood mice and bank voles caught in each trapping session, the total for each session being pooled for the duration of the study. Theoretically, an individual caught in a certain trap more than once in the same session should only be counted once so as not to bias the results with trap addiction. In this study such a method results in too few data and testing against the Negative binomial resulted in an unacceptably high number of expected values being ignored. Therefore in this analysis all captures at a trap station were included.

10.2.2 Habitat use at Matley Wood

The movement of wood mice between different habitats at Matley Wood was examined by a combination of trapping, using grids and lines, and radio-telemetry. The relative positions of the different vegetation communities and the positions of trapping grids and lines are shown in figure 10.1. The trap lines were established in February 1983 and trapping began in March following the trapping of the woodland grid. Each trap line was run for 3 trap nights without a prebaiting period, trapping in the sequence of woodland grid, woodland edge, grassland, gorse and heathland. Unfortunately, each line was only trapped twice from March to June before public interference necessitated termination of all work at this site.

Most studies of movement in small rodents have involved the use of C.M.R. techniques; however, in this study where populations were very small, these techniques demanded a large amount of effort for little data return and therefore radio-telemetry was employed in conjunction with trapping to assess movement. Due to equipment failure the results of this will only be commented on in the discussion (section 10.4).

Figure 10.1 A sketch map of the Matley Wood study area showing the relative positions of the six habitat types (woodland, woodland edge, grassland, acid grassland, gorse and heathland), and of the trapping grids and trap lines. Trap lines were ten trap stations long at 10m spacings, woodland trapping grid was 7x7 at 15m spacings and the acid grassland grid was 8 x 6 at 15m spacings; two traps were placed at each trap station. See text for trapping dates and periods.


MAIN TRAPPING GRID
MATLEY WOOD
(OAK WITH SWEET CHESTNUT)
WOODLAND EDGE
(OAK WITH BIRCH & HOLLY)
Trap Lines
GRASSLAND (THICK BRACKEN & SCATTERED HOLLY)
GORSE (A)
GORSE (B)
ACID GRASSLAND
TRAPPING GRID
(LIGHT BRACKEN COVER)
Calluna HEATHLAND
Calluna

10.3 RESULTS

10.3.1 Microdistribution

Spatial distribution

1) Variance mean ratio

Preliminary examination of spatial distribution using the variance mean ratio revealed all ratios to be < 1 indicating contagious distributions.

2) Negative binomial

Comparison of distribution with the negative binomial (table 10.1) revealed all captures to agree with this model indicating a contagious distribution.

10.3.2 Distribution in relation to ground cover

Figure 10.2 shows the frequency of captures of wood mice and bank voles in relation to the cover of bracken and, for Howse Copse and the ungrazed Denny Pen, brambles. These distributions have been compared to the expected using a G test for goodness of fit. The results of these tests (shown on figure 10.2) indicate that distribution of voles within different cover classes of bracken in Pound Bottom Wood and the Denny Pen and distribution of wood mice at Backley Inc and the Denny Pen vary significantly from that expected. Only within the Denny Pen does the distribution of voles in different cover classes of brambles vary significantly from that expected.

Table 10.1 Results of negative binomial tests on the distribution of captures of A.sylvaticus and C.glareolus about 0.81ha tapping grids within Open New Forest woodland (sites 1 to 4), one ungrazed 5ha New Forest woodland Pen (site 5) and two woodlands outside the New Forest (sites 6 & 7).

Site	χ^2	df	p
A.sylvaticus			
1. Island Thorns Inc	13.15	11	>0.05
2. Backley Inc	5.12	7	>0.05
3. Sloden Inc	3.63	5	>0.05
4. Matley Wood	7.23	6	>0.05
5. Ungrazed Denny Pen	11.37	11	>0.05
6. Howse Copse	4.84	10	>0.05
7. Pound Bottom Wood	5.82	7	>0.05
C.glareolus			
1. Ungrazed Denny Pen	21.52	13	>0.05
2. Howse Copse	13.23	11	>0.05
3. Pound Bottom Wood	7.23	7	>0.05

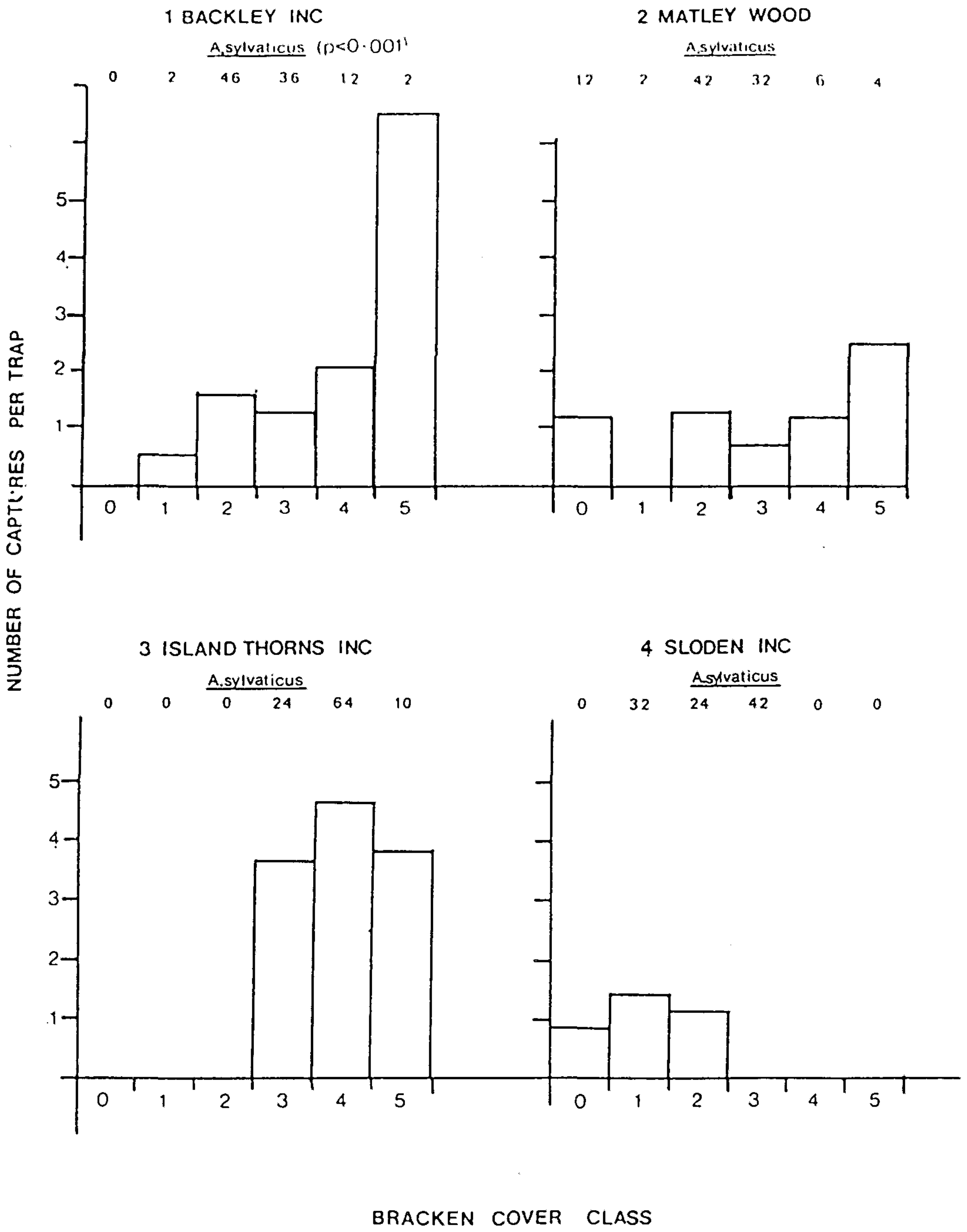


Figure 10.2 The frequency of captures of A.sylvaticus and C.glareolus within different cover classes (see text) of bracken (P.aquilinum) and brambles (R.fruticosa) about 0.81 ha trapping grids within Open New Forest (sites 1 to 4), Enclosed New Forest (site 5) and outside New Forest (sites 6 & 7). (Numbers of traps within each cover class and significant departures from random distributions are shown).

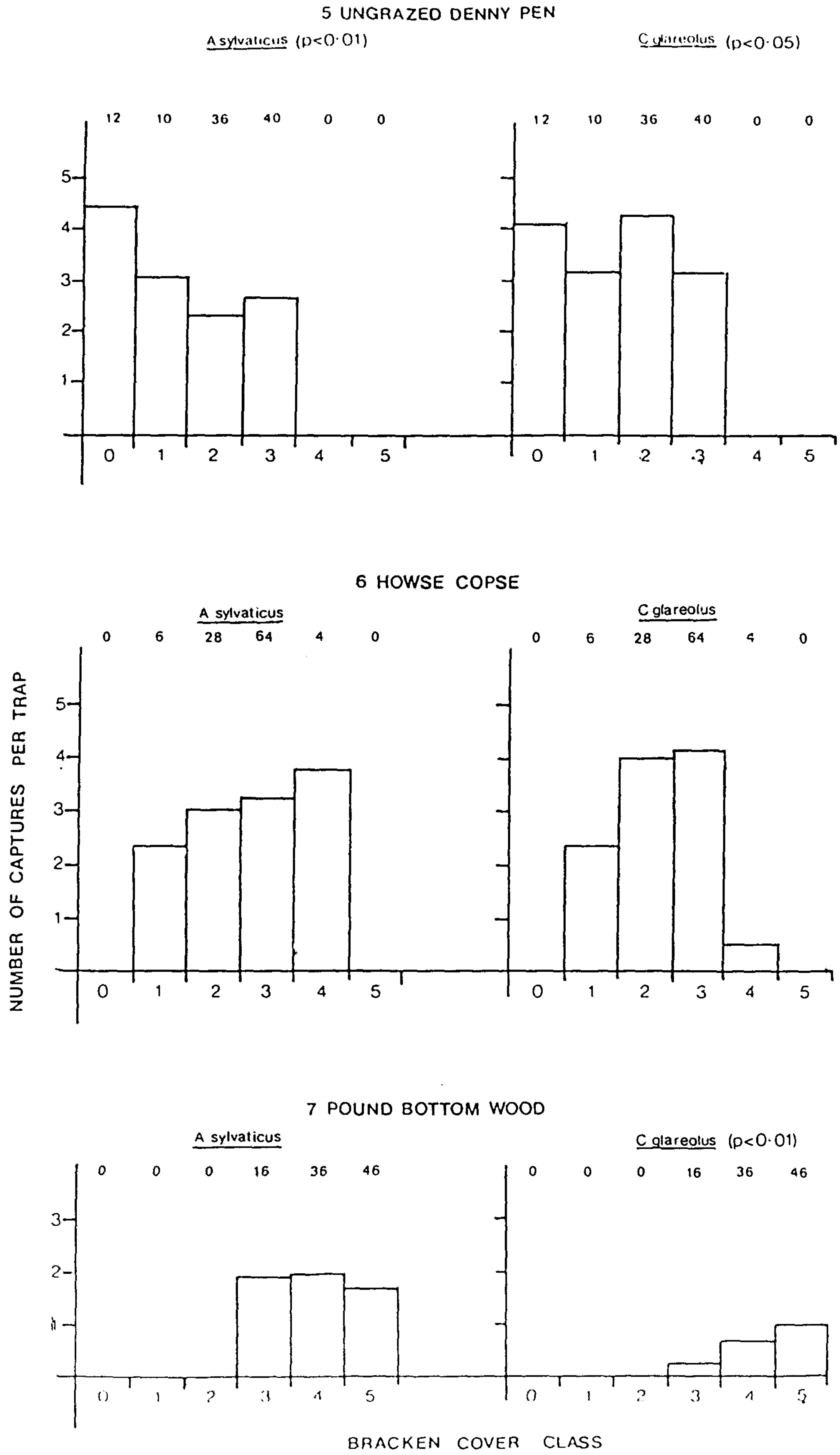


figure 10.2 continued

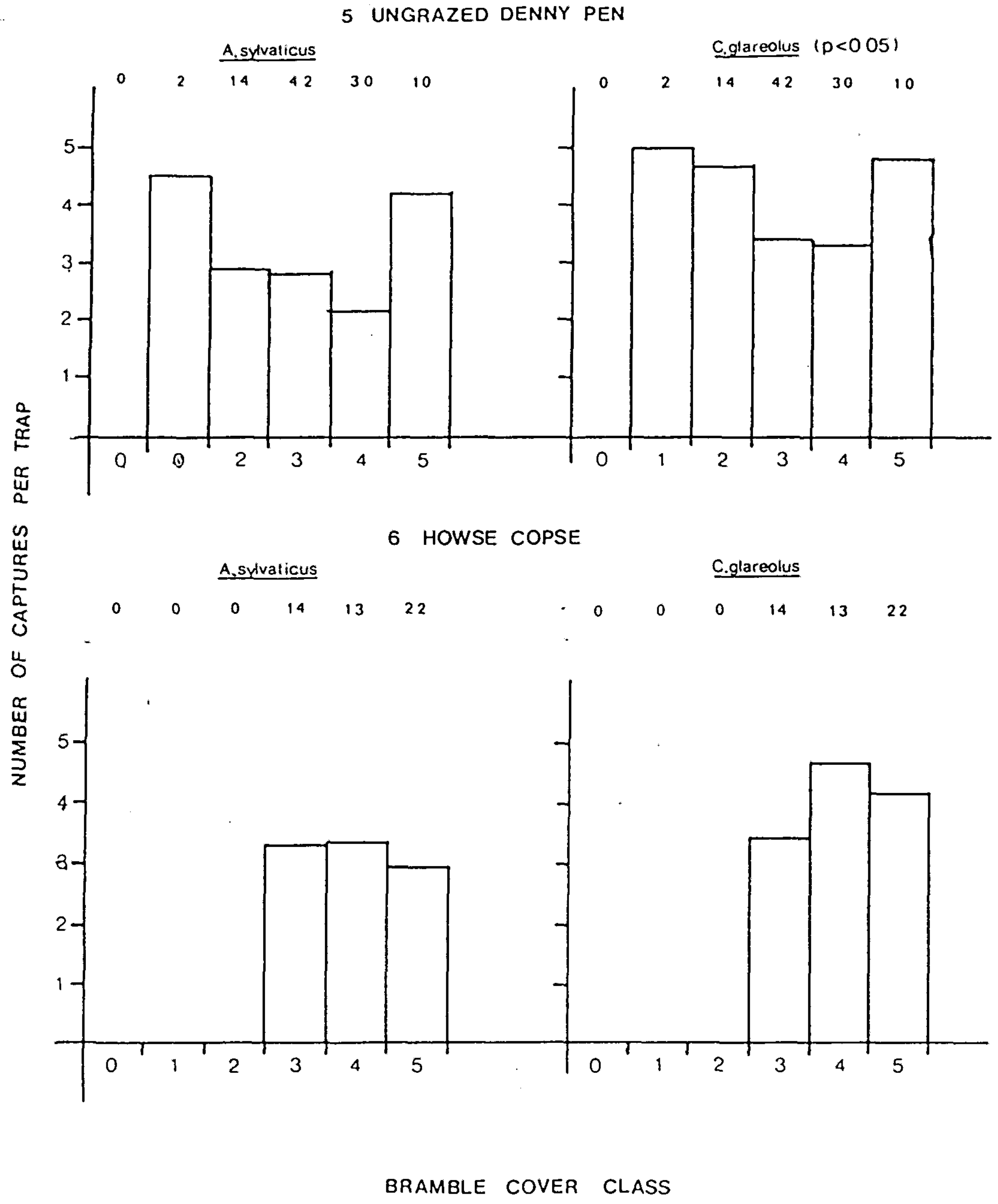


figure 10.2 continued

10.3.3 Habitat use at Matley Wood

The numbers of wood mice caught on the grid and trap lines are presented in table 10.2. The sites of initial capture of those recaught in different habitats are presented in table 10.3. The main movement between habitats was between the woodland edge and the grassland between the woodland and the gorse (figure 10.1).

10.4 DISCUSSION

The most obvious effect of large herbivore grazing within the New Forest woodlands is the removal of vegetation from the shrub layer (Chapter 4), and it is suggested that this is responsible for the reduced diversity of small rodent species within the grazed woodlands in comparison to the ungrazed and outside ones (Chapter 7). This analysis is not intended to be an exhaustive examination of microdistribution in relation to vegetative cover but an examination of the distribution of rodents in single and multi-species communities in relation to the shrub layer and the use of habitats adjacent to the woodland.

