POPULATION ECOLOGY OF *LASIUS FLAVUS* F.

ON CHALK GRASSLAND.

Submitted for the degree of PhD

by

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PART ONE

ABSTRACT AND CONTENTS

Abstract.

Lasius flavus F. is a common ant species on chalk grasslands in the south of England. This thesis examines the effects of the management regimes and environmental conditions of these grasslands, on the characteristics of the ant populations.

The null hypothesis of the study was that the characteristics of *L. flavus* populations are not significantly affected by variation in:

1) management procedures,

2) the physical environment,

3) the biological environment.

The ant populations, management regimes and environmental characteristics of twenty sample areas were investigated and subjected to intensive analysis to examine this hypothesis.

The null hypothesis was rejected. The population of ants that an area of chalk grassland supports, depends on both the management of that area and the environmental conditions.

In the short term (2 to 4 years) more intense management leads to significant reductions in the sizes of the soil mounds built by the ant colonies, and reductions in the sexual productivity and sexual investment ratios of the colonies. In the longer term (over 10 years) the density of mounds is also reduced.

The most important environmental characteristic of the grasslands is the soil water regime. Drier areas support a lower density of colonies with smaller mounds.

The numbers of root aphids (the major food source of the ant) are reduced by increased grazing intensity. Other invertebrate groups are also affected by the management regime and the physical environment of the sample areas.

It is suggested that increased grazing pressure and lower soil water contents reduce the productivity of chalk grassland and the abundance of soil invertebrates. This reduces the abundance of the food sources of the ants.

The information gained from this study is used to suggest a management plan for the establishment and conservation of dense populations of *L. flavus* on chalk grasslands.

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PART TWO

THE INTRODUCTION

CHAPTER ONE

Introduction to and aims of the project

1.1. The importance of social insects.

Many social insects are known to be extremely important within their ecosystems, achieving in natural ecosystems an almost unique abundance amongst invertebrate groups (Tobin 1989, Wilson 1987).

The importance of many winged social Hymenoptera as pollinators is well known (Gauld and Bolton 1988). The importance of termites may be under perceived, although, they too can reach high densities and be important in their ecosystems, for example in terms of soil turnover and modification (Wood and Sands 1978, Lobry de Bruyn and Conacher 1990).

Amongst the social insects, ants are the most conspicuously abundant, for example, Tobin (1989) has found that on tropical rainforest trees, ants may account for over 50% of the individual insects found and around 50% when considered in terms of biomass (see also May 1989). Throughout many other ecosystems ants are also in dominant positions. For example, in North American forests ants are the dominant invertebrate scavengers (Fellers 1982). In South America, leafcutter ants are often the dominant invertebrate herbivore (Lofgren and Vander Meer 1986). Army ants can be considered as the dominant invertebrate predator in the ecosystems they inhabit (Gotwald 1982) and *Solenopsis invicta** has become a serious and dominant pest in many areas (Lofgren and Vander Meer 1986).

Wilson (1987) considers the ants as one of the most ecologically

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* Barring the next species mentioned, all authorities of latin names of organisms are given in the index at the end of this volume.

successful groups of organisms, due to their abundance and long fossil history. Petal (1978) in discussing the role of ants in ecosystems suggests a number of ways in which ants are important, including as predators, prey, in terms of occupying space, their nest characteristics and also in simple terms of energy flow.

The ant Lasius flavus (Fabricius 1781) is considered by some authors as the most common ant species in the British Isles (Collingwood 1957). It is particularly frequent on chalk grasslands in the south of England.

1.2. Chalk grasslands.

Chalk grasslands represent a plagioclimax community of plants and animals, overlying chalk bedrock, which occur only as the result of grazing, both by animals controlled by Man, sheep and cattle, and independant of Man, eg. rabbits (Oryctolagus cuniculus). In the absence of such grazing the grassland will revert to scrub and then to woodland in a successional sequence (Tansley 1939, Wells 1980).

The area of land covered by chalk grassland has, for a long time, been in decline in the south of England (see section 2.2.) and active conservation of it has been necessary (Jermy and Stott 1973, Prescott 1983). Chalk grassland is a valued resource (Jermy and Stott 1973, Smith 1980) and much research has been carried out in order to establish the extent of the decline that has occured (Blackwood and Tubbs 1970), ways of conserving the remnants and even recreating areas of grassland after they have been lost (Wells 1978, 1987).

1.3. Conservation.

Conservation, when concerned with biology, is defined by Usher (1973) as follows.

> Biological conservation is essentially concerned

> with the interaction between Man and the environment.
>
> Fulfillment of conservation strategies for a biological resource requires the resourses' management in perpetuity on the basis of a sustained production of the resource or biotic component of the environment and a sustained demand on the resource or environment by Man.

The resources referred to in the definition can be almost anything, from the very general, such as a whole class of ecosystem, eg. tropical rainforest, to the very specific, such as a single variety of a single species, eg. the British Large Blue butterfly, *Maculinea arion*.

The resource is often only considered worthy of conservation in 'the eye of the beholder', for example a small group of arachnologists may be concerned over the conservation of a small Lyniphiid spider, while most people would be unconcerned by its loss.

In this thesis the resource being considered is the ant *L. flavus* and more particularly its presence in the kinds of numbers and conditions which lead to the production of a grassland studded with large numbers of large ant mounds (see Figure 1.1 for example). This type of habitat has attracted attention from both ant specialists and a whole range of other biologists (Elton 1966 and Edington and Edington 1972 for example).