The investigation into movement of wood mice between habitats at Matley Wood, although temporally short, did reveal that the animals made use of most available habitats and moved freely between them. At the time of this study, winter/late spring, more wood mice were caught in the grassland between the woodland and acid grassland than in any other habitat and the radio-tagged animals too spent considerable time in this area. All trap defined movements were in the direction away from the woodland and between adjacent habitats, three animals initially caught on the woodland grid being recaught in the woodland edge and gorse, four animals moving from the woodland edge to the grass, and five animals moving from the grassland to the gorse. No animals, however, moved into the woodland grid though. There

Table 10.2 The numbers of wood mice (<u>Apodemus sylvaticus</u>) caught within six different habitats at Matley Wood within the New Forest during spring 1983. the relative positions of the trap lines are shown in figure 10.1.

Habitat	Week	Number of animals caught		
		♂	♀	Total
Woodland	9	3	3	6
	15	1	1	2
	20	5	6	11
Woodland edge	9	6	5	11
	16	2	2	4
Grassland	10	15	3	18
	17	2	1	3
Gorse A	11	1	6	7
	16	2	2	4
Gorse B	11	0	5	5
	16	1	2	3
Heathland	12	0	0	0
	17	0	0	0

Table 10.3 Trap defined movements of (Apodemus sylvaticus) between different habitats (shown in figure 1) at Matley Wood in the New Forest during spring 1983.

2♂ moved from Gorse A to Gorse B

1♀ moved from Gorse B to Gorse A

4♂ & 1♀ moved from grassland to gorse

1♀ moved from woodland to gorse via grassland

1♂ & 1♀ moved from woodland to woodland edge

3♂ & 1♀ moved from woodland edge to gassland

1♀ moved from woodland to grass

was also a continuous interchange between the two gorse trap lines suggesting that the wood mice are resident in these areas and explore them quite fully. As this was not a period of recruitment, this movement cannot be attributed to dispersion in the way that was suggested for the wood mice within the Denny Pens (Chapter 8).

The amount of ground cover, principally bracken, increases as one progresses away from the woodland across the grassland to the gorse. In the summer months bracken covers the acid grassland too and, as revealed in Chapter 7, wood mice are caught in this habitat in these months. In the winter the cover on the grasslands soon disappears due to trampling of the bracken litter but in the woodland edge and adjacent grassland areas, the cover remains quite dense as the large herbivores do not appear to make such extensive use of these areas. At this time the cover in the woodlands is also low, there is no bramble cover due to grazing and the bracken is dying back. Bank voles are almost totally absent from Matley Wood and so, as suggested by Montgomery & Bell (1981), the mice might be exhibiting a preference for areas of dense cover in the absence of competition.

The results of analysis of microdistribution within the woodlands do not endorse this theory. Distribution about trapping grids in relation to bracken cover at most sites did not differ significantly from that expected, with only the wood mice at Backley Inc showing a preference for cover. Within the ungrazed Denny Pen, both mice and voles appeared to select areas of low bracken cover, whereas voles caught at Pound Bottom Wood did exhibit a preference for bracken cover.

In comparison to bracken, brambles offer a more dense vegetation and, in the presence of both, rodent distribution may be related more to the latter; of course, the two plant species may also interact, but the study of cover analysis suggests cover of both species to be high in all quadrats (Chapter 4); this may be related to canopy structure, both species growing better in areas where the canopy is more open.

Distribution of wood mice and bank voles in relation to bramble cover revealed only one significant departure from that expected: the distribution of bank voles in the Denny Pen. This distribution does not reveal a preference for any particular degree of cover; it appears, as with the wood mice (figure 10.2), that the voles were caught more often in the areas of high or low cover and less in the intermediate areas.

In the presence of both species, one might expect the animals to be caught in different habitat types, the bank voles excluding wood mice from their preferred habitat. This is not revealed in these data, although an examination of the number of each species caught at each grid point reveals separation (Howse Copse: $G = 152.81$ $df=48$ $p<0.01$).

This would be expected as the two species are probably caught at different times: bank voles are active throughout the day but are more diurnal in the presence of wood mice (Brown 1956) whereas mice are primarily nocturnal (Montgomery & Gurnell 1985; but see recent telemetry work by Wolton 1983) so, once caught, bank voles stop the trap from catching further animals. Therefore the wood mice would have fewer traps in which to be caught and the bank voles, but not necessarily the mice, would exhibit their preference for cover.

From these data it appears that within one site at least, Matley Wood, wood mice make extensive use of marginal habitats. This study is unable to take account of changes in spatial distribution due to reproductive condition, age or food supply, but it is possible to suggest that at the time this study was performed, the amount of ground cover outside the woodland was greater than within due to the prescence of bracken on the grassland and the removal, by large herbivores, of vegetation from the woodland floor. Therefore, the mice selected this habitat.

Within the woodlands where only wood mice were present, the only evidence to suggest selection for dense ground cover in the shrub layer is from Backley Inc, but the bracken cover over the woodland floor at most sites was quite uniform and this is a subjective assessment of what animals may select for. It would therefore appear that the reduction in ground cover due to grazing, and the resulting absence of competitors, is not influencing the distribution of wood mice. Other studies (Montgomery, 1980b; Gibson, 1981) have found correlations between other vegetation strata and small rodent captures, but these are in areas where the ground cover is not subjected to heavy grazing and is stucturally more complex. In the woodlands where both species were present there again appears to be little consistent evidence of voles or mice selecting for or against vegetation cover, but this may be due to the uniform nature of the cover types studied (Chapter 4).

CHAPTER 11

PREDATION UPON WOODLAND RODENT POPULATIONS

11.1 INTRODUCTION

Small rodents are important prey to mammalian, avian and reptilian predators (Chapter 1), and these predators may have a profound affect on the distribution and demography of such rodent prey. During the period of this study, variations in small rodent abundance and distribution have been found between the grazed New Forest and the outside sites. In woodlands and heathlands outside the Forest a greater diversity and number of rodents has been found, the actual number of rodents in the New Forest woodlands being approximately half that found in the outside woodlands due chiefly to the absence of bank voles. Since the total rodent biomass within the Forest is low, one can hypothesise that a) the ecology of predators within these areas may be affected by low prey availability and that b) the reduced cover within the deciduous woodlands makes wood mice more vulnerable to predation.

There are several species of predator within the New Forest (table 11.1) but in most cases the actual number of each appears to be small: Insley (1977) reported that density of adult foxes was 0.75/km compared to densities 10 times greater in other parts of Britain (Lloyd 1980). Tubbs (1982) notes that during the same period as Insley's study there was only one pair of kestrels (Falco tinnunculus) per 18km compared to densities of a pair per 2km on farmland. Badgers (Packham 1984) and common buzzards (Buteo buteo) (Tubbs & Tubbs 1985) are at low densities too. Apart from studies on smooth snakes (Spellerberg & Phelps 1977; Goddard 1981,1984), there have been no studies on the abundance of other predators, such as adders (Vipera berus), which might be present in high numbers. Within the New

Table 11.1 Predators of small rodents known to be resident within the New Forest (various sources).

Mammals	
Red fox	(*Vulpes vulpes*)
Badger	(*Meles meles*)
Stoat	(*Mustela erminea*)
Weasel	(*Mustela nivalis*)
Aves	
Kestrel	(*Falco tinnunculus*)
Buzzard	(*Buteo buteo*)
Tawny owl	(*Strix aluco*)
Reptiles	
Adder	(*Vipera berus*)
Smooth snake	(*Coronella austriaca*)
Grass snake	(*Natrix natrix*)

Forest woodlands, tawny owls are probably the most abundant predator and are known to feed extensively on small rodents in other areas (Southern 1954,1969; Hirons 1976; Wendland 1981,1984). Again there is little published data on the diet of this species within the New Forest (Mikkola 1983; Hirons 1984).

This study has revealed low densities of small rodents within the Forest woodlands and it suggested that this is due to a reduction in habitat suitability through large herbivore grazing. The reduction in ground cover may increase the susceptibility of the rodents to predation and so affect their demography. This chapter examines the diet of tawny owls from within the New Forest woodlands and compares it with published data from woodlands not subjected to intensive grazing by large herbivores and where ground cover is known to be greater and so susceptibility to predation is presumed to be less. This work was carried out in conjunction with Dr Graham Hirons in his study on the ecology of raptors of the New Forest. The data on tawny owl diet within the New Forest includes information gained earlier in the study and previously published (Hirons 1984).

11.2 METHODS

11.2.1 Diet Analysis

Between 1982 and 1984 tawny owl diet was studied by the analysis of prey remains in pellets cast at roost sites (Glue 1970). Tawny owl roost sites were found by systematic searching of the birds' territories and location of roost sites used by owls fitted with radio-transmitters (Hirons unpublished). Tawny owl pellets came from two woodlands trapped in the small rodent studies, Matley Wood and Island Thorns Inc., and two other woodlands, Studley Wood (GR:SU235 165) and Stubby Inc (GR:SU325 045). Pellets were dried at 80 c for 48 hours and analysed individually.

Identification of prey was based on skulls, jaws, isolated cheek teeth and, if no skeletal remains were present, fur (following Day 1966). No attempt was made to differentiate between A.sylvaticus and A.flavicollis. The presence of a bird was indicated by the powdery matrix of the pellet, skeletal remains being used to assess size (Yalden 1977).

11.3 RESULTS

11.3.1 Occurrence of prey items in tawny owl pellets

The frequency of occurrence of prey items in 101 tawny owl pellets collected betweeen 1982 and 1984 is given in table 11.2. The data have been divided into winter (November to April) and summer (May to October) as the availability of the major prey item, small mammals, is known to vary in these periods (Chapter 7) and their offtake has been found to vary seasonally (Southern 1954,1969; Hirons 1976), especially in relation to the breeding season.

Beetles (primarily Geotrupes and Typhoeus) accounted for 50% of the total prey items but only 4.5% of the total weight of prey. Overall small rodents, mice, bank voles and field voles, accounted for 40% of items and made the largest contribution in weight (61.7%). Of this total Apodemus species accounted for 32% of total items (52.6% by weight). Other vertebrates accounted for the rest of the diet (11%) but, due to their large size, were responsible for a large proportion by weight (28.2%). After Apodemus, small birds were the most common prey.

Examination of diet by pellet analysis has methodological drawbacks: Lowe (1980) found that 40% of wood mice, 33% of bank voles, and 15% of field voles eaten by a captive owl were not recovered in pellets and it is assumed that losses occur in other items too. As small rodents are the major component of the diet the relative importance of each species (table 11.3) has been corrected following Lowe

Table 11.2 Summer (May to October) and winter (November to April) variation in the prey items, their relative numbers and weights, identified in 101 tawny owl pellets collected from Open deciduous New Forest woodlands between 1982 and 1984.

Prey	May to October			November to April			Overall		
	Items		Weight	Items		Weight	Items		Weight
	Number	%	%	Number	%	%	Number	%	%
Mice	39	35.4	48.1	39	30.0	60.5	78	31.6	52.6
Bank vole	2	1.8	2.1	9	6.9	12.5	11	4.6	6.8
Field vole	2	1.8	2.8	7	5.4	12.6	9	3.8	7.4
Grey squirrel	1	0.9	6.8	0	0.0	0.0	1	0.4	3.8
Rabbit	1	0.9	13.7	0	0.0	0.0	1	0.4	7.8
Common shrew	5	4.5	2.7	3	2.3	2.1	8	3.4	2.5
Birds	11	10.0	18.8	3	2.3	6.4	14	5.9	13.7
Slow worm	1	0.9	1.3	0	0.0	0.0	1	0.4	0.8
Coleoptera	48	43.6	3.2	69	53.1	5.9	117	49.4	4.6
	110			130			140		

Conversion to weight based on Hirons (1976) and Yalden (1977).

Table 11.3 Seasonal change (summer and winter) in the relative importance of three small rodent species in the diet of tawny owls (Strix aluco) within Open New Forest deciduous woodland from the actual occurrence in the diet (% pellet) and after correction for losses in digestion (% corrected) (correction based on data from Lowe 1980).

	May-October		November-April		Overall	
Rodent prey	% pellet	% corrected	% pellet	% corrected	% pellet	% corrected
Apodemus sylvaticus	86.6	89.8	70.9	71.4	78.9	79.8
Clethrionomys glareolus	4.4	5.1	16.3	15.8	11.5	11.4
Microtus agrestis	4.4	5.1	12.7	12.7	9.4	8.7

(1980). The relative importance of Apodemus increases to 80% of rodent prey for the year, 89.9% in summer and 71.4% in winter, voles accounting for approximately equal proportions of the remaining 20%. As correction has not been made for other prey items, percentage weight of prey (table 11.2) is based on the number of items found in the pellets.

There is little seasonal difference in the occurrence of major dietary items (table 11.2) except for the decrease in the number of birds and an increase in the number of voles taken in the winter.

11.4 DISCUSSION

Tawny owls are generalised predators taking a range of invertebrate and vertebrate prey items (Southern 1954; Wendland 1981,1984; Mikkola 1983) but small rodents, principally Apodemus and bank voles, commonly account for more than 60% of identifiable prey items in deciduous woodland (Southern 1954).

Small rodents accounted for 40% of identifiable prey items taken by the owls in the Forest (table 11.2) and made the largest contribution by weight (66.7%). Apodemus were the principal small rodent species consumed (79.8% of rodent items; 32% of total and 52.6% by weight of the total) with both vole species accounting for only 8.4% of the total items (14.1%) by weight. If one corrects for items not regurgitated (Lowe 1980) the importance of Apodemus increases to 83% (table 11.3). These data are similar to those from a small scale study by Mikkola (1983, table 28). The order of occurrence of prey in this study is almost identical to Mikkola's (1983), the exception being the number of invertebrates. Coleoptera, principally Dor Beetles, were the most common prey item in the current study (50%), whilst Mikkola found insects as a group to be of little importance. Dor beetles are found in the dung piles of large herbivores and so their availability is expected to be high. The difference between Mikkola´s findings and these here may be related to the areas from where he collected pellets: if he collected them from an ungrazed enclosure the amount of dung present would have been low and, at the time of his study, 1971, ponies and cattle were actively removed from the Inclosures; however, he does not give site information.

The occurrence of field voles and bank voles in equal numbers is unexpected, since, although small numbers of bank voles were caught in the Forest woodlands, no field voles were caught. However, the territories occupied by the owls do have small areas of habitat, such as woodland fringe, which probably contain low numbers of voles.

If one compares the diet of the New Forest owls with data from other deciduous woodland (Southern 1954, 1969, Wytham Woods, Oxon)(table 11.4), similarities are found in the relative importance of prey: vertebrates constitute most of the diet, small rodents being the single biggest contributor. There are also seasonal changes in the importance of the different items: at both sites small rodents contribute less in the summer months, this being counterbalanced by a large increase in the offtake of moles in Wytham Woods. Within the New Forest no moles were recorded in the owls´ diet but a corresponding increase in the offtake of other vertebrates, principally birds, occurs (table 11.2).

As in Southern´s (1954) study others have shown the importance of invertebrate prey (Glue 1970; Hirons 1976; Mikkola 1983) with both Coleoptera and earthworms forming a large part of the items identified but, as shown here, not making a large contribution to the weight of prey. Hirons (1976) found that tawny owls returned to the nest with a large number of earthworms but during the current study no earthworms were found in the pellets. This is interesting as

Table 11.4 A comparison of the relative importance (by weight) of the major prey items in the winter and summer diet of tawny owls (Strix aluco) from within the New Forest and Wytham Woods, Oxon. (Wytham data calculated from Southern 1954).

	New Forest		Wytham Woods	
Prey	Winter	Summer	Winter	Summer
Rodents	85.6%	53.0%	65.5%	41.5%
Moles	0.0%	0.0%	7.5%	27.0%
Other Verts.	8.5%	43.3%	26.0%	29.5%
Beetles	9.5%	6.5%	1.0%	2.0%

Table 11.5 A comparison of the relative importance (by weight) of small rodents to the winter and summer diet of tawny owls (Strix aluco) from within the New Forest and Wytham Woods, Oxon. (Wytham data calculated from Southern 1954).

	New Forest		Wytham Woods	
Rodent species	Winter	Summer	Winter	Summer
Apodemus	60.5%	48.1%	26.2%	17.3%
Clethrionomys	12.5%	2.1%	27.5%	16.6%
Microtus	12.7%	2.8%	11.5%	7.6%

Packham (1984) showed earthworm densities within the Forest woodlands to be low, and it appears that the owls are compensating by the increased offtake of beetles. Of course, as dung density is high, the owls may in fact be selecting the most vulnerable prey.

Other prey items, such as birds and other mammals, did not contribute greatly to the number of prey items but are significant in their weight contribution, especially the birds (table 11.2). However, it is obvious that small rodents contribute the most and, as this component is 80% *Apodemus*, the actual offtake of these species may be quite high in comparison to Wytham Woods.

Comparison of the importance of small rodents between Wytham Woods and the New Forest reveals some interesting differences (table 11.5). In Wytham small rodents account for over one half of the winter diet, wood mice and bank voles being caught in equal amounts and accounting for most of this total. In the summer the total contribution made by rodents decreases by one third to 41.4%, again wood mice and bank voles being caught in equal amounts.

In the New Forest small rodents also constitute the major weight of prey but their importance is greater in both winter (85.6% Forest, 65.5% Wytham) and summer (53.0% Forest, 41.5% Wytham). However, within these totals the relative importance of mice and voles is quite different (table 11.5). In the winter months *Apodemus* contribute nearly three quarters of the rodents consumed by the Forest owls, both vole species accounting equally for the remaining rodent prey. In Wytham Woods during the winter, *Apodemus* and bank voles contribute almost equal amounts (40%) and the same ratios are maintained in the summer. In the Forest, however, the relative importance of *Apodemus* increases to just under 90%, both vole species again accounting equally for the remaining items. This shows that *Apodemus* are far more important to the diet of tawny owls in the New Forest.

It also suggests that they are either more abundant, more available to predation or that other prey are not present and so the owls have to feed on rodents.

In Wytham Woods variation in predation of bank voles and wood mice has been attributed to the habitats selected by the rodents and the feeding preference of the owls (Southern & Lowe 1968,1982): mice being caught from areas of reduced cover and the owls taking more wood mice than bank voles even when bank vole density is far greater than that of the wood mice (Southern & Lowe 1982). The reduction in rodent predation in Wytham Woods is partly attributed to reduced availability due to the vegetation and there also appears to be a wider range of prey available, the owls compensating for the reduced abundance and availability of the rodents by utilising other vertebrate prey. Although there was some alteration in the numbers of each prey species taken in the New Forest there is little variation in the range of items, this implies that they are not present; if they were available the owls, being faculative feeders, would take them.

Hirons (1976) demonstrated that tawny owl territory size is inversely related to small rodent abundance. Due to the absence of bank voles from the New Forest woodlands (Chapter 7) the total abundance of small rodents in these areas is approximately half that of the outside sites, and therefore one might expect territory sizes of the Forest owls to be greater than those in areas of higher rodent abundance. However, comparison of tawny owl territory sizes from within the New Forest with areas outside and from other studies (table 11.6) does not support this hypothesis. Territories are approximately the same size in grazed and ungrazed areas of the Forest and similar to those in outside sites and Wytham Woods.

This indicates that the owls are able to compensate in some way for the lower abundance of rodent prey. The

Table 11.6. Mean territory size per pair of Tawny owls (*Strix aluco*)in different areas of woodland. New Forest data (Hirons unpublished), Wytham Woods & Forest of Ae data from Hirons (1976).

Woodland	Mean territory size (ha)+/-SE	No. of pairs
New Forest (ungrazed)	23·4 ± 1·9	11
New Forest (grazed)	17·5 +2·1	10
Outside New Forest	17.9 ±1·9	12
Wytham Woods (Oxon.)	18·2 ±2·1	31
Forest of Ae	46·1 ±7·1	17

birds do capture both bank voles and field voles within the Forest, even though the former rarely and the latter never appeared in the trapped populations, but, as they constitute such a small proportion of the diet (table 11.2) and there is limited suitable habitat for them, their contribution to rodent abundance over the whole territory will be small. The range of alternative prey items, and their relative importance, taken by the Forest owls is less than in Wytham Woods (table 11.2) this being especially true in the summer months; therefore the birds are not compensating for the reduction in rodent abundance by increased use of alternative prey.

As the Forest owls do not have larger territories, and the importance of other prey is not markedly increased, there is an indication that in the Forest small rodents must be the most available prey all year, whereas in Wytham Woods it is suggested that the spring growth of vegetation (Southern & Lowe 1982) and low rodent abundance at this time reduces their availability and that the birds feed on other prey (Southern 1954). Due to large herbivore grazing within the Forest, the only spring growth of vegetation is bracken, but this is unlikely to afford the same type of cover to the rodents as brambles and other species so their physical availability to the owls may not be dramatically reduced. Their numerical availability is known to decrease at this time of year (Chapter 7) but, from the diet of the owls it appears that they are still quite vulnerable to predation. Of course, there is little information on the availability of other prey but owls, being faculative feeders, would take them if they were available. It appears from the restricted range of items identified, and the importance of the rodents, that alternative prey are not available. Therefore the owls have little choice but to feed upon the rodents.

In the winter months the overall importance of small rodents in the diet in both studies increases (table 11.4) at this time they are not only numerically very abundant (Chapter 7 & Southern & Lowe 1982) but the annual vegetation has died back and so they are physically more vulnerable. Within the Forest this vulnerability would be greater because when the bracken dies back there is no vegetation affording cover. This probably explains the greater increase in predation on both vole species in the Forest. One factor which is hard to measure is the activity of the rodents. Normally in the autumn and winter months there is abundant tree seed, but in this study there was not (Chapter 5). Therefore, the rodents may have been foraging more actively and for longer periods, which would again have increased vulnerability. It is difficult to comment on the importance of other prey at this time but it appears that prey items of any significant weight, such as birds, decrease in importance; this may be due to their decreased availability, or increased availability of the rodents, leading to greater predation on the most vulnerable prey.

The analysis of tawny owl diet therefore suggests that the birds are removing a considerable number of rodents, and this intense predation may be having a dramatic effect upon rodent demography. If, as suspected, wood mice are more available to the owls, their mean life expectancy should be less than in habitats affording greater cover. Examination of cohort survival (Chapter 9) did not reveal any significant differences in survival between age groups within sites nor between cohorts from grazed and ungrazed sites. From the findings of the owl diet analysis this is not expected.

This result may be due to the limitations of such a small data set used in the survival analysis, but may also indicate that other factors played an important role in wood mouse survival during the course of the study. For example little is known about the effects of other predators; in the Forest Tubbs (1982) suggested there are few other small mammal predators, whilst in other woodlands (e.g. Wytham (King 1980; Southern & Lowe 1982)) there are mustelid predators as well as tawny owls. The low autumn tree seed crop (Chapter 5) has been identified as one factor but others, such as the weather, may have played some part. During the summer months it is not clear what other factors may be acting upon the populations.

CHAPTER 12

GENERAL DISCUSSION

12.1 INTRODUCTION

The New Forest offers a range of vegetation communities for small mammals, some, such as deciduous woodland and heathland, covering very large areas, whilst others, such as valley bogs and arable land being localised, and small in size. The New Forest therefore has the potential to contain a wide range of small mammal species.

Large herbivores have a dominating influence upon vegetation communities and may affect all aspects of the community and its environment. Within the New Forest intensive large herbivore grazing has been maintained for hundreds of years, and many of the Forests vegetational communities have developed as a result of this long history of grazing (Putman *et al.* 1981). In particular the structure of the woodlands and grasslands reflect the impact of large herbivores. Alteration of vegetation characteristics by large herbivores affects habitat suitability for many other species and, depending upon their preference, the effect may be a reduction or increase in habitat suitability. For example, grazing in grasslands reduces suitability for some invertebrate species and results in alteration of diversity and abundance (Holmes, Smith & Johnston 1979; Hutchinson & King 1980), but the creation of short grass pastures by cattle increases its suitability for, and use by, european hares (*Lepus europeus*) (Frylestam 1979). With knowledge of the habitat requirements of a species it is therefore possible to predict the effects of large herbivore grazing upon the composition of other fauna.

For small mammals the major effect of grazing is probably the reduction in living standing crop and structure of vegetation *i.e.* the amount of cover afforded. This is the factor identified by most workers as being of primary importance to small rodents (Hansson 1978; Gurnell 1985). One would therefore expect that alteration of vegetation by the removal of shelter would affect the diversity and abundance of rodents found within the habitat by exclusion of those species preferring cover, and alteration in abundance of those species remaining due to a reduction in habitat suitability. This is the finding of many previous studies (*e.g.* Birney *et al.* 1976) and this study.

12.2 DECIDUOUS WOODLAND

It is clear that, of the vegetation types sampled in this study, the deciduous woodlands contain the largest populations of small rodents. Previous studies on the effects of modification of woodland habitats have shown that a reduction in field and shrub layer vegetation leads to a loss of those species preferring cover and an overall reduction in diversity (for birds see Casey & Hein 1983; Bock & Bock 1983; for small mammals see Borrecco *et al.* 1979; Halvorson 1982; Martell 1983a; Singer *et al.* 1984). Those species that have more specialised habitat requirements are often totally excluded, the more generalist ones being restricted in abundance and performance.

Gurnell (1985) has recently reviewed the ecology of woodland small rodent communities and notes that deciduous woodland habitat can contain up to seven small rodent species in Britain (more in central Europe), but that some species, such as the common dormouse (*Muscardinus avellanarius*), have localised distributions (Arnold 1984) and specific habitat requirements. The successional state of the woodland is therefore most important, habitat structure altering as succession progresses. In mature woodland two species, wood mice and bank voles, are the most commonly found rodents, with yellow necked mice being found mainly in the south-east of England. However, these species exhibit habitat preferences related to their activity patterns and diet (Chapter 1, section 1.3). In summary, bank voles show a strong preference for woodlands with a dense field and shrub layer, such as those characteristic of the mid successional stages; wood mice and yellow necked mice appear to have no preference for cover in these lower strata (but see Chapter 1, section 1.3.1). However, these microhabitat associations do vary in the presence of competitors (Chapter 1, section 1.3.4).

The comparison of grazed New Forest woodlands, outside sites with low levels of grazing and the ungrazed New Forest site clearly showed that a long history of grazing has led to an almost total loss of shrub layer, a field layer that is kept very short and a lack of regeneration in the New Forest (Chapter 4). From this, and the knowledge of small rodent habitat preferences, it is reasonable to predict that species with a preference for dense ground cover will be absent or in low numbers in the grazed woodlands due to habitat unsuitability. This is exactly what was found in this study. The intensive trapping of the woodland sites revealed that small rodent diversity was lower in the grazed New Forest woodlands than either the low grazed or ungrazed sites. There is some indication that diversity increases as grazing intensity decreases, this being due to the almost total absence of bank voles, the species which prefers cover, from the grazed woodlands; the reduction of cover through grazing must be the cause of absence of this species.

Habitat modification also affects other species which show a preference for ground cover; shrews were found to be absent from the grazed woodlands, whilst they were often caught in the ungrazed Denny Pen and at Howse Copse and led to a greater small mammal diversity in these ungrazed sites (Chapter 7).

An important component of diversity is the equitability of species. In the two sites, Howse Copse and the ungrazed Denny Pen, wood mice and bank vole populations were of similar sizes. However, within the other low grazed outside site, Pound Bottom Wood, bank vole numbers were very variable and generally at lower levels than wood mice. Although total large herbivore habitat use, as measured by faecal accumulation, was found to be similar for this and the New Forest sites, the actual grazing pressure in the latter was greater due to the presence of large numbers of ponies (Chapter 3). The vegetation analysis revealed this site to be very similar to the two Forest plantations, Island Thorns and Backley Incs, except for a greater biomass of grass in the field layer and of bracken in the shrub layer. This probably afforded a more suitable habitat for bank voles and so they were able to attain and maintain greater numbers than the Forest vole populations.

Although populations of wood mice were present at all sites, they were more abundant in Howse Copse and the ungrazed Denny Pen than the other sites for the duration of the study (Chapter 7). This may indicate that, although the grazed woodlands were not unsuitable for this species, the populations were not attaining levels seen in the areas subjectively assessed to be more suitable. However, this comparison is complicated by a number of factors. Previous studies (e.g. Kikkawa 1964) have shown how variable wood mouse populations can be over quite small areas, and the demographic characteristics of all wood mouse populations within this study were similar (Chapter 8), and the same as those recorded elsewhere. Therefore the variability in population size between grazed and ungrazed sites might not be due to differences in habitat suitability but due to local variations in population fluctuations. Also, comparison of wood mouse population size with data from the National Small Mammal Survey conducted over the same period as this study (Chapter 7) revealed that, at the start of this study in 1982, the number of mice caught in deciduous woodlands was very low throughout the country. Flowerdew (unpublished) suggests poor autumn seed crops and bad weather in 1982 were responsible for the initial low numbers, and increases in latter years of the Survey sites are correlated to better seed crops in those years, the rate of recovery of populations being different in various study areas. Therefore differences between the populations in grazed and ungrazed woodlands may have been masked by the low sizes of the populations. Only more long term studies comparing populations within grazed and ungrazed habitats will clarify differences between areas.

Of course habitat factors other than vegetation cover are also important to small rodents. A number of workers have shown that, after a good autumn tree seed crop, overwinter survival of small rodents is good and that populations are larger in the following year (e.g. Smyth 1966). In the autumns of 1982 and 1983 the tree seed crop was poor at all sites in this study (Chapter 5). This was probably a major factor contributing to the small population sizes seen in this study as compared to others. Although all populations exhibited well-documented seasonal changes in abundance and population structure, leading to high autumn populations, the low overwinter survival caused fast declines in numbers (Chapter 9) to levels from which recovery was very slow. The data suggest that populations of wood mice were gradually increasing in the outside sites (Chapter 7, figure 7.3) but, again, the study was too short to prove this.

As the autumn tree seed crop is so important to small rodent populations, one can suggest that all populations under study here were being supressed by a shortage of food, differences between population size and structure of grazed and ungrazed areas being masked by the overriding influence of this. This might explain why the analysis of the woodland rodent population structure revealed no differences between populations in the different areas, whereas other studies have revealed demographic differences between rodent populations in 'sub-optimal' and 'optimal' habitats, such as poor juvenile survival (e.g. Martell 1983a).

Although overwinter survival and population success of wood mice can be correlated with autumn tree seed crop, the fact that no differences were found in survival of other groups throughout the year is harder to explain. Measurement of survival here cannot distingiush between mortality and dispersion (Chapter 9), so, although minimum survival is not different for age and sex classes and between sites, the reason for the loss may be different. Again, only continued long term studies will clarify this.

There are various other aspects of habitat modification by large herbivores that could be investigated. This study has examined the effects on supply of the autumn tree seed crop but this is only one food source for small rodents. As has been mentioned previously (Chapter 1, section 1.3.2) woodland small rodents are not dietary specialists and exhibit seasonal changes in their diet in relation to food availability. Large herbivore grazing not only alters the physical structure of the habitat but may also be altering food availability. This may be in the form of direct competition with the more herbivorous bank voles, or indirect competition with the omnivorous wood mice by reduction in habitat suitability for invertebrates, which form an important part of the diet in the spring and summer months (Watts 1968).

12.3 HEATHLAND

The sampling intensity, and hence number of animals caught, on the heathland study sites was smaller than that in the deciduous woodlands, but the differences in diversity and abundance of small rodents on the heathlands between

Forest and adjacent sites (Chapter 7) are probably the most striking examples of how habitat modification may affect other species. The heathlands adjacent to the Forest hold permanent populations of wood mice and populations of harvest mice; on the Forest heaths only wood mice were found, and this was only on two occasions (one individual at each, out of seven trapping sessions in the two and one half years of the study). Total small mammal diversity (including both rodents and insectivores) was also greater in the adjacent heaths as shrews were caught at these sites on a number of occasions.

The vegetation study of the heathlands revealed adjacent areas to be older, have a greater plant diversity and be structurally more complex than the Forest heaths (Chapter 4). This is, however, thought to be largely due to the differences in management rather than grazing since both this study (Chapter 3), and previous ones (Putman _et al._ 1981), show this vegetation is not extensively used by large herbivores. Burning of heathland is more regularly practised within the New Forest, and the reduced grazing and burning over the adjacent heaths means the vegetation affords a suitable habitat for small rodents and possibly insectivores. The vegetation offers a high degree of cover and it is probable that food supplies are more plentiful, the greater cover of _Molinia_ increasing seed supplies and the nature of the vegetation leading to a greater invertebrate biomass.

The more complex vegetation structure and decreased disturbance from large herbivores is probably most important for harvest mice. These favour areas of thick vegetation and avoid areas of excessive disturbance by livestock (Harris 1979). The absence of this species from the New Forest trapping results is certainly a direct effect of the management of the heathlands, but its absence from the trapping results does not mean it is absent from the Forest. There a many areas, such as railway embankments and farmland which, although small in area, would be suitable for this species. Also, Hirons (1984) has recently found that harvest mice comprised 15% of the diet of kestrels resident in the Forest, though where they were caught is not known.