The definition also emphasizes the sustained nature of the presence of the resource (and the demand for it) ie. in this context that the population of ants is maintained over time. This is an indication of the need for biological management of the system in which the resource

Figure 1.1.

Large population of mounds of **L. flavus** on Beacon Hill, Aston Rowant.

occurs, in this case chalk grassland management by a variety of means such as grazing and cutting of pasture.

The conservation of this particular resource, like many other conservation goals, may not be compatible with other aims of conservation on chalk grasslands, as seen from other 'eyes'. Wells (1980) suggests such a dilemma exists over the conservation of both invertebrates, and species rich plant assemblages on chalk grasslands.

1.4. L. flavus.

Much is in fact already known of the biology of this species of ant. It has been much studied in the past and almost any general ant or social insect textbook will contain numerous references to it (see Wilson 1971, Sudd and Franks 1987 and Brian 1983 for example). It is abundant and easily available over much of Europe and it has been and remains, a favoured species for ant research. It is even recommended for use by several authors for use in school projects (King and Woodell 1975, Wratten and Fry 1985 and Skinner 1988 for example). The current extent of this knowledge of the species will be discussed in Chapter Three. However, there remains much more to be discovered, for example, in the field of the sexual production of colonies about which little has been published (Wright 1990).

The ant, just like chalk grassland, has been considered as a valuable conservation resource and conservation measures (transplantation of colonies) have been described by Box (1987).

We can thus conclude that both the ant Lasius flavus and chalk grasslands are valued conservation resources. It is then interesting to find that despite the obvious abundance of this ant on chalk grasslands (see Figure 1.1.) little has been done to research the links between the ecology of this ecosystem and the biology of the ant.

1.5. The aim of the study.

This thesis will concentrate on two main points.

a). The interaction between the management and environment of chalk grasslands and the populations of *L. flavus* found on them. This will be done by examination of the characteristics of sample populations of *L. flavus* present under a variety of management and environmental conditions.

b). How our knowledge of the population characteristics of this ant, in these differing situations, can be used in the conservation of the ant in the ecosystem.

CHAPTER TWO

Chalk grasslands.

2.1. Introduction.

There has been possibly more written on the subject of chalk grasslands and their flora and fauna than any other British ecosystem (White 1789, Hudson 1923, Tansley 1939, Lousley 1950, Smith 1980 to cite just a few of the better known works). This is probably due to two things, firstly their geographical position (in the south of England and therefore nearer to the centres of early academic study) and secondly, the undoubted richness of the flora which in turn produces a rich fauna. Chalk grasslands have, though, for many years, possibly centuries, been in decline.

2.2. The historical decline of chalk grasslands.

Large areas of chalk grassland have been lost over past centuries. Many sites have been destroyed as a result of increasing agricultural pressure (see Figure 2.1). Other areas have been abandoned and invaded by scrub.

The historical decline in the area of chalk grasslands began in the 18th Century when the agricultural emphasis shifted from livestock (mainly sheep) grazing pasture lands, to arable farming (Blackwood and Tubbs 1970). Vast tracts of downland were lost, the process accelerating during the Napoleonic wars, when rising grain prices induced farmers to convert more of their pasture land to cereal production. Blackwood and Tubbs (1970) suggest that in this period this was such a drastic process that in 1815 the area of chalk grasslands left was similar to that in 1966.

Since then, as grain prices have fluctuated, areas have alternately been converted to agricultural production and then abandoned. The

Figure 2.1.

Looking out from the south slope at Old Winchester Hill.

Note the contrast between the Nature Reserve in the foreground and the agricultural land beyond. Much of this agricultural land would have been managed as sheep grazed chalk pasture in the past.

introduction of myxomatosis around 1954 (Fenner and Ratcliffe 1965, Mead-Briggs 1977) and the consequent reduction in the rabbit population also led to large areas reverting to scrubland (Thomas 1960, 1963).

The survey of Blackwood and Tubbs (1970) found about 43,546 hectares of chalk grassland remaining, with just under 70% of this in Wiltshire. Most of these sites consisted of steep escarpment slopes that were unsuitable for arable crops. Since that survey it is likely that further large areas have been lost, particularly since the onset of the Common Agricultural Policy (Prescott 1983). Chatters (1990) discusses the loss of species rich chalk grassland on the Isle of Wight. Since 1956 about 56% of the Island's chalk grassland has been lost to agriculture, building land etc. On East Wight the annual rate of destruction has been about 5% per year since 1980.

Much of the remaining area of chalk grassland in southern England only exists because it has been acquired and managed as nature reserves. Chalk grasslands, even more so than many other habitats, need to be actively managed to maintain their biological interest (see section 2.4.).

2.3. The characteristics of chalk grassland.

2.3.1. The soil. In Britain chalk grassland is classified in the group of calcareous grasslands (Ratcliffe 1977), which also includes grasslands on Jurassic limestone, Carboniferous limestone, Magnesian limestone and Devonian limestone, plus a few other isolated outcrops of other rocks. The soils on these materials all have certain characteristics (Ratcliffe 1977):-

1) A high pH, usually in the region 6.5 to 8.5.

2) A high available calcium content, 300-1,000 mg calcium/ 100g soil

3) A high free calcium carbonate content, (30 to 75%).

4) Often a high organic matter content, (7 to 20%).

Chalk grasslands are normally found on shallow soils (up to 35cm. deep), developed directly from the parent chalk (Shimwell 1973). There are three major soil types, rendzinas, which develop on the steeper slopes, brown rendzinas on more gentle slopes on damper situations, and brown calcareous soils which have lower pH's (6 to 7), less free carbonate and more clay content.