12.4 ACID GRASSLAND

The short New Forest grasslands are not ideal habitats for small rodents, especially field voles which exhibit a strong preference for thick vegetation. As expected, very few rodents were found in this habitat, and only at times when bracken cover was present, and this is certainly due to the intense large herbivore use of the areas and the resulting short vegetation. At present large herbivore densities there is no opportunity for this habitat to become suitable for such species. However, the radio-tracking and trapping at the Matley Wood site revealed that wood mice do make use of the grassland habitat, but were concentrated in areas adjoining the woodland. As wood mice move to sources of food (Flowerdew 1972), it is not clear whether the trap-defined movements were in response to the input of food via the traps or related to other factors such as movement to natural food sources or dispersion. The limited radio-tracking did reveal that the mice make full use of the grassland; it is suggested however that they are not resident in the habitat but possibly in others such as the gorse.

12.5 PREDATION

This, and previous studies, have shown how important cover is to bank voles and they are obviously absent from the grazed woodlands because insufficient shelter is available; as discussed in Chapter 1, section 1.3.5, this is related to the activity of this species and their susceptibility to predation. Some studies suggest that, in the presence of bank voles, wood mice have no preference for vegetative cover but that in their absence, wood mice do reveal such a preference (Montgomery & Bell 1981). This preference for cover would be beneficial to the mice as it would decrease their vulnerability to their main predators within woodlands, the tawny owl. Within the New Forest woodlands, it has been found (Chapter 11) that the owls prey extensively upon wood mice, and, even though wood mouse and total rodent abundance is low they form the major part of the birds' diet. As large herbivore grazing has removed cover the vulnerability of the rodents to tawny owls must be increased (a similar situation suggested for predation on reptiles (Janzen 1976)), or the owls must spend a larger proportion of their time catching the rodents. The first factor certainly occurs and the latter is likely as there is little other food available to the owls.

The indication that predation pressure on wood mice is high in the Forest woodlands suggests that survival may be reduced due to mortality. If one assumes predation pressure not to be so high in the areas with greater ground cover, one would expect survival there to be greater, but it is not (Chapter 9) and therefore other factors must be playing an important role; this is, however, where one cannot distinguish between mortality and movement except to say that, due to predation mortality is likely to be higher in the grazed Forest woodlands.

The effects of predation upon small rodent demography are variable but, as noted previously, in some systems predators can remove almost all the annual small rodent production (Erlinge *et al.* 1983), and removal is greater at low rodent densities (Ryskowski *et al.* 1973). If the same factors are acting upon New Forest wood mouse populations then predation is probably contributing to maintaining populations at low levels which is thus a direct result of habitat modification by large herbivores. It is, however, impossible to separate the effects of predation and autumn food supply because insufficient data are available and the latter is thought to be responsible for the poor survival of animals at all sites.

If wood mice have been found to select areas of cover in the absence of bank voles (Montgomery & Bell 1981), one might expect mice in the Forest to exhibit the same behaviour, so decreasing their vulnerability. However, the field and shrub flora of the Forest woodlands are sparse and evenly distributed, providing little cover, and it is not surprising to find that captures about the Forest trapping grids were regular (Chapter 10), there being no cover for the animals to select.

This study has not investigated the diet of predators on the New Forest heathlands but there is some information available indicating the levels of predation pressure. Goddard (1981,1984) investigated the diet of reptiles in the New Forest heathlands, studying mainly smooth snakes but with small samples of adders and grass snakes (Natrix natrix). He found that nestling small mammals, primarily shrews, were the main dietary item of smooth snakes and adders but found only one mammalian prey item in the grass snakes. A more detailed study of the diet of adders in a similar habitat in Dorset (Prestt 1971) also revealed adders to feed extensively on small rodents.

Goddard (1984) compared smooth snake densities at three heathland sites, one enclosed and ungrazed and two unenclosed and grazed, and found the highest density of snakes in the grazed regenerating area. This study has revealed small mammals to be most abundant in the unmanaged regenerating habitats. Food availability is an important habitat component and so the abundance of prey is probably one explanation of Goddard's findings. It is also, therefore, unlikely that snake densities would be high on the large tracts of managed Forest heathlands.

In addition to predation from reptiles, small mammals on heathlands are also susceptible to predation by kestrels. Although there is some information on the diet of kestrels within the Forest (Hirons 1984), it has not been clarified where these birds catch their prey. They are able to cover large areas within and outside the Forest and so a wide range of vegetation types is available to them; as noted above, harvest mice form a large proportion of the diet but were not trapped on the Forest study sites.

The data on kestrel diet are interesting because they reveal these birds to be preying heavily on lizards, this must be in compensation for the scarcity of their most common prey, field voles, from the Forest, which has occurred through grazing altering grasslands and management altering heathland habitats. This makes an interesting comparison to the diet of the tawny owls where modification through grazing has reduced abundance of their main prey, bank voles. However, it is suggested, above, that the reduction in cover by grazing has been beneficial to the owls by increasing the availability of wood mice. It is therefore suggested that large herbivore grazing and management not only affect the distribution of small rodents and small mammals through habitat modification, but indirectly influence the distribution of reptilian predators and the diet of avian, predators, and may subsequently be affecting other ecological aspects of these species. This opens a completely new area needing study, some of which is currently in progress.

12.6 SUMMARY

Although the New Forest is a conglomerate of vegetational communities, the maintenance of large herbivore grazing and management practices has led to these communities generally being unsuitable for small mammals through the reduction in vegetation cover. It is therefore not surprising that this study has revealed a low small rodent and small mammal diversity and low abundance within the grazed New Forest habitats compared with ungrazed areas.

Within the deciduous woodlands, large herbivores are responsible for the low plant diversity and reduced vegetation cover which has led to the absence of species such as the bank vole and insectivores. Small rodent populations within these study areas were all at very low levels at the beginning of this study, and the low autumn mast production in both 1982 and 1983 obviously had a dominating influence on all populations, by reducing overwinter survival and hence population increase. Therefore, the study was unable to identify differences in the sizes of rodent populations or demographic aspects as reported elsewhere for species in ´sub-optimal´ habitats. In years of high mast production large herbivore offtake may be very high and it is suggested that this is a possible route for direct interaction between small rodents and these grazers, and one which may lead to restriction of rodent success in these woodlands.

Large herbivore grazing of grassland habitats has made them unsuitable for grassland small rodents and other small mammals, but it is apparent that wood mice do use these areas. Management practices are probably more responsible for the alteration of heathland habitats than large herbivore grazing. As with the New Forest woodlands, habitat suitability of Forest heathlands for small rodents and insectivores is reduced and has led to very low numbers being present.

It is suggested that the removal of vegetation cover has led to the increased vulnerability of woodland small rodents to predation. Although the overall number of predators is small, the actual offtake by one species, the tawny owl, is high in comparison with that found in other studies. It is not clear if this is due totally to increased wood mouse availability or the lack of other prey but this high level of predation probably restricts small rodent population increases within these woodlands. Examination of results from other studies suggest that the reduction in suitable habitats for rodents throughout the Forest might also be affecting the ecology of other predators.

This study has quantified the subjective observations that large herbivore grazing does indirectly influence small rodent distribution, diversity and abundance within the New Forest. There is still a gap in our general knowledge of the ecology of small mammals in managed areas and the New Forest offers an ideal habitat in which to perform such studies. However, to give quantitative information on the effects of management these studies will need to be long term. Although there have been a number of studies on other areas of the Forests ecology, there are still many aspects of the influences of herbivores upon the Forest, and the resulting effects on other species that could be examined, and there is surely a case for concurrent multidisciplinary studies. In doing so a more complete picture of the ecology of this unique area can be developed to aid in the future management and conservation of the area.

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APPENDIX 1

LARGE HERBIVORE FAECAL ACCUMULATION

Table A1.1 The monthly large herbivore faecal accumulation within deciduous woodland study sites. Sites 1 to 4 Open New Forest, and site 5 outside New Forest. All sites were visited once a month and all faeces found recorded and removed. The 1982 data are total accumulation of faeces in six 100m^2 (10m x 10m) quadrats. 1983 data are total accumulation of faeces in seven 95m x 1m transects.

Site & Species						Woodland						
1982	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Ponies												
1.Island Thorns Inc	3	3	0	0	0	3	0	0	1	0	3	1
2.Backley Inc	-	-	-	-	-	0	0	0	0	1	0	0
3.Matley Wood	3	3	0	0	0	3	0	0	1	0	3	1
4.Sloden Inc	0	0	0	0	0	0	0	0	0	3	1	0
1983	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1.Island Thorns Inc	2	2	3	2	1	0	0	0	0	0	1	0
2.Backley Inc	0	1	1	3	0	0	0	0	0	0	1	0
3.Matley Wood	4	6	4	5	5	3	4	-	-	-	-	-
4.Sloden Inc	2	5	1	0	2	0	1	2	1	1	3	2
Deer												
1983	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1.Island Thorns Inc	1	6	0	0	0	0	3	0	0	1	0	1
2.Backley Inc	-	-	-	-	-	4	3	2	2	8	5	4
3.Matley Wood	0	0	0	0	0	1	0	0	0	1	2	0
4.Sloden Inc	0	0	0	0	0	0	0	0	0	0	3	0
5.Pound Bottom Wood	-	-	-	-	-	0	0	0	0	1	0	1
1983	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1.Island Thorns Inc	7	8	0	1	1	0	0	0	0	1	0	0
2.Backley Inc	7	8	6	4	3	4	2	2	2	0	3	3
3.Matley Wood	2	0	1	0	0	0	0	-	-	-	-	-
4.Sloden Inc	7	3	3	0	2	1	2	0	3	3	1	2
5.Pound Bottom Wood	10	14	2	0	2	1	1	1	2	0	1	1

Table A1.2 The monthly accumulation of large herbivore faeces within six 100m^2 (10m x 10m) quadrats on <u>Calluna</u> heathland within the New Forest (sites 1 to 4) and outside the New Forest (site 5). Data were collected in the same manner as for woodlands.

Site & Species	Heathland 1982											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Ponies												
1.Island Thorns Inc	1	1	0	0	0	2	3	3	0	0	2	0
2.Backley Inc	-	-	-	-	-	2	0	0	0	0	0	1
3.Matley Wood	0	6	7	5	0	0	0	0	2	0	0	0
4.Sloden Inc	0	0	0	0	0	0	0	0	0	1	0	0
Cattle												
1.Island Thorns Inc	0	0	0	4	0	0	0	0	0	0	0	0
3.Sloden Inc	0	0	0	0	0	2	0	0	0	0	0	0
Deer												
2.Backley Inc	-	-	-	-	-	0	1	1	0	5	3	6
3.Matley Wood	0	0	0	0	0	0	0	0	1	0	0	1
5.Pound Bottom	0	0	1	1	0	0	0	1	3	1	0	0

APPENDIX 2

TRAPPABILITY AND THE USE OF EAR-TAGS

2.1 INTRODUCTION

Demographic studies of small rodent populations require a proportion of the animals to be caught at least once before any estimation of population size or structure can be made. Most studies assess populations by Capture Mark Recapture (C.M.R.) methods employing traps of various kinds, usually some form of live capture box or pitfall trap (Twigg 1975b), whereas for non C.M.R. studies kill traps may be used.

All data obtained is therefore highly dependent upon trap efficiency; unfortunately each trap has it´s own limitations, and different types of trap sample populations differently. For example, Grant (1970b) found Longworth traps (Chitty & Kempson 1949) to be more efficient at trapping heavier species; these traps rely upon the animal tripping a treadle which a heavier animal is more likely to do. There are of course many types of trap available but they all have similar practical limitations.

The actual trappability of species, for example, bank voles (Andzezewski, Petrusewicz & Waszkiewicz-Gliwicz 1967; Gliwicz 1970), varies between individuals and with age, the juveniles being retrapped less often than the adults; it also varies with reproductive condition (Jensen 1975), non reproductive sub-adults and postreproductive adults being less trappable than reproductive animals. These responses to traps are behavioural (Stoddart 1982) and mechanical. Pitfall traps are simple to use and, as they do not rely upon working mechanisms to trap the animals, they catch greater numbers and a wider range of species (Williams & Braun 1983). Pitfall traps have been found to sample wider cross sections of M.townsendii (Beacham & Krebs 1980) and

M.pennsylvanicus (Boonstra & Rodd 1984) populations than box traps, with juveniles being caught less often in the latter, but box traps were more successful at catching the larger M.pennsylvanicus. This may be due to their ability to jump higher from pitfalls or to differences in the depth of trap used in each study. Although Chelkowska (1968) demonstrated the same sampling differences for bank voles it was also found that pitfalls caught fewer wood mice, again probably because of their ability to jump.

Non-random sampling of rodent populations is often further complicated by climatic factors. The capture of mice is known to decrease on moonlit nights (Marten 1973) and increase during periods of heavy rain (Sidorowicz 1960), although Gurnell (1976) found the opposite response to rainfall from wood mice in Britain. Extremes of climatic changes may also cause trap deaths, especially in bank voles (Perrin 1975). This is an important consideration if one is using C.M.R. techniques but, unlike the effects of climate and efficacy, trap deaths can be reduced.

It should therefore be apparent that any study of rodents relying on trapping is dependent upon factors that one has little control over, but, with care, one can increase trap efficacy and adequately sample populations. Care in the positioning of traps (Gurnell & Langbein 1983) and the use of bait clearly enhances the probability of the capture of small rodents in box traps (Chitty & Kempson 1949); and the practice of prebaiting further increases the number caught (Pelikan, Zejda & Holisova 1972; Gurnell 1980) and the rate of capture (Babinska & Bock 1969) but it can lead to trap addicted animals and immigration which affects density estimates from C.M.R. studies.

Obviously for C.M.R. studies animals caught have to be identifiable if recaught which requires marking them in some manner. For small rodents there are a number of methods available, some permanent and some temporary, examples being toe-clipping, fur-clipping, marking with dye, leg-ringing or ear-tagging (Twigg 1975a). The handling of animals for marking may alter their behaviour and thus their response to traps. Hirons (pers.comm.) found that European woodcock (Scolopax rusticola) fitted with small radio transmitters altered their behaviour for approximately 24 hours before returning to normal behaviour patterns. It would seem reasonable to suggest that handling and marking of small rodents may affect their behaviour, albeit temporarily, thus altering their trappability.

As mentioned above studies of small rodents often include some attempt to estimate population density, and the behavioural responses of the animals may affect such estimations. There are in fact many different methods for estimating population density from trapping results (Seber 1973) and this area is still the focus of much attention (Hilborn, Redfield & Krebs 1976; Renzulli, Flowers & Tamarin 1980; Bondrup-Nielsen 1983 and Nichols, Hines & Pollock 1984). As the name suggests, Capture Mark Recapture methods rely on all or part of the marked population being recaught and, therefore, the effects of trapping technique and behavioural response of the animals may affect both the initial capture and recapture of animals, so introducing a bias into any density estimation.

There are various assumptions underlying population estimates from C.M.R. studies; Southwood (1978) lists four which underlie most methods:

1) The marked animals are not affected (in behaviour or life expectancy) by being marked and the marks will not be lost.

2) The marked animals become completely mixed in the population.

3) The probability of capturing a marked animal is the same as that of any member of the population; that is the population is sampled randomly with respect to mark status, age and sex *i.e.* there is equal catchability. This

assumption has two aspects: firstly that all individuals of the different age groups and of both sexes are sampled in the proportion in which they occur; secondly, that all the individuals are equally available for capture irrespective of their position in the habitat.

4) Sampling must be at discrete time intervals and the actual time involved in taking the samples must be small in relation to the total time.

Southwood (1978) lists four further assumptions: two for the Lincoln Index (Lincoln 1930):

1) The population is a closed one or, if not, immigration and emigration can be measured or calculated.
2) There are no births or deaths in the period between sampling or, if there are, allowance must be made for them.

and two for the more complex stochastic methods where either migration, natality or mortality or all three are occurring and where these methods require a series of sampling occasions:

1) Being captured one or more times does not affect the animal´s subsequent chance of capture. This is a further extension of the assumption of equal catchability, number (3) above.
2) Every marked animal has the same probability of surviving through the sampling period. This means that if mark status is anyway related to age then mortality must be independent of age; it must act randomly on the population and some individuals must not be at greater risk.

Obviously no method of population estimation is perfect and most have their own particular limitation, however, as all methods rely upon the recapturing of animals, if the number of animals caught or recaught is small, as in the present study, any estimate is subject to wide variation (Blower, Cook & Bishop 1981). In studies where data are scarce and there is failure to fulfil the underlying assumptions of the model the error estimation will be amplified.

Recently Fairley (1983) has suggested that toe-clipping and leg-ringing have a short term effect on wood mouse retrappability: newly marked animals being less likely to be caught the following day than those marked previously. In this study a combination of toe-clipping and ear-tagging was used on the populations of mice and voles. In the light of Fairley's findings, and knowledge of how density estimations may be affected by such behavioural changes, it was decided to examine the retrappability of ear tagged and toe-clipped animals within and between trapping sessions. In this case, ear-tagged animals were also toe-clipped so differences in trappability between animals toe-clipped and those toe-clipped with ear-tags are being examined.

2.2 PRELIMINARY STUDY ON THE USE OF EAR-TAGS

Before ear-tags were employed in the main study, an examination into the success of ear-tags and the retrappability of these animals in comparison with toe-clipped animals was performed. This preliminary study was carried out within the grounds of Southampton University at Chilworth (G.R: 402 183) just north of the main campus. The study area was a small block of mixed deciduous woodland dominated by mature oak with an understorey of birch and almost 100% cover of brambles on the woodland floor.

A standard grid of 7 x 7 trap stations with two Longworth traps at each point was established within the woodland in January 1982 and was trapped every four weeks until December 1982. Trapping routine varied slightly for each period but was always preceded by 24 hours prebaiting; trapping then followed for at least four days, and sometimes five. All animals caught were subjected to the examinations previously described (Chapter 6). After examination, every animal was toe-clipped for individual recognition; every other animal of each species caught was then given a small metal ear tag using a pair of modified fine nose pliers as applicators (Plate A2.1) (tags were Monel Metal size 1 tags supplied by the National Band and Tag Co., Kentucky). Animals were then released as normal. Due to the small number of captures at each session it was not possible to alternate tagging sexes.

2.2.1 RESULTS

A total of 98 wood mice, 78 bank voles and 6 yellow necked mice were caught in 9 trapping sessions between January and December 1982, 50% of which were given ear-tags. Too few yellow necked mice were caught to be included in the comparison of tagging and retrappability. As trapping data came from individual trapping sessions a 2 way ANOVA was performed on the data for mice and voles, examining differences in time and capture frequency, using type of tagging as replicates for each cell. To make use of all available data only the first three trapping days were used in the analysis. These two tests proved not to be significant (mice:F ratio =0.0, d.f. 3,16 $p>0.05$ and voles: F ratio = 0.22, d.f. 3,16 $p>0.05$). Therefore these data for individual time periods were pooled and a G-test of heterogeneity performed comparing the frequency of capture for ear and toe-tagged animals of each species; this test showed there to be no difference in the the frequency of capture of toe-clipped and ear-tagged animals for each species (mice:G=3.29 d.f. 3 $p>0.05$ and voles :G=3.49 d.f. 3 $p>0.05$). From these results it was concluded that frequency

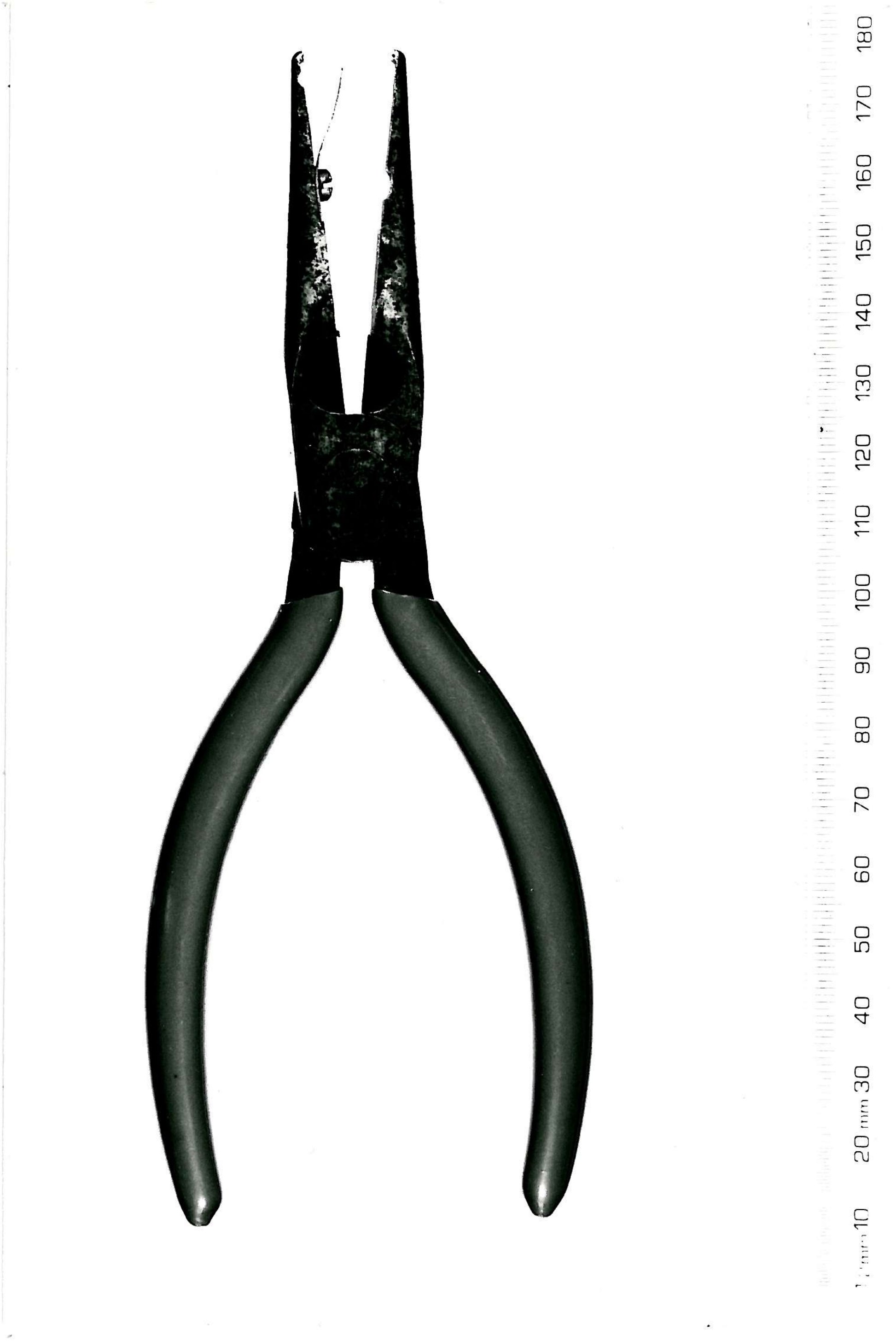


Plate A2.1 Modified fine-nosed pliers used to apply the Monel Metal ear-tags of capture within a session for both species was not affected by the mode of tagging.

2.3 EFFECTS OF EAR-TAGGING ON RETRAPPING WITHIN AND BETWEEN SESSIONS

The main questions being examined here are:

1) Is there any difference in the short term retrapping of newly ear tagged and toe-clipped mice and voles i.e. recapture one day and recapture two days later?.

2) Is there any difference in the retrapping of these animals in the next session?.

If the two above questions prove negative then the data for ear-tagged and toe-clipped animals can be combined and then all data examined to study the short term effects of toe-clipping and ear-tagging on retrappability.

Two sets of data are presented: that from the Chilworth study and that from the main study after the usefulness of ear-tags had been assessed. The definitions of "new" and "old" animals are:

1) New animals are those caught for the first time. To be included in the day 1 recapture group they must have been caught initially the previous day. To be included in the day 2 recapture group they must have been caught two days earlier.

2) Old animals are those caught new at the previous session. Therefore animals are excluded after one session of recaptures.

2.3.1 RESULTS

Effects of ear-tagging and toe-clipping upon recaptures of new and old animals

The monthly data for each session from each site were pooled and the retrappability of ear-tagged and toe-clipped animals compared using Wilcoxon´s matched-pairs test. For both wood mice and bank voles this resulted in no significant differences between the retrappability of the two classes (mice:$T = 41$, N used $=17$, $Z = -1.6805$ $p= 0.14$; voles:$T = 1$, N used $= 6$, $Z = 0.1048$ $p=0.46$). It was therefore felt that the retrapping data for ear-tagged and toe-clipped animals could be pooled for analysis of differences in recapture of ´new´ and ´old´ animals.

Retrappability of new and old animals

The monthly data for all sites were pooled and treated in the same manner as above. For bank voles no significant difference was found between the retrappability of old and new animals. The same analysis of the wood mouse data revealed a significant difference between retrapping of the two groups of animals ($T = 30$, N used $= 18$, $Z = -2.4170$, $p<0.02$). As these were pooled, day 1 and day 2 recapture data (see above), the data were split into these two recapture groups and again tested for differences in retrappability between new and old animals. Both these tests gave no significant differences within the two recapture groups (Day 1: $T = 1$, $N = 4$, $Z -1.4605$ $p=0.07$; Day 2: $T = 3$, $N = 4$, $Z = -0.7303$ $p=0.23$).

Success of ear-tags

Of 234 wood mice tagged with ear-tags 125 were recaught in subsequent trapping sessions and 9 (7.2%) of these had lost their tags. On average those tags were lost after 1.6 months. Obviously fewer bank voles were tagged, 59 in total, and of these 35 were recaught in subsequent sessions, again 9 (25.7%) had lost their tags but the average time before loss was 3 months.

Duration of residence of animals

The data from Chilworth and the main study were combined to enable comparison of duration of residence (see Chapter 9) for ear-tagged and toe-clipped wood mice and bank voles. Duration of residence was compared using a Mann Whitney U test, both species sexes being tested independently and then, as no significant differences were obtained, combined to compare overall residence of animals.

The results of these tests are presented in table A2.1 and show that no significant differences in duration of residence between ear-tagged and toe-clipped animals was found.

2.4 DISCUSSION

2.4.1 Use of ear-tags

The use of ear-tags in small rodents is not new (Scott 1942). Fullager & Jewell (1965) compared the effectiveness of a number of tagging methods and found no problems with them in the laboratory but in the field trials it was found that whilst the tags were retained for the two weeks of the study, four months later all previously tagged animals had lost their tags. Leg-rings have been used in a number of predation studies where workers have wished to identify individual prey (e.g. Southern & Lowe 1968). However, problems with the fixing of rings and of subsequent serious injury to the animals can occur (Fullager & Jewell 1965). In this study some problems were initially incurred until the new type of applicator was developed and then the tags were easily placed into the base of the ear and, as the results show, very few were lost.

2.4.2 Trappability

Analysis of the retrapping data revealed no change in trappability due to ear-tagging. Fairley (1983) suggested that toe-clipping or leg-ringing decreased the short term retrappability of wood mice; there is little evidence in this study to support this hypothesis but this may be due to the small sample size. Some recent unpublished work by Le Boulenge and co-workers using "Michel" clips suggested that it was the toe-clipping of bank voles and wood mice that resulted in altered behaviour rather than the ear-tagging. If this were the case in this study, one would not expect a difference between the two groups of tagged animals as they were both toe-clipped.

2.4.3 Duration of residence of tagged animals

No significant differences in the duration of residence between the two groups of animals were found in this study. Due to the small sample sizes it is not possible to separate animals on the basis of season, but, as no differences were found in duration of residence between seasons in the main study (Chapter 9) it is suggested that this effect would be minimal on this analysis. This finding is quite important when one considers the basic assumptions underlying C.M.R. population estimates where one assumes that the marking of an animal does not affect it in any manner that will alter its trappability. Recently Pavone & Boonstra (1985) have reported that survival of male M.pennsylvanicus was reduced, but not significantly, by toe-clipping which is important since altered survival obviously alters the trappability of an animal.

From the results of this investigation it is suggested that small ear-tags are a successful method of markng small rodents. It is suggested that this method of marking has no adverse affect on the retrappability of animals. Therefore one is justified in treating the recapture data for both groups of animals together as is done for the analysis of population size (Chapter 7) and the following estimations of population density.

Table A2.1 Mann-Whitney U tests on duration of residence of toe-clipped and toe-clipped with ear-tags A.sylvaticus and C.glareolus.

A.sylvaticus	Males	U = 37.0	p = 0.8906
	Females	U = 87.0	p = 0.0605
	Combined	U = 285.5	p = 0.2063
C.glareolus	Males	U = 52.5	p = 0.8600
	Females	U = 88.0	p = 0.6448
	Combined	U = 282.5	P = 0.7256

APPENDIX 3

ESTIMATION OF DENSITY OF WOODLAND RODENT POPULATIONS

3.1 INTRODUCTION

There are many methods available for estimating population density from capture mark release recapture studies (Seber 1973) and, although each method is subject to some specific form of limitation, as they rely upon the ratio of marked to unmarked animals if the number of animals caught is small, as in the present study, any estimate is subject to wide variation. Thus analysis to date has been based on direct estimates of actual numbers of animals known to be alive in the study area. However, in order that the reader may make comparisons between these results and those of other published studies it was decided to estimate density of the wood mouse and bank vole populations within the deciduous woodlands.

As different studies have used a variety of methods of estimation, five of the most commonly used have been applied to the data from this study. These are:

a) Calendar of Captures (Petrusewicz & Andrzejewski 1962).
b) Mean Petersen estimate (Seber 1973).
c) Baileys triple catch (Bailey 1951,1952).
d) Haynes modified Lincoln Index (Hayne 1949).
e) Jolly´s stochastic method (Jolly 1965).

Estimation of actual population number from the Mean Petersen, Bailey´s triple catch and Hayne´s method were performed on data from each trapping week (three trap nights) for the monthly and seasonal numbers of rodents caught. Jolly´s method was employed on the same data but, as this method uses a series of samples over longer time periods the numbers of individuals caught in each trapping week were pooled and entered as a single value. This calculation was performed by using an ALGOL program ´PEST´ (R.J. White unpublished) which is available on the University of Southampton ICL 2976 computer. As described in Chapter 7, the Calendar of Captures method is a simple value of the number of individuals known to be alive at a particular time in the study.

3.2 Conversion to density

To estimate actual density one has to calculate the effective trapping area of one´s trapping grid. This is normally performed by adding a boundary strip of one half the average home range, or average distance moved by the species, to the size of the trapping grid (Dice 1949). Many studies employ trap lines in association with trapping grids in an attempt to assess movement of individuals, or more recently, one is able to employ more advanced techniques such as radio-telemetry (Wolton 1983). Due to the intensive trapping in this study it was not possible to use trap lines, so the average distance moved has been calculated on the basis of individual movements about the grid over a number of trapping sessions. For accuracy this method requires to be performed on a large number of individuals with a high recapture rate and to be split into different seasons: previous studies on movements of small rodents have revealed that movement varies with the fecundity of animals, male mice being more active and females possibly becoming territorial in the breeding season, and between age groups, juveniles tending to disperse more than adults (a full account of movement in mice and voles can be found in the recent review by Wolton and Flowerdew 1985).

Unfortunately the number of animals caught and recaught in this study was too small to enable calculation of movement for different seasons and separate age and sex classes and so only those animals caught on a minimum of three different trapping sessions were used in the calculation. Juveniles and sub-adults were excluded from the analysis unless they remained in the population as adults in which case they would be included if they also fulfilled the criteria of three recaptures.

As the number of recaptures was low throughout the study (Chapter 8, table 8.2) very few adult animals fulfilled the above criteria and data from only three sites were used: Island Thorns Inc from within the New Forest, Howse Copse from outside, and the ungrazed Denny Pen.

The calculated average distances moved of wood mice and bank voles (below) were not found to be significantly different for each species between sites (Mann Whitney U test). Despite this estimates of distance moved in the ungrazed Denny Pen were kept separate from the other two sites as the available habitat was limited by the perimeter fence of the pen. For estimates of average distance moved in the grazed areas the data from Howse Copse and Island Thorns Inc were pooled. The resulting estimates of average distance moved are:

Ungrazed Denny Pen	*A.sylvaticus*	60.47m +/- 29.19
	C.glareolus	50.35m +/- 29.50
Island Thorns Inc & Howse Copse.	*A.sylvaticus*	63.64m +/- 34.77
	C.glareolus	60.62m +/- 25.82

obviously, as no voles were caught within Island Thorns Inc, this estimate is based on data from Howse Copse only.

The effective trapping area of the study site grids was therefore calculated by adding one half of the above averages as a boundary strip to the actual grid dimensions of 95m x 95m. In the case of the Denny Pens correction had to be made for the limited area of habitat available: the boundary strip was only added on two sides of the grids as they adjoined the boundary with other habitats.