The soils are extremely free-draining (Painter 1971) and this together with the high summer temperatures that are reached by the soil surface (Smith 1980) contributes to the development of drought conditions in the summer months. The consequences for the invertebrate fauna are likely to be as important as those for the flora. Both Tansley (1939) and Smith (1980) commented that the flora of the downs must be limited by the extreme summer minimum water content values of the soil.

In summary typical chalk grassland soils are free draining, nutrient poor and alkaline. It is the very lack of nutrients in the soil that is considered to lead to the species richness of the plant communities (Harding 1973, Rizand et al 1989).

2.3.2. The flora. Chalk grasslands are justly famous for the richness and diversity of their plants (Lousley 1950). Smith (1980) points out how the attractive nature of the chalk flora, described by writers such as Defoe (1724) and Cobbett (1830), induced the early phytosociologists to intensively study it. In Britain, for example, the work of Tansley (1911, 1922, 1939) is well known. Tansley (1939) gave a list of 15 species which occurred in more than 80% of samples from chalk grasslands and which can be considered constant.

Grasses:- *Avenula pubescens*

Briza media

Festuca ovina

F. rubra

Koeleria macrantha

Others:- *Carex flacca*

Cirsium acaule

Leontodon hispidus

Linum catharticum

Lotus corniculatus

Pimpinella saxifraga

Plantago lanceolata

Sanguisorba minor

Scabiosa columbaria

Thymus serpyllum

More recently Shimwell (1973) phytosociologically described the main communities of chalk grasslandas belonging to two Associations;

1) Cirsio-Brometum, a typical chalk grassland characterised by the presence of *Cirsium acaule*, *Bromus erectus*, *Brachypodium pinnatum* and *Asperula cynanchica*, and

2) Agrosto-Campanuletum rotundifoliae, a *Festuca-Agrostis* dominated grassland generally lacking the two grass character species of the first association and where mesophilous species such as *Anthoxanthemum odoratum*, *Holcus lanatus*, *Prunella vulgaris* and *Veronica chamaedrys* are of high constancy.

Within both these associations there are a large number of sub-associations and many of these remain to be satisfactorily described and classified (Shimwell 1973) although some progress is being made (Willems 1978). In an earlier study Shimwell (1971b) established that 79.4% of the plants on calcareous grasslands were hemicryptophytes, that is bearing their overwintering buds at ground level (Raunkiaer 1934).

Perring (1959) emphasized the importance of variation in topography of chalk grasslands in determining the distribution and abundance of a large number of plants species.

2.3.3. The fauna. In contrast to the flora, the invertebrate fauna has been less well studied, and it is only comparatively recently that more intensive study has begun. In his review of the ecology of the English chalklands Smith (1980), discussing the invertebrates of grazed chalk grassland, cites only one source of information before 1954, and the majority of the references are from the 1960's and 70's.

The principle source of information at the present time is the Nature Conservation Review, (Ratcliffe 1977). Chalk grasslands are treated here within the framework of British calcareous grasslands. The review points out how scanty our knowledge of most of the invertebrate fauna is and that most attention is paid to the more popular groups, such as the Lepidoptera, of which there are several distinctive chalk species. For example, the Adonis, Chalkhill and Small Blues, (Lysandra bellargus L. coridon, Cupido minimus), Silver Spotted Skipper, Hesperia comma among the butterflies, and moths such as the Mother Shipton, Callistege mi and Burnet moths, Zygaena spp. Ratcliffe (1977) reports a number of spiders as characteristic of calcareous grassland, such as Zelotes praeficus and Xysticus bifasciatus. A number of other species of spider confined to chalk grassland are only locally frequent eg. Phrurolithus minimus.

Morris (1967, 1968, 1969a, 1971a) has made a more specific study of the invertebrate faunas of grazed and ungrazed chalk grassland, but despite this it is clear that much work remains to achieve a comprehensive knowledge of the invertebrate community characteristics on chalk grasslands.

2.4. Management of chalk grasslands.

As noted in Chapter One, chalk grasslands represent a plagioclimax community which arises as the result of grazing, both by animals controlled by Man, sheep and cattle, and independent of Man eg. rabbits. Active management is needed to maintain its floristic and faunistic interest.

The practical aspects of this management for conservation purposes have been considered by a variety of authors, notably perhaps by Wells (1965, 1969, 1971 and 1973) for the botanical interest and Morris (1969b, 1971b and 1973) for the invertebrate interest. The practical options of management are discussed by Green (1973). Methods of management include grazing (by sheep and other animals), mechanical cutting and burning. The timing of use of the management procedure adopted is also important and depends on the required goals of the management plan and the situation of the individual grassland being considered (Green 1973, Morris 1973, Wells 1973, NCC 1982). Most studies of chalk grassland management procedures have focussed on the botanical implications. There has been a relative lack of work on the effects of cutting and grazing on invertebrate and other animal communities, on chalk grassland, and indeed, on most European grassland ecosystems (Bakker 1989).

2.5. **Lasius flavus** and chalk grasslands.

It is surprising that little reference is made to L. flavus in any of the works discussed in this Chapter, particularly when considering the obvious abundance of its mounds on many chalk grasslands (Figure 1.1). The work presented in this study should provide information to correct this omission and to examine in detail some of the effects of management procedures on chalk grassland ecology.

CHAPTER THREE

The ant Lasius flavus.