3.3 Calculated density

All calculated densities per trapping area for both seasonal and monthly data are presented in tables A3.1 & A3.2. These numbers are very widespread, often suggesting very large or very low densities when only small numbers of animals were known to be alive. A discussion of the limitations of these methods can be found in Seber (1973), but, the wide variations from the actual number known to alive arise from the low number of recaptures, both within and between sessions (see Chapter 8 table 8.2 & Chapter 9 table 9.2). This affects the Jolly estimate more than the other three as this method relies on between session retrappability. The other methods use less information from within a session but still produce wide variations from the actual number known to be alive. Comparison of the Calendar of Captures estimate (tables A3.1 & A3.2) with the other estimates reveals them to often be similar, but there are sessions where the number recaught was small and serious underestimates may occur at these times.

As the number of recaptures in this study were consistently low, actual density estimations have been taken from the Calendar of Captures method which makes use of all available data. The actual density per ha, +/- minimum and maximum estimate, are presented in figures A3.1, A3.2, A3.3 & A3.4, and, as one would expect, these follow the same seasonal changes revealed in the variation in actual number caught (Chapter 7, figures 7.1 & 7.2).

The densities of mice and voles were quite high in all sites in December 1983, but, in general, the density of voles at Howse Copse and the ungrazed Denny Pen were always greater than that of wood mice at these sites.

Table A3.1 A comparison of five different seasonal estimates of the size of *A.sylvaticus* and *C.glareolus* populations, between 1982 and 1984, from within Open New Forest (sites 1 to 4), outside New Forest (sites 5 & 6) and Enclosed New Forest (site 7) deciduous woodlands.

1.Island Thorns Inc *Apodemus sylvaticus* Seasonal Estimates

Week	Cal	L.I	Bailey's	Hayne's	Jolly
1982					
3	8	8 (0.0)	4 (3.1)	8 (0.0)	-
16	1	1 (0.0)	0 (0.0)	0 (0.0)	2 (0.5)
30	2	2 (0.0)	0 (0.0)	2 (0.0)	3 (0.7)
45	24	20 (3.6)	8 (3.2)	24 (0.0)	24 (0.9)
1983					
3	23	17 (1.5)	19 (15.4)	28 (0.3)	18 (2.8)
22	20	12 (0.0)	7 (4.2)	15 (0.0)	312 (313.0)
37	38	32 (0.0)	40 (18.4)	38 (0.7)	252 (314.0)
49	18	14 (2.8)	8 (5.3)	17 (0.0)	0 (0.0)
1984					
10	7	4 (1.4)	4 (3.5)	6 (0.0)	0 (0.0)
22	0	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)

2.Backley Inc *Apodemus sylvaticus* Seasonal Estimates

1982					
17	1	0 (0.0)	0 (0.0)	0 (0.0)	-
31	0	0 (0.0)	0 (0.0)	0 (0.0)	17 (2.0)
46	16	10 (3.5)	14 (8.6)	18 (0.0)	35 (13.7)
1983					
5	16	0 (0.0)	0 (0.0)	0 (0.0)	13 (5.7)
21	7	5 (0.7)	3 (2.3)	7 (0.2)	19 (2.2)
38	24	15 (0.7)	41 (30.6)	16 (0.0)	8 (1.6)
47	6	5 (0.7)	1 (1.3)	8 (0.0)	5 (1.5)
1984					
9	4	2 (1.0)	0 (0.0)	3 (0.5)	0 (0.0)
21	2	2 (0.0)	2 (0.0)	1 (0.8)	0 (0.0)

3.Sloden Inc *Apodemus sylvaticus* Seaonal Estimates

1982					
8	2	1 (1.4)	0 (0.0)	1 (0.0)	-
18	0	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.0)
32	0	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.0)
47	9	6 (7.7)	96 (85.3)	12 (0.0)	11 (1.5)
1983					
5	9	4 (0.7)	0 (0.0)	6 (0.3)	23 (10.1)
21	5	2 (0.0)	0 (0.0)	4 (0.3)	24 (21.1)
38	24	18 (9.9)	11 (6.9)	25 (0.0)	24 (1.8)
47	11	4 (3.5)	0 (0.0)	0 (0.0)	81 (75.5)
1984					
9	8	6 (0.7)	0 (0.0)	0 (0.0)	21 (17.8)
23	6	3 (1.4)	0 (0.0)	2 (0.0)	-

4.Matley Wood Wood *Apodemus sylvaticus* Seasonal Estimates

1982					
4	6	6 (2.1)	3 (2.0)	6 (0.0)	-
23	0	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.0)
36	9	7 (2.1)	4 (2.8)	6 (0.0)	10 (1.0)
49	34	31 (5.6)	41 (18.8)	39 (3.0)	32 (0.9)
1983					
4	13	15 (2.1)	8 (5.3)	9 (0.4)	35 (28.4)
23	11	13 (4.2)	133 (101.6)	6 (2.0)	-

Table A3.1 continued

5.Howse Copse Apodemus sylvaticus Seasonal Estimates

Week	Cal	L.I.		Bailey´s		Hayne´s		Jolly	
1982									
9	3	3	(2.1)	2	(1.6)	6	(0.4)	-	
22	0	0	(0.0)	0	(0.0)	0	(0.0)	1	(0.0)
37	1	0	(0.0)	0	(0.0)	0	(0.0)	2	(0.5)
48	26	32	(19.1)	15	(12.3)	37	(0.4)	24	(.)
1983									
4	27	39	(27.3)	18	(12.4)	37	(0.8)	130	(90.8)
20	10	8	(0.7)	4	(2.8)	11	(0.0)	11	(3.2)
39	34	30	(5.5)	127	(81.5)	36	(0.6)	93	(59.9)
48	19	10	(3.0)	24	(19.5)	13	(0.3)	58	(23.4)
1984									
10	13	6	(0.7)	0	(0.0)	6	(0.1)	12	(7.6)
22	6	0	(0.0)	0	(0.0)	0	(0.0)	0	(0.0)

5.Howse Copse Clethrionomys glareolus Seasonal Estimates

1982									
9	12	10	(2.1)	5	(3.6)	12	(0.0)	-	
22	8	4	(1.3)	1	(1.1)	4	(0.7)	55	(45.0)
37	8	6	(2.8)	1	(1.0)	8	(0.0)	9	(0.9)
48	48	15	(4.2)	14	(9.9)	18	(0.0)	142	(50.7)
1983									
4	31	14	(4.2)	0	(0.0)	11	(0.3)	73	(22.0)
20	13	13	(3.3)	11	(8.1)	14	(0.0)	35	(11.0)
39	21	11	(5.1)	6	(5.8)	16	(0.0)	25	(5.8)
48	28	23	(4.2)	58	(41.7)	31	(0.3)	27	(3.4)
1984									
10	10	1	(1.4)	0	(0.0)	13	(0.1)	32	(26.1)
22	9	7	(1.4)	4	(3.4)	9	(0.1)	-	

6.Pound Bottom Apodemus sylvaticus Seasonal Estimates

1982								
18	0	0	(0.0)	0	(0.0)	0	(0.0)	-
31	0	0	(0.0)	0	(0.0)	0	(0.0)	-
46	23	19	(4.9)	13	(7.0)	24	(0.0)	-
1983								
3	6	0	(0.0)	0	(0.0)	0	(0.0)	-
22	4	1	(1.4)	0	(0.0)	2	(0.0)	-
37	44	53	(16.2)	38	(18.9)	46	(0.0)	-
49	7	9	(7.0)	0	(0.0)	12	(1.1)	-
1984								
9	4	0	(0.0)	5	(4.1)	0	(0.0)	-
21	2	1	(1.0)	0	(0.0)	1	(0.0)	-

6.Pound Bottom Clethrionomys glareolus Seasonal Estimates

1982								
18	3	2	(0.7)	13	(7.0)	0	(0.0)	-
31	1	1	(0.0)	2	(2.0)	0	(0.0)	-
46	6	0	(0.0)	0	(0.0)	0	(0.0)	-
1983								
3	1	0	(0.0)	0	(0.0)	0	(0.0)	-
22	2	2	(2.1)	3	(2.3)	0	(0.0)	-
37	18	16	(0.7)	38	(18.9)	19	(1.4)	-
49	4	0	(0.0)	0	(0.0)	0	(0.0)	-
1984								
9	2	2	(0.0)	0	(0.0)	0	(0.0)	-
21	1	1	(1.4)	2	(1.5)	0	(0.0)	-

7.Ungrazed Denny Pen Apodemus sylvaticus Seasonal Estimates

1983									
6	32	27	(1.4)	92	(69.0)	36	(0.3)	-	
24	22	15	(0.0)	10	(5.1)	16	(0.0)	64	(22.0)
36	31	30	(3.5)	48	(24.1)	34	(0.0)	47	(14.0)
46	14	13	(7.0)	24	(20.1)	17	(0.3)	22	(7.3)
1984									
10	12	14	(5.6)	4	(4.0)	9	(0.0)	14	(4.6)
22	6	2	(3.5)	0	(0.0)	4	(4.0)	-	

7.Ungrazed Denny Pen Clethrionomys glareolus Seasonal Estimate

1983									
6	24	26	(9.8)	17	(12.1)	32	(0.0)	-	
24	39	28	(2.8)	24	(11.7)	34	(0.1)	97	(15.2)
36	27	16	(5.6)	10	(6.4)	8	(0.0)	49	(4.4)
46	43	34	(12.7)	21	(13.0)	40	(0.0)	108	(28.8)
1984									
10	24	15	(2.8)	22	(14.8)	18	(0.3)	27	(5.4)
22	22	18	(6.3)	20	(13.5)	22	(0.0)	-	

Table A3.2 A comparison of five different monthly estimates of the size of A.sylvaticus and C.glareolus populations, between 1982 and 1984, from within Open New Forest (sites 1 to 4), outside New Forest (sites 5 & 6) and Enclosed New Forest (site 7) deciduous woodlands.

1.Island Thorns Inc Apodemus sylvaticus Monthly estimates

Week	Cal.	L.I.		Bailey's		Hayne's		Jolly	
1982									
45	24	21	(4.9)	11	(5.7)	26	(0.2)	-	
3	15	16	(2.1)	19	(15.4)	28	(0.3)	66	(10.5)
8	21	16	(3.5)	15	(12.6)	21	(0.0)	136	(32.1)
13	16	6	(8.4)	0	(0.0)	13	(0.0)	465	(431.0)
19	20	18	(4.9)	31	(19.1)	18	(0.0)	79	(16.1)
22	21	13	(2.8)	4	(2.7)	18	(0.8)	202	(103.0)
30	12	9	(0.0)	2	(1.4)	10	(0.1)	60	(26.8)
37	35	33	(0.7)	42	(19.5)	39	(0.3)	47	(7.3)
44	31	7	(9.8)	63	(54.9)	14	(0.0)	128	(60.5)
49	22	10	(0.7)	7	(5.3)	17	(0.0)	97	(44.1)
1983									
2	14	7	(6.3)	69	(48.4)	12	(0.1)	57	(23.5)
6	9	5	(0.0)	2	(2.0)	11	(0.2)	156	(158.0)
10	6	0	(0.0)	4	(3.5)	7	(0.1)	44	(41.8)
14	3	0	(0.0)	0	(0.0)	0	(0.0)	9	(7.5)
18	1	0	(0.0)	0	(0.0)	0	(0.0)	0	(0.0)
22	0	0	(0.0)	0	(0.0)	0	(0.0)	-	

2.Howse Copse Apodemus sylvaticus Monthly Estimates

1982									
48	26	28	(5.1)	10	(8.6)	33	(0.1)	-	
1983									
4	12	20	(6.2)	26	(14.0)	23	(0.0)	23	(90.6)
9	8	3	(3.1)	35	(30.7)	6	(0.0)	135	(107.0)
15	4	1	(1.0)	0	(0.0)	1	(1.0)	55	(40.5)
20	11	8	(6.2)	4	(2.8)	11	(0.0)	24	(4.5)
23	10	2	(3.2)	0	(0.0)	19	(0.4)	35	(6.5)
30	12	6	(0.1)	0	(0.0)	12	(0.7)	204	(189.0)
39	34	30	(0.9)	127	(81.5)	35	(0.0)	70	(18.5)
44	19	7	(4.4)	5	(3.3)	7	(0.0)	540	(493.0)
48	15	10	(1.2)	24	(19.0)	13	(0.3)	54	(4.1)
1984									
2	24	22	(8.5)	29	(17.7)	28	(0.0)	132	(31.8)
6	16	9	(3.2)	8	(5.1)	11	(0.0)	121	(40.3)
10	12	0	(0.0)	0	(0.0)	0	(0.0)	260	(239.0)
14	9	0	(0.0)	0	(0.0)	0	(0.0)	108	(96.0)
18	7	0	(0.0)	0	(0.0)	0	(0.0)	42	(35.3)
22	7	0	(0.0)	0	(0.0)	0	(0.0)	-	

2.Howse copse Clethrionomys glareolus Monthly Estimates

1982									
48	43	22	(8.5)	12	(7.8)	40	(2.0)	-	
1983									
4	31	27	(12.7)	60	(47.0)	42	(0.0)	109	(0.0)
9	20	9	(5.6)	16	(11.6)	10	(0.0)	45	(0.0)
15	13	3	(4.9)	63	(56.6)	8	(0.0)	50	(0.0)
20	17	9	(1.4)	7	(4.6)	11	(0.5)	53	(0.0)
23	14	10	(0.7)	33	(23.6)	11	(0.0)	546	(499.0)
30	12	5	(3.4)	24	(11.2)	9	(0.0)	98	(67.0)
39	22	10	(0.7)	6	(5.8)	16	(0.0)	26	(0.0)
44	30	6	(8.4)	0	(0.0)	27	(0.2)	525	(480.0)
48	33	25	(0.7)	39	(25.5)	32	(0.0)	39	(0.0)
1984									
2	24	43	(13.4)	105	(137.0)	76	(0.1)	59	(0.0)
6	19	8	(8.5)	2	(1.3)	14	(0.0)	38	(0.0)
10	12	1	(1.4)	0	(0.0)	14	(0.0)	106	(32.6)
14	8	15	(0.7)	0	(0.0)	2	(0.0)	45	(32.6)
18	7	4	(0.0)	2	(1.7)	5	(0.0)	43	(34.9)
22	7	8	(2.2)	12	(10.4)	11	(0.1)	-	

Table A3.2 continued

3.Pound Bottom *Apodemus sylvaticus* Monthly Estimates

Week	Cal.	L.I.		Bailey´s		Hayne´s		Jolly	
1982									
46	24	21	(5.6)	13	(7.0)	24	(0.0)	-	
1983									
3	6	0	(0.0)	0	(0.0)	0	(0.0)	1	(0.0)
8	7	4	(2.2)	2	(2.0)	7	(0.0)	2	(0.4)
13	4	2	(0.0)	0	(0.0)	4	(0.0)	30	(23.2)
19	4	1	(1.0)	0	(0.0)	0	(0.0)	12	(3.7)
22	8	6	(3.5)	3	(2.3)	8	(0.0)	36	(33.7)
30	5	0	(0.0)	0	(0.0)	0	(0.0)	28	(26.4)
39	40	36	(9.1)	38	(18.9)	46	(0.1)	48	(29.3)
44	10	7	(1.4)	2	(2.0)	11	(0.0)	36	(27.3)
49	6	1	(0.0)	2	(1.5)	2	(0.0)	-	

3.Pound Bottom *Clethrionomys glareolus* Monthly Estimates

1982									
46	6	0	(0.0)	0	(0.0)	0	(0.0)	-	
1983									
3	1	0	(0.0)	0	(0.0)	0	(0.0)	1	(0.0)
8	1	0	(0.0)	0	(0.0)	0	(0.0)	2	(0.4)
13	2	0	(0.0)	0	(0.0)	0	(0.0)	30	(23.2)
19	1	0	(0.0)	0	(0.0)	0	(0.0)	12	(3.7)
22	2	0	(0.0)	0	(0.0)	0	(0.0)	36	(33.7)
30	3	1	(1.4)	0	(0.0)	2	(0.0)	28	(26.4)
39	18	15	(0.7)	27	(20.4)	19	(1.4)	49	(29.3)
44	11	6	(0.7)	5	(3.1)	7	(0.0)	36	(27.3)
49	4	0	(0.0)	0	(0.0)	0	(0.0)	-	

4.Ungrazed Denny Pen *Apodemus sylvaticus* Monthly Estimates

1983									
46	14	13	(7.0)	26	(20.1)	17	(0.0)	-	
1984									
2	15	8	(0.1)	5	(4.2)	16	(0.4)	68	(31.7)
6	15	8	(2.2)	31	(27.2)	8	(0.0)	83	(30.7)
10	12	7	(0.7)	3	(4.0)	7	(0.0)	87	(31.4)
14	10	9	(2.1)	3	(5.8)	7	(0.0)	343	(339.0)
18	7	7	(4.2)	8	(6.4)	4	(0.0)	60	(41.2)
22	7	3	(4.2)	0	(0.0)	0	(0.0)	-	

4.Ungrazed Denny Pen *Clethrionomys glareolus* Monthly Estimates

1983									
46	43	34	(12.7)	21	(13.0)	40	(0.1)	-	
1984									
2	35	24	(3.1)	16	(9.3)	30	(0.0)	217	(522.0)
6	23	0	(0.0)	0	(0.0)	0	(0.0)	50	(0.0)
10	25	13	(6.4)	16	(11.8)	18	(0.3)	207	(86.6)
14	20	5	(3.2)	1	(1.0)	6	(0.0)	156	(76.2)
18	21	14	(2.2)	8	(6.1)	18	(0.0)	78	(26.3)
22	22	19	(0.7)	21	(15.0)	22	(0.1)	-	

Figure A3.1 Seasonal changes in calculated density (+/- minimum and maximum ha^{-1}) (Calendar of Captures estimate) of A.sylvaticus populations within Open New Forest (sites 1 to 4), Enclosed New Forest (site 5) and outside New Forest (sites 6 & 7) deciduous woodlands.