3.1 Taxonomy.

3.1.1. The ants. Ants are generally considered to be confined in a single family, the Formicidae, of a single superfamily, the Formicoidea, in the suborder Apocrita, Order Hymenoptera (Wilson 1971). Alternatively, Gauld and Bolton (1988) place the Formicidae in the larger superfamily Vespoidea. The family has been divided into 12 subfamilies by Taylor (1978) of which the Sphecomyrminae (Wilson, Carpenter and Brown 1967) are the only subfamily without living species. The subfamily Formicinae, in which the genus Lasius is found, is considered to be one of the most advanced (Wilson 1971, Taylor 1978).

3.1.2 The genus **Lasius**. The taxonomy of this genus was extensively revised by Wilson (1955) and this review still remains the most comprehensive examination of it. Collingwood (1979) claimed the genus contained about 42 species with a holarctic distribution, with 14 species found in Europe. There are either 7 or 8 members of the genus found in the British Isles (Collingwood 1957, 1979, Bourne 1973, Bolton and Collingwood 1975), depending on the status accorded to Lasius mixtus and L. umbratus.

3.2. Nomenclature.

Lasius flavus is one of the most common ants in the genus. It has previously been known under a variety of names, both common and Linnaean, for example the Yellow Hill Ant (Morley 1953), the Common Yellow Ant (Step 1924), the Yellow Ant (Step 1932) and the Turf Ant (Duncan 1896). This author prefers to use the Yellow Meadow Ant which seems an appropriate description of the species. It has in the past, been placed in the genera Acanthomyops (Morley 1953), Donisthorpea (Donisthorpe 1915) and originally Formica (Gould 1747).

3.3. The distribution of L. flavus.

3.3.1. World distribution of L. flavus. L. flavus is a holarctic species In Europe it is an abundant species from Ireland in the west (O'Rourke 1950) to the USSR in the east (Kusnetskov-Urgamskij 1925), and from Scandinavia in the north (Collingwood 1979) to Central Italy and Spain in the south (Menozzi 1922). It has also found across large areas of North America (Buren 1944 and Talbot 1965 for example) and in Japan (Hayashida 1960). Wilson (1955) usefully summarises the information on its distribution.

3.3.2. The British distribution of L. flavus. The records of the Biological Records Centre at Monks Wood (Barrett 1979) show its presence over most of Britain. It is recorded from 49 of 68, 100 km. squares (Barrett 1979). The records are concentrated in the south of England, where, as Barrett (1979) notes, most of the ant recording has taken place. Like most species of ants L. flavus is undoubtedly much under recorded in the British Isles. Collingwood (1957) suggests it is possibly the most common of the 47 native species of ant in Britain. In Ireland O'Rourke (1950) gives useful information on its distribution, showing it to be present in 20 of the 40 Irish vice counties as defined by Praeger (1901).

3.4. The habitats in which L. flavus occurs.

3.4.1. The necessary attributes of the habitats. L. flavus has three main requirements of its habitats.

a). A suitable temperature regime, with enough warm days in the year for the brood to develop in one season. The distribution of L. flavus is limited in north Europe by cold temperatures and short summer seasons.

b). A suitable moisture regime. The ants can apparently survive temporary inundations such as are found on salt marshes at spring tides. It is probable that pockets of air are trapped in the galleries of the nest. The workers are very susceptible to desiccation, rapidly dying in dry conditions, although the queens are more hardy, (pers. obs.). It is likely that L. flavus is unable to colonise environments that are prone to long periods of dryness.

c). A sufficiently developed soil. Boomsma and De Vries (1980) demonstrated that in a sand dune ecosystem, L. flavus was excluded from the early succession. A large part of the food of L. flavus consists of root aphids and their exudates, (see section 3.9). Without a sufficient supply of organic matter in the soil the plants upon which the aphids depend will not be able to grow successfully.

3.4.2. The types of habitats. L. flavus can be found in a great variety of habitats throughout its range. In north Europe it is typically found in permanent to semi-permanent grass pastures and, where it is warm enough, on the periphery of woodlands. Apart from the typical mound building of the species it will also nest under stones (Gosswald 1932, Elmes 1974, Collingwood 1979), the stones acting as a heat sink. The stone nesting habit is also found in the lowlands of southern Europe (Wilson 1955), although as a source of heat stones are presumably less important in these regions, although they may act to maintain temperatures in otherwise cooler evenings.

The species can be found in marshy areas (Skwarra 1929, Gosswald 1932), damp meadows (Blackith et al 1963), in salt marshes, (Woodell 1974), and tidal meadows (Nielsen et al 1976). In southern England and probably in other regions L. flavus is common in gardens (contrary to the findings of Gosswald (1932) in continental Europe), and in surburban areas, and is even found in frequently mown lawns and recreational areas, eg. Blackheath in London, (pers. obs.).

Oddly, Hayashida (1960) appears to report that this species was most common in peat bogs in a lowland area of Japan.

3.5. Nest characteristics of *L. flavus*.

3.5.1. General characteristics. *L. flavus* is an underground species, the workers seldom appearing above ground (Wilson 1955), although the large soil mounds that the workers often build are conspicuous. (see Figure 1.1). In common with many other soil dwelling ants the nests of *L. flavus* consist of a central complex of galleries with tunnels radiating out (Brian and Downing 1978). Brian (1983) suggests the tunnels may extend down as far as 2 metres in suitable soils. The distance to which they may radiate outwards is unknown, although the core samples taken between pairs of nest mounds by Pontin (1978) suggest that over a metre is possible. Nielsen et al (1976) also found considerable numbers of workers in soil cores 30 cm. or more away from the nest mound.

3.5.2. The soil mound. The characteristics of the soil mounds which *L. flavus* build, have attracted much attention. This soil mound is an extremely variable structure, changing in response to many geographical and local environmental factors.

3.5.2.1. The purpose of the mound. The main purpose of the mound is to act as a solarium, in particular to catch the early morning sunlight, in order to warm up the brood as soon as possible after the cooler night. It has often been observed that the mounds are not circular in shape, being larger in the south-east to north-west axis (Huber 1810, Linder 1908, Forel 1928). The ants place more soil on the south-eastern side (Linder 1908), thus enlarging it compared to the north-western side. The taller south-eastern side will then present more area to the morning sun. The north-western side may also catch the light of the setting sun and warm the nest longer into the evening than surrounding areas.

Many mounds show this type of orientation, particularly in the Swiss mountains where it is very marked (Donisthorpe 1915). In other mounds it can be by no means as clear. It is less obvious in younger, smaller mounds for example (pers. obs.). Other factors can also interfere with the orientation, such as the trampling of animals while grazing on steep slopes (see plate 11 in Brian 1977).

3.5.2.2. Other functions of the mound. As well as acting as a solarium the mounds can raise the level of the colony above that of a high water table, for example in marshy areas. This was first suggested by Richardson (1894), and more recently Waloff and Blackith (1962) demonstrated how the level of the water table affected the size of mound. In observations made at Silwood Park, in Berkshire, England, they concluded that in freely drained areas with a low water table the ants tended not to construct mounds. In areas where the drainage was less good and the water table higher, mounds of above average size were built. Blackith et al (1963) noted how mounds on a pasture in Devon, England, increased in size when the water table rose due to the damming of a stream.

3.5.3. The sizes of mounds. The ants can build up the mounds to large sizes. Donisthorpe (1915) mentions that he found one about one metre in height, although they are usually much smaller. Waloff and Blackith (1962) found, in their Area 3, that in 60 mounds chosen at random the mean height was 22 cm. with a range of 6 to 37 cm., and the mean largest diameter of the mounds 72 cm. with a range of 37 to 145 cm.

3.5.4. <u>Soil movements by the ants.</u> Growth of mounds occurs by the piling up of soil particles on the surface of the mounds by the worker ants. Soil particles are generally seen to be brought to the surface of the mounds (presumably from galleries excavated underground in and around the mound) when conditions are damp, usually after overnight rain or a heavy dew.

Pickles (1942) estimated that when the ants were active an average of 10 grams of soil per day was brought up to the mound surface. King (1972) estimated a maximum accretion rate of 1340 cm^{-3}. per year per colony. Using this accretion rate Wells et al (1976) and King (1981b) were able to estimate the age of ant mounds and correlate this to the known history of the grasslands they inhabited.

3.5.5. <u>The mound soils</u>

3.5.5.1. <u>The soil components.</u> The chemical components of the mound soil have been investigated on a number of occasions to see if they differ from surrounding soils. King (1977a) has summarised the data of other authors, together with his own, and concludes that there is little chemical difference save for a small increase in potassium content, and a smaller increase in the amount of phosphorus.

In data from acidic grassland on the Gower Peninsula King (1981a) found that the ph, exchangeable hydrogen and potassium ion contents of mound soils were not significantly different from pasture soils, while the total exchangeable bases were significantly higher and the organic matter content significantly lower.

On chalk grassland at Aston Rowant King (1977a) found that the ant mound soils did not differ significantly from surrounding pasture soils in terms of calcium content or, extractable phosphorus. The content of organic matter was significantly lower at 14.2% compared to 16.85%, as was the nitrogen content in the same samples.

3.5.5.2. Water contents of mound soils. Mound soils tend to be drier than the surrounding pasture ones. King (1977a) in a series of measurements of the mean percentage water content, found from a sample of 5 mounds that the top 5 cm. of mound soil was drier than that of the surrounding pasture. Further he found that the soil of the south facing aspect of the mound was drier than that of the north aspect. The mounds have more variable microclimates than surrounding level ground, with the south aspect recording very high temperatures, and the north aspect being cooler. This was particularly conspicuous when snow, frost and dew remained longer on the north sides, than on the south sides of the mounds or the surrounding pasture (King 1977a).

3.5.5.3. Particle sizes of mound soils. Haarlov (1960) observed that the maximum size of a soil particle carried by a worker of *L. flavus* was 2 x 4 mm. The maximum jaw width of the workers was 0.65 mm. and the workers preferred to manipulate soil particles under 0.75 mm. in diameter when given a choice of sizes. Wells et al (1976) found a lack of particles over 0.5 mm. in diameter in mounds, in contrast to surrounding grassland. King (1977a) says that in mounds at Aston Rowant, Oxfordshire, England, the median size of the structural aggregates in mound soils is lower than the surrounding grassland, although no figures are given, and that the mounds are virtually stoneless compared to the pasture soils (0.1% compared to 6.7%). The worker ants are unable to manipulate large stones. This also results in a lower bulk density for the mound soils, 0.45 compared to 0.56 g/cm^{-3}.

3.5.5.4. The pH of mound soils On chalk grasslands the pH of mound soils can be higher than that of the surrounding pasture due to the bringing up of chalk subsoil particles by the ants (King 1977a). However, in his data from Aston Rowant, King (1977a) found that the ant mound soils did not differ significantly in pH from surrounding pasture soils.