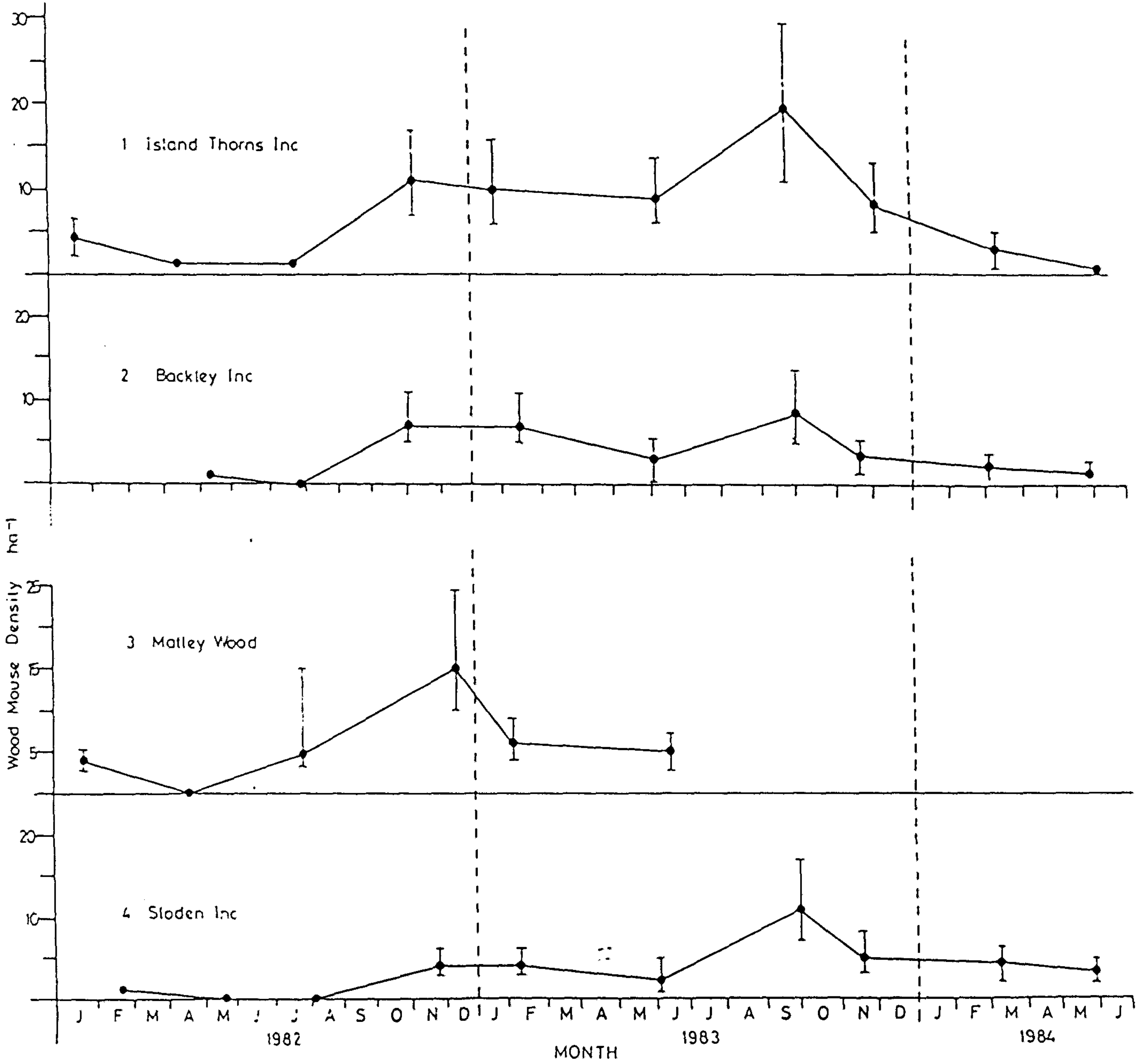

1 Island Thorns Inc
2 Backley Inc
3 Matley Wood
4 Sloden Inc
Wood Mouse Density ha⁻¹
30
20
10
20
10
25
15
5
20
10
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
1982
1983
1984
MONTH

fig. A3.1 continued

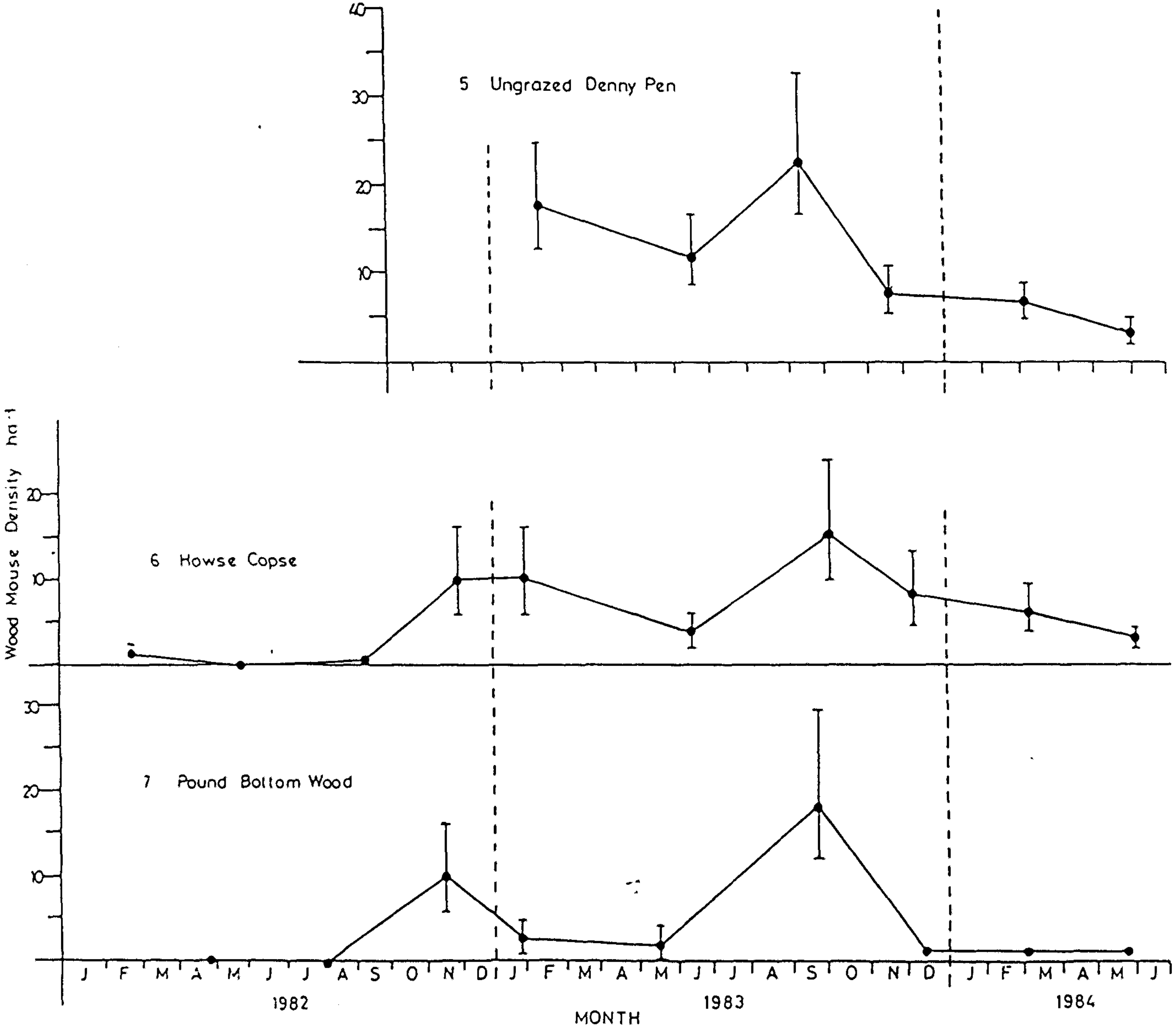


Figure A3.2 Seasonal changes in the calculated density (+/- minimum & maximum ha^{-1}) Calendar of Captures estimate) of *C.glareolus* populations from within Enclosed New Forest (site 1) and outside New Forest (sites 2 & 3) deciduous woodlands.

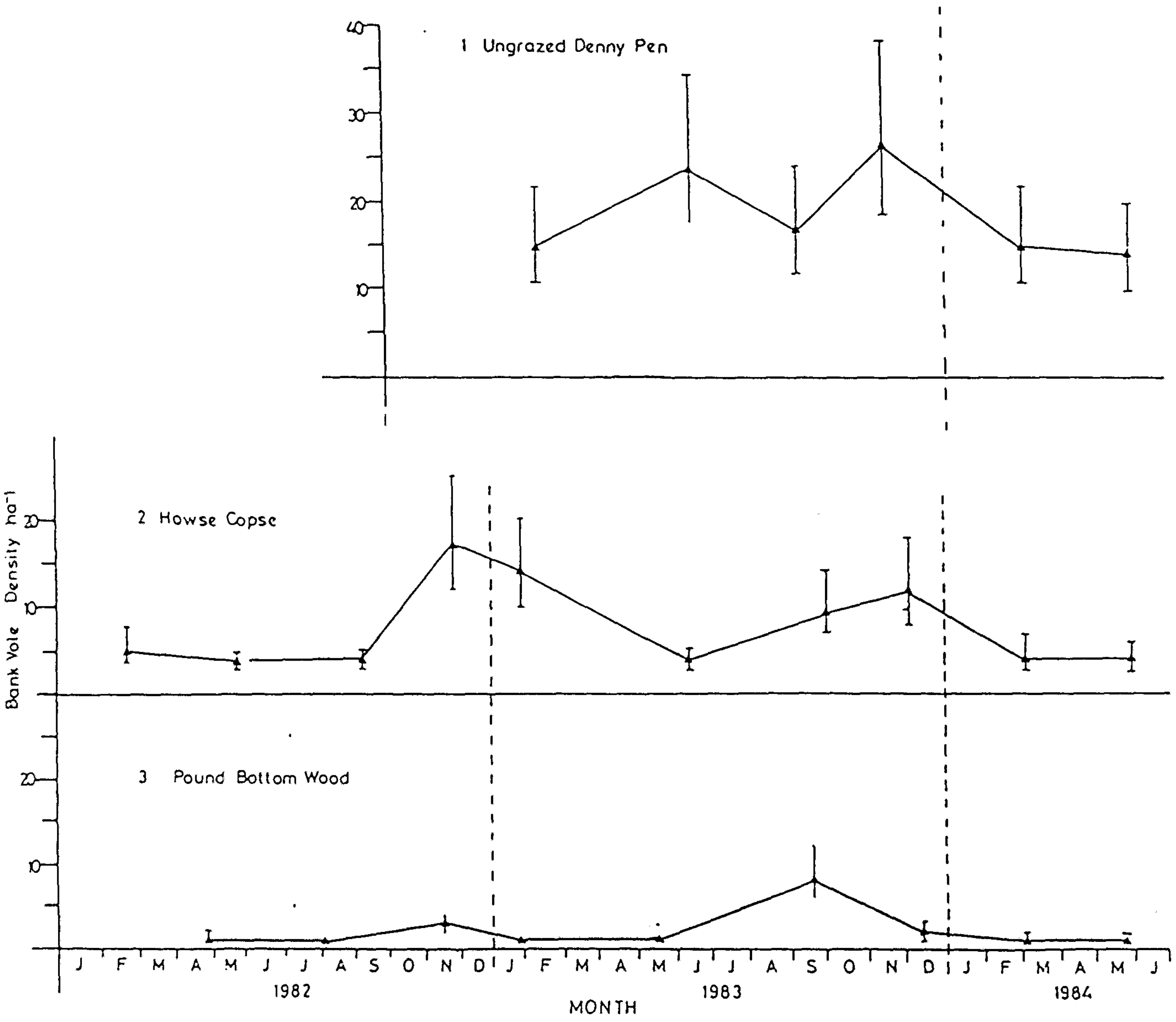
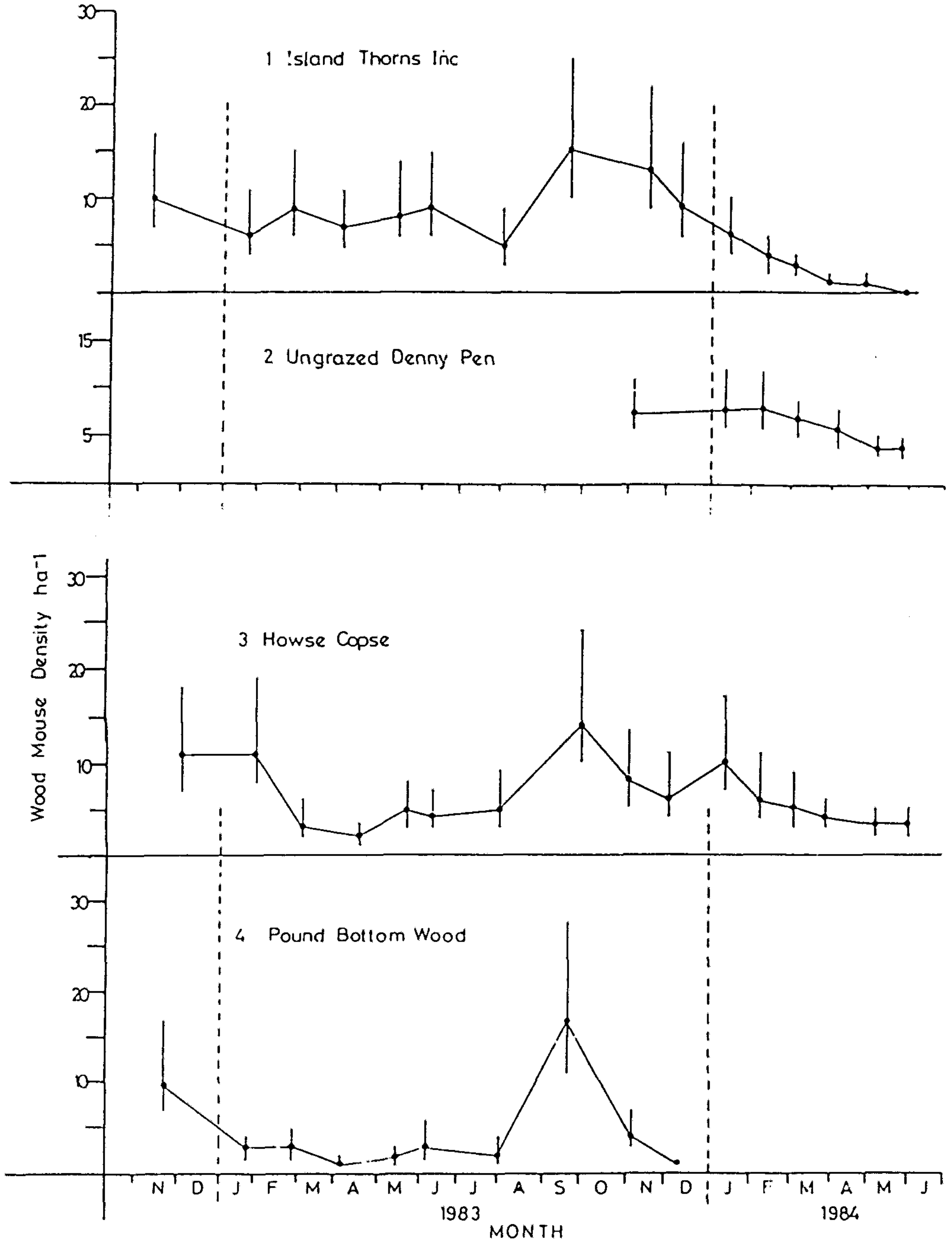

40
30
20
10
1 Ungrazed Denny Pen
Bank Vole Density ha^{-1}
20
10
2 Howse Copse
20
10
3 Pound Bottom Wood
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
1982
1983
1984
MONTH

Figure A3.3 Monthly changes in calculated density (+/- minimum and maximum ha^{-1}) (Calendar of Captures estimate) of *A.sylvaticus* populations within Open New Forest (site 1), Enclosed New Forest (site 2) and outside New Forest (sites 3 & 4) deciduous woodlands.