On acid grassland at Thornhill, Yorkshire Pickles (1940a,b) observed that the pH of soils in mounds was greater than that of the surrounding pasture. From the data given in his paper (Pickles 1940b) the following figures have been calculated. The mean pH of the mound soil was 5.05+/-0.11* and of the pasture soil 4.37+/-0.10. There were 21 pairs of samples. Haarlov (1960) found no significant differences in mound and surrounding soils on Danish pastures, although his sample sizes were very small. Grubb et al (1969) and Lambley (1967) did find that mound soils were significantly different (slightly higher pH). King (1981a) found no significant differences between mound soils and surrounding soils on the Gower Peninsula in Wales. While the studies above have come to differing conclusions it is interesting to note that in all the studies mentioned above mound soils were on average of a higher pH than the corresponding surrounding soils.

3.5.6. <u>The growth of mounds.</u> The growth rates of mounds at Silwood Park (Berkshire, England) have been examined by Waloff and Blackith (1962). They followed the progress over several years of a group of eighteen small mounds, of which, originally, eleven were up to 2.5 cm. high, five from 5 to 10 cm. high, and the other two, 15 and 17.5

All figures in this thesis, given in the form XX+/-XX represent a mean and the standard error of that mean, not the standard deviation, unless otherwise stated.

cm. high. The increases in size of these mounds were measured for 8 years. Little is known of the early growth of *L. flavus* colonies, and so Waloff and Blackith (1962) were unable to estimate the age of their smallest mounds. For the purposes of their calculations they assumed they were 1 year old. This can be considered extremely unlikely for the largest of their sample mounds. Little is known of the early growth rates of mounds but it is clear that a considerable time is required before the colony gets large enough to build a mound of significant size. Observations indicate that newly founded colonies do no more than throw up a little surface soil.

The mounds were variable in their growth rates, but the following regression equations were produced, firstly relating diameter to age:

$$x = 2.77z + 5.48$$

x = greatest diameter
y = maximum height
z = age in years

secondly relating height to age:

$$y = 0.90z + 0.39$$

and thirdly relating diameter to height:

$$x = 1.80y + 6.36$$

Combining the data from these mounds with data from sets of older mounds in the same areas, they concluded that in general, for an increase in height of 1 cm. a mound would increase its maximum diameter by 2.45 cm.

3.5.7. Colonies of *L. flavus* that do not build mounds. Whilst the construction of a permanent earth mound is one of the characteristic features of a colony of *L. flavus*, there are circumstances in which mounds are not constructed. For example in Europe colonies of *L. flavus* have been observed on many occasions to be without mounds. On steep slopes and areas of dry sandy soil the mounds are not stable and will collapse and in areas of high rainfall they may be knocked down by the rain (Brian 1977). Brian (1977) also suggests that in the lowlands of southern Europe mounds are not built at all, and that this may be due to the worker ants being unable to manipulate the hard soils, although evidence for this is not presented. In many areas of recreation grassland in southen Britain mounds are not in evidence although colonies are clearly present. In this case it is likely that either trampling or mowing prevents the formation of mounds.

In America Wilson (1955) states that he has never seen a mound built by this species. Talbot (1965) describes some of these American nests, located in Livingstone County, Michigan. She examined these nests by careful excavation. There were no soil mounds.

> "Nests of *Lasius flavus* were widespread near the surface, but did not go deep. Larger nests sprawled out in very irregular shapes for 0.81 square metres or more. Smaller ones might occupy 0.18 to 0.27 square metres. Often the ground was honeycombed with chambers of various shapes, so that it looked like a piece of magnified coarse bread. The smooth cavities were almost touching and were connected by several short galleries. They varied greatly in size from tiny cells to those as large as 3.5 x 2.4 x 1.3 cm. Chambers began immediately below the surface, but were most plentiful between 2.5 and 10 cm. deep."

The reasons why the workers do not build soil mounds at all in America are not known and this is an aspect of the biology of the species that merits further investigation.

3.6. The effects of the presence of *L. flavus* on the soils they inhabit.

The considerable amount of digging that these ants undertake has some effect on the soils they live in. Drainage can be improved by ant tunnels and galleries, (Green and Askew 1965), and soil characteristics changed (Czerwinski et al 1971, King 1977a). For example pH can be increased by the activity of *L. flavus*, the worker ants bringing up chalk subsoil particles to the surface (King 1977a). Wells et al (1976) calculated that the soil contained within the ant mounds on the Porton Ranges (Wiltshire) was equivalent to a layer up to 5 cm. deep over the whole grassland. Like earthworms, *L. flavus* workers are involved in considerable soil turnover and their importance should never be overlooked.

3.7. The flora of the mounds.

The nest mounds of *L. flavus* are usually covered by vegetation, the roots of which help stabilise and bind together the loose mound soils. It has been noticed on several occasions that the soil mounds tend to have a different flora to that of the surrounding area (Grubb et al 1969 on chalk heath, Thomas 1962, Griffiths 1968, Wells et al 1976 and King 1977a on chalk grassland, Haarlov 1960 on a tidal meadow, Woodell 1974 and Kay and Woodell 1976 on a saltmarsh and King 1981a on acidic grassland), also see Figure 3.1. King (1977a,b,c) has undertaken the most thorough study of this phenomenon, examining the flora of mounds on chalk grassland and comparing it to that of the surrounding pasture.

Grubb et al (1969) gave a list of factors which might be of importance in influencing the flora of a mound. These factors are listed and commented on below.

a).

b)

Figure 3.1.

Mounds of *L. flavus* covered with

a) *Helianthumum nummularium.*

b) *Thymus serpyllium.*

1) Less shading and root competition on the mounds. The surfaces of mounds, being raised above the surrounding vegetation may well be less subjected to shading than surrounding pasture. It is difficult to be precise on root competition for mound plants compared to non-mound plants, but King (1977a) states that ant hills in summer frequently have a plant cover of only 5 to 20%. The rest of the mound surface is covered by bare soil, due to soil being thrown up by the worker ants smothering the surface vegetation.

2) Better aeration of mound soils. As already discussed King (1977a) has commented on the lower bulk density of the ant mound soils, due to the general absence of large particles. This structure of the mound soils and their dryness would suggest that aeration is likely to be better in mound soils than in pasture soils.

3) A more extreme temperature regime. The observations discussed in section 3.5. indicate that the mounds are subject to more extreme temperature variation than ordinary soils. It would seem probable that this could affect the plants growing on the mounds.

4) Less acid soil, (here Grubb et al (1969) are specifically referring to chalk heath). In section 3.5.5.4. it was concluded that mounds do tend to have a higher pH than surrounding soil. However, King (1977a) concludes that except on chalk heath this is likely to have a minimal effect on the flora.

5) Selective eating, moving and bringing to the mound of plant seeds. Grubb et al refer to Ridley (1930) as evidence for movement and eating of seeds, but L. flavus is not specifically mentioned in his book. There is no evidence to suggest that L. flavus mound flora is modified in this way (King 1977a), although floras associated with other ant species most certainly are (Beattie 1985).

6) Burial of plant seeds. King (1977c) clearly demonstrated the effect that burial can have on seedling germination and establishment. Of 10 plants which he examined, all of which were common chalk grassland plants only 4 showed any ability to overcome burial. Burial is an important factor in determining the success of seed germination on mounds.

7) Soil is continually being brought up in occupied mounds so that plants are smothered. King (1977a) reports that on active mounds the apparent vegetation cover of 5 to 20% may be a result of an initial cover of 80% being smothered by soil in the Spring. The bare surface is then reinvaded by plants that are capable of growing up through this soil. Other plants incapable of growing through the soil, such as rosette species are killed. Smothering of plants is therefore a powerful selective factor on the flora of the mounds.

7) Drought is more intense. Kings' (1977a) figures again support this statement. He also suggests that the growth of *Festuca rubra* and *F. ovina* on the mounds is limited by water availibility.

8) Animal disturbance of mounds. Many animals can affect the mounds of *L. flavus*. Rabbits will dig into the mounds, evidently liking the soft soil, and will also urinate and defecate on them. The mounds are preferentially grazed by sheep (Piggott 1955, Griffiths 1968, pers. obs.), and may be poached (trampled into mud) by cattle, badgers (*Meles meles*) or sheep sleeping on them. Thus effects on the flora are likely to be considerable.

9) Plants being harmed by the activities of root aphids. King (1977a) concluded that this was a minor effect if it existed at all. He found no evidence of it in his work.

King (1977a,b,c) concluded that the ant mounds have a distinctive flora with two types of plants dominating, firstly those that could survive being smothered by soil excavated by the worker ants, such as the stoloniferous species Agrostis stolonifera and Galium verum, and secondly fast growing annuals such as Linum catharticum and Medicago lupulina which can flower before being covered with soil. He also suggested that the presence of ant mounds with their different flora from the surrounding grassland will help enhance the variety of plant species present in an area of chalk grassland.

Thus it is possible that the aim of conserving ant mounds may have a desirable side product in helping maintain or even increase the diversity of the grassland they inhabit. The ant mounds on chalk grassland provide a quite different set of soil characteristics to those to be found in the surrounding pasture. As such they can almost be considered as a habitat within a habitat and have considerable conservation value. Woodell and King (1990) have also stressed the importance of the mounds of colonies of L. flavus in this respect.

3.8. The life cycle of **Lasius flavus.**

3.8.1. The founding of colonies. After the mating flight, the fertilised queens land and look for somewhere to build the first small brood chamber. They may enter small crevices in the ground or actively dig in suitable soil (Waloff 1958). More than one unrelated queen may join together at this stage, and Waloff (1958) has shown that in artificial nests this improves the survival chances of the queens, increases the number of eggs laid and speeds their development. These queens will later usually separate (Wassman 1910, Waloff 1958), each taking some of the brood. Waloff and Blackith (1962) observed the gradual division of a small nest mound into two separate mounds and this is possibly a natural example of two queens separating after jointly founding a nest. Older, large nests are very infrequently found with more than 1 queen (Donisthorpe 1915, Anderson 1970).

3.8.2. The growth of the colony. The first eggs may be laid almost immediately after the mating flight and digging of the brood chamber After hatching from the eggs, the larvae pass through three stages or instars, the queen/s feeding them on trophic eggs and salivary secretions derived from the fat reserves accumulated when they were gynes in the parent colony. The colony may overwinter with larvae in one or more of the three stages, or, if conditions are suitable, the larvae may pupate and the first workers emerge before winter. Once the first brood has matured they forage for food for the queen and for themselves, and enlarge the nest. The queen is free to concentrate on egg laying. The queen lays eggs each year from which workers develop. Some may complete their development in the same year, but many overwinter as larvae and emerge in the following year (Peakin 1985). The population expands year by year, but little is known of the dynamics of this process, although Pontin (1963) estimates that in the early phase of exponential growth the worker population could double each year. The amount of mortality of colonies, from the queens digging the first brood chamber, up to when the colony becomes firmly established, is unknown as yet.

3.8.3. The production of sexuals. The colony is said to be mature when it starts to produce sexuals, ie. winged males and/or gynes, (Brian 1965). Males and gynes are produced from eggs laid the previous summer which probably overwinter as third instars, with the largest destined to become the gynes. (Peakin 1985). In the following spring the largest larvae rapidly increase in size, being preferentially placed in the warmest parts of the nests (pers. obs., Peakin 1960) and developing faster than the smaller larvae which are kept in cooler parts of the nest (Peakin 1960).

After emergence from their pupae, the gynes rapidly gain weight, as much as doubling it in only two or three weeks, putting on the fat reserves necessary to rear their first workers. The gynes do not fly until this process is complete, despite the occurrence of suitable weather conditions. The males probably do not increase their body weight in the same period (Boomsma et al 1982, Peakin 1972).

3.8.4. The mating flight. Flights typically occur in mid August in Britain, on days when there is little wind and it is usually, although not always, warm and sunny. Often large numbers of colonies will have their sexual flight at the same time and often with the sexuals of other species as well, particularly those of *L. niger*. This can lead to extremely large swarms of winged ants. This type of synchronised mating flight allows greater genetic mixing to occur with gynes and males from many different colonies flying together. Major flights of sexuals are not uncommon, but smaller flights can occur on other suitable days, when only some colonies are prepared for the flight. The remarkable synchronisation of the flights of individual colonies contrasts strongly with other species in which this does not occur, for example *Tetramorium caespitum*.

Mating occurs during the sexual flight. The gynes are able to support the weight of the much smaller males while flying. It seems likely that some gynes may be inseminated by more than one male (Forel 1928), such polyandry being often recorded in social insects (Page 1986). It has also been demonstrated in other members of the genus *Lasius*, (Imai 1965, Van der Have 1987).

Many queens are lost during the marriage flight, eaten by birds such as swallows, Hirundo rustica and swifts Apus apus, and after landing, by birds such as starlings, Sterna vulgaris and sparrows, Passer domesticus. Sparrows have been seen gorging themselves on queens, catching one at a time, rubbing off the wings on a rough surface, eating the queen and then catching another (pers. obs.).

After mating the queens land to search for nest sites, and the males die.

3.9. The food of **Lasius flavus.**

As L. flavus is a subterranean species it has proved difficult to establish precisely what the workers eat. The relationship between L. flavus and aphids has been known for a long time, (Lubbock 1882) but its precise nature remained unknown. In 1955 Wilson stated, "it has generally been assumed that the main food of this species consists of the secretions of Homoptera maintained in the nests (cf. Eidmann 1926), but food habits have never been well investigated."

Since then Pontin has shown in a series of papers (1958, 1961, and particularly 1978), that the food of this species consists of three main components, the secretions of root aphids, ie. honeydew, the aphids themselves (particularly young instars), and a variety of small invertebrate prey. Many species of aphids have now been associated with L. flavus, several as obligate myrmecophiles. Without the ants the aphids foul themselves in their own honeydew. The ants may also dig chambers around the plant roots for the aphids (Pontin 1978).

Pontin (1978) was able to correct the still widely held view that the aphids were confined to roots in the nest mound (Eidmann 1926, Czerwinski et al 1971), confirming the earlier observations of Carey and Diver (1937). Pontin (1978) found worker ants associated with underground aphids in soil cores up to 1 metre outside the mound. Nielsen et al (1976) also found worker ants up to 1 metre away from the mound.

Aphid relationships with L. flavus will be further discussed in Chapter Eighteen.

3.10. The relationships of **Lasius flavus** with other organisms.

L. flavus plays an important role in the lives of many animals. Some of the animals which feed on it are of economic importance, for example the Grey Partridge, Perdix perdix (Potts 1970), and some are rare and in need of protection, for example the Chough Pyrrhocorax pyrrhocorax (Cowdy 1973). For both of these species L. flavus is an important component of their food. Potts (1970) gives some details of the feeding of Grey Partridge chicks on the adults and pupae of the ant. The adults will take the chicks to a mound and dig in it, and then with the chicks, feed on the ants. Indeed, from a selection of young birds up to two weeks old, ants constituted 31% of the food items found in the crops of the birds, and most of these ants were adults and pupae of L. flavus. Potts (1970) also collected two chicks in which L. flavus constituted 86% of the food items. The Green Woodpecker, Picris viridis also feeds on this ant (Edington and Edington 1972), particularly in winter, and its characteristic damage to the nest mounds (conical holes on the mound surface) is frequently seen on chalk grassland. Other corvids may also feed on the ant at times (Cowdy 1973, Coombs 1978).

The extent to which other organisms feed on L. flavus is less well known, but it is certainly preyed upon by Lasius niger (Pontin 1961) and Myrmica scabrinodis (Collingwood 1979). Other groups which may feed on L. flavus workers include some spiders (Jones 1983) and pseudoscorpions (Legg and Jones 1988).

Richards and Waloff (1954) decribed how mounds of *L. flavus* at Silwood Park, Berkshire provided oviposition sites for the grasshoppers, *Chorthippus brunneus*, *C. parallelus*, *Omocestus viridulus* and *Stenobothrus lineatus*. These species prefer to lay their eggs on patches of bare warm soil and the mounds of *L. flavus* provided the majority of such sites available. Indeed, *C. brunneus* eggs were laid only on ant mounts, *C. parallelus* almost always on mounds and the for the other 2 species a majority of eggs were laid on ant mounds. Again, it could be assumed that a loss of the ants would thus lead to a large reduction in the grasshoppers.

Within the nests of *L. flavus* are found many organisms known as myrmecophiles. Some of these species rely on the ants