1 Island Thorns Inc
2 Ungrazed Denny Pen
3 Howse Copse
4 Pound Bottom Wood
30
20
10
15
5
30
20
10
30
20
10
Wood Mouse Density ha-1
N D J F M A M J J A S O N D J F M A M J
1983
1984
MONTH

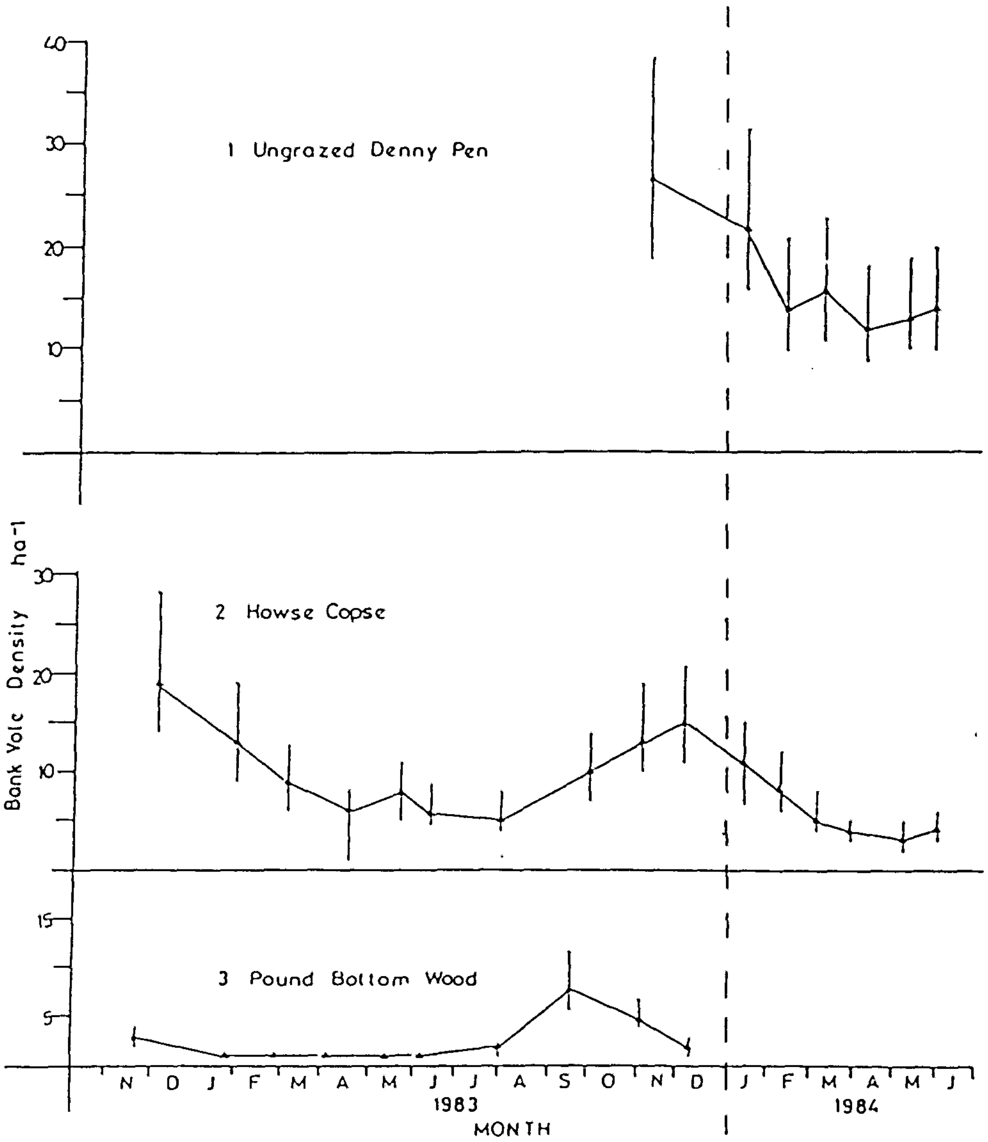


Figure A3.4 Monthly changes in the calculated density (+/- minimum and maximum ha^{-1}) (Calendar of Captures estimate) of C.glareolus populations from within Enclosed New Forest (site 1) and outside New Forest (sites 3 & 4) deciduous woodlands.

APPENDIX 4

TRAPPING DATA

The number of individuals of small rodents (A. sylvaticus, C. glareolus & A. flavicollis) and insectivores (S. araneus & S. minutus) caught during each three night trapping period within Open New Forest (sites 1 to 4), Enclosed New Forest (sites 5 & 6) and outside (sites 7 & 8) deciduous woodlands between January 1982 and June 1984. (All trapping grids 7 x 7 trap stations, 2 traps per station, at 15m spacing.)

1. Island Thorns Inc.

A. sylvaticus

Week no.	Total Caught		♂♂			♀♀	
		J	S	A	J	S	A
1982							
3	8	0	0	3	0	2	3
1	1	0	0	1	0	0	0
30	2	0	0	1	0	0	1
45	26	1	2	13	5	2	4
1983							
3	10	0	0	4	0	0	6
8	18	0	3	5	2	4	4
13	14	0	0	6	0	2	6
19	21	0	1	10	0	2	8
22	21	0	1	9	0	1	10
30	12	2	1	5	1	0	3
37	35	6	8	6	8	1	6
44	9	0	0	4	1	3	1
49	17	2	4	3	0	5	3
1984							
2	14	0	3	5	0	0	6
6	9	0	0	6	0	0	4
10	6	0	0	3	0	0	3
14	3	0	0	1	0	0	2
18	1	0	0	0	0	0	1
22	0	0	0	0	0	0	0

1. **Island Thorns Inc.** (contd.)

C. glareolus

Week no.	Total Caught	♂♂ J	♂♂ S	♂♂ A	♀♀ J	♀♀ S	♀♀ A
1982							
3	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0
1983							
3	0	0	0	0	0	0	0
8	1	0	0	1	0	0	0
13	0	0	0	0	0	0	0
19	2	0	0	1	0	0	1
22	1	0	0	0	0	0	1
30	1	0	0	0	0	0	1
37	1	0	0	1	0	0	0
44	1	0	1	0	0	0	0
49	1	0	0	0	0	0	1
1984							
2	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0

A. flavicollis

Week no.	Total Caught	♂♂ J	♂♂ S	♂♂ A	♀♀ J	♀♀ S	♀♀ A
1982							
3	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0
1983							
3	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0
30	1	0	1	0	0	0	0
37	3	0	0	1	2	0	0
44	1	0	0	1	0	0	0
49	1	0	1	0	0	0	0
1984							
2	1	0	1	0	0	0	0
6	1	0	1	0	0	0	0
10	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0

S. araneus

Total Caught
2
0
2
1
0
0
0
0
0
0
0
0
0
0
0
0
0
0
0

2. Matley Wood

A. sylvaticus

Week no.	Total Caught	♂♂			♀♀		
		J	S	A	J	S	A
1982							
4	6	0	0	2	0	0	4
23	0	0	0	0	0	0	0
36	9	2	2	2	1	1	1
49	34	11	0	6	7	5	5
1983							
4	6	0	3	0	0	0	3
21	11	0	0	5	0	0	6

C. glareolus

Week no.	Total Caught	♂♂			♀♀		
		J	S	A	J	S	A
1982							
4	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0
1983							
4	2	0	0	0	0	0	2
21	1	0	0	0	0	0	1

A. flavicollis

Week no.	Total Caught	♂♂		
		J	S	A
1982				
4	1	0	0	1
23	0	0	0	0
36	0	0	0	0
49	0	0	0	0
1983				
4	0	0	0	0
21	0	0	0	0

3. Sloden Inclosure

A. sylvaticus

Week no.	Total Caught		♂♂			♀♀	
		J	S	A	J	S	A
1982							
8	2	0	0	1	0	0	1
18	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0
47	10	0	3	4	1	1	1
1983							
5	8	0	1	5	0	0	2
21	5	1	0	2	1	0	1
38	25	6	3	6	6	1	5
47	9	0	0	7	1	0	1
1984							
9	7	0	0	4	0	0	3
23	6	0	0	4	0	0	2

A. flavicollis

Week no.	Total Caught		♂♂			♀♀	
		J	S	A	J	S	A
1982							
8	3	0	0	1	0	0	2
18	1	0	0	1	0	0	0
32	0	0	0	0	0	0	0
47	1	0	0	1	0	0	0
1983							
5	7	0	0	2	0	0	5
21	4	0	0	2	0	0	2
38	3	0	0	1	0	0	2
47	4	0	1	1	0	0	2
1984							
9	3	0	0	1	0	0	2
23	9	0	0	6	0	1	2

4. Backley Inclosure

A. sylvaticus

Week no.	Total Caught	♂♂			♀♀		
		J	S	A	J	S	A
1982							
17	1	0	0	1	0	0	0
31	0	0	0	0	0	0	0
46	16	3	1	4	1	3	2
1983							
5	16	1	1	6	0	1	7
21	7	1	0	2	1	1	2
38	16	1	4	2	3	4	2
47	7	0	1	4	0	0	2
1984							
9	4	0	0	2	0	0	2
21	2	0	0	1	0	0	1

5. Ungrazed Denny Pen

A. sylvaticus

Week no.	Total Caught	♂♂ J	♂♂ S	♂♂ A	♀♀ J	♀♀ S	♀♀ A
1983							
6	31	1	0	14	1	0	15
24	21	0	0	13	0	0	8
36	33	2	6	13	0	1	11
46	15	0	2	7	0	0	6
1984							
2	12	0	0	7	0	0	5
6	9	0	0	5	0	0	4
10	9	0	0	4	0	0	5
14	9	0	0	4	0	0	5
18	8	0	0	3	0	0	5
22	7	0	0	4	0	0	3

C. glareolus

Week no.	Total Caught	♂♂ J	♂♂ S	♂♂ A	♀♀ J	♀♀ S	♀♀ A
1983							
6	24	1	3	1	4	5	10
24	37	1	0	14	4	0	18
36	18	0	3	6	0	1	8
46	35	0	0	15	0	4	16
1984							
2	31	0	0	8	0	0	23
6	16	0	0	5	0	0	11
10	17	0	2	3	0	1	11
14	8	0	0	3	0	0	5
18	15	0	0	6	0	0	9
22	20	0	0	9	0	0	11

5. Ungrazed Denny Pen (contd.)

A. flavicollis *S. araneus* *S. minutus*

Week no.	Total Caught		♂♂			♀♀		*S. araneus* Total Caught	*S. minutus* Total Caught
		J	S	A	J	S	A		
1983									
6	0	0	0	0	0	0	0	3	0
24	1	0	0	1	0	0	0	3	0
36	0	0	0	0	0	0	0	1	1
46	0	0	0	0	0	0	0	6	1
1984									
2	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	2	0
14	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0

6. Denny Pen Grazed

A. sylvaticus

Week no.	Total Caught		♂♂			♀♀	
		J	S	A	J	S	A
1983							
6	6	0	3	1	1	1	0
24	6	1	1	2	0	0	2
36	10	0	2	1	4	0	3
46	1	0	1	0	0	0	0
1984							
2	5	0	0	2	0	0	3
6	2	0	0	0	0	0	2
10	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0

7. Howse Copse

A. sylvaticus

Week no.	Total Caught		♂♂			♀♀	
		J	S	A	J	S	A
1982							
9	3	0	0	3	0	0	0
22	0	0	0	0	0	0	0
37	1	0	0	0	0	1	0
48	26	0	11	3	4	7	1
1983							
4	27	0	3	9	0	12	3
9	6	0	0	3	0	0	3
15	1	0	0	0	0	0	1
20	9	0	0	4	0	0	5
23	10	0	0	7	0	1	3
30	9	0	0	5	0	0	4
39	32	0	4	14	1	2	11
44	16	0	0	10	0	0	6
48	15	0	2	7	0	1	5
1984							
2	24	0	0	14	0	0	10
6	16	0	1	9	0	0	6
10	3	0	0	1	0	0	2
14	4	0	0	3	0	0	1
18	4	0	0	2	0	0	2
22	6	0	0	5	0	0	1

C. glareolus

Week no.	Total Caught		♂♂			♀♀	
		J	S	A	J	S	A
1982							
9	12	0	0	7	1	0	4
22	6	0	1	3	0	0	2
37	7	0	0	5	0	0	2
48	45	5	21	2	8	9	2
1983							
4	31	0	7	5	1	11	7
9	18	0	0	9	0	7	2
15	11	0	0	4	0	0	7
20	16	0	0	12	0	0	4
23	13	0	0	8	0	0	5
30	5	0	0	3	0	0	2
39	13	0	0	6	1	1	5
44	14	0	0	8	0	0	6
48	29	0	6	19	0	0	5
1984							
2	18	0	0	7	0	0	11
6	17	0	1	7	0	4	5
10	8	0	0	2	0	1	5
14	4	0	0	2	0	0	2
18	6	0	0	4	0	0	2
22	9	0	0	6	0	0	3

7. Howse Copse (contd.)

A. flavicollis								S. araneus	S. minutu
		♂♂			♀♀				
Week no.	Total Caught	J	S	A	J	S	A	Total Caught	Total Caught
1982									
9	1	0	0	1	0	0	0	3	2
22	0	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0	5	5
48	2	0	0	2	0	0	0	8	0
1983									
4	3	0	0	2	0	0	1	2	0
9	0	0	0	0	0	0	0	2	0
15	1	0	0	0	0	0	1	4	3
20	0	0	0	0	0	0	0	16	4
23	1	0	0	0	0	0	1	0	0
30	0	0	0	0	0	0	0	0	0
39	4	0	0	2	0	0	2	10	0
44	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	2	0
1984									
2	0	0	0	0	0	0	0	0	1
6	1	0	0	1	0	0	0	0	1
10	0	0	0	0	0	0	0	1	0
14	0	0	0	0	0	0	0	1	0
18	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0

8. Pound Bottom Wood

A. sylvaticus

Week no.	Total Caught		♂♂			♀♀	
		J	S	A	J	S	A
1982							
18	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0
46	24	2	7	3	5	0	7
1983							
3	2	0	0	1	0	0	1
8	7	0	0	1	0	0	6
13	5	0	0	5	0	0	0
19	4	0	0	3	0	0	1
22	6	0	0	5	0	0	1
30	5	0	1	1	1	0	2
37	39	0	5	15	6	0	13
44	10	0	0	4	0	0	5
49	2	0	0	2	0	0	0
1984							
9	1	0	0	0	0	0	1
21	2	0	0	1	0	0	1

C. glareolus

Week no.	Total Caught		♂♂			♀♀	
		J	S	A	J	S	A
1982							
18	3	0	0	2	0	0	1
31	0	0	0	0	0	0	0
46	1	0	0	1	0	0	0
1983							
3	5	0	3	0	0	2	0
8	1	0	0	0	0	0	1
13	2	0	0	1	0	0	1
19	1	0	0	1	0	0	0
22	2	0	0	1	0	0	1
30	3	0	0	1	1	0	1
37	18	1	1	9	1	0	6
44	11	0	2	4	0	0	5
49	4	0	0	0	0	0	4
1984							
9	2	0	0	0	0	0	2
21	2	0	0	0	0	0	2

8. Pound Bottom Wood (contd.)

	A. flavicollis				*S. araneus*
Week no.	Total Caught	♂♂			Total Caught
		J	S	A	
1982					
18	0	0	0	0	0
31	0	0	0	0	0
46	0	0	0	0	2
1983					
3	0	0	0	0	0
8	0	0	0	0	0
13	0	0	0	0	0
19	1	0	1	0	0
22	0	0	0	0	0
30	0	0	0	0	0
37	0	0	0	0	3
44	4	1	1	2	2
49	2	0	0	2	0
1984					
9	0	0	0	0	2
21	0	0	0	0	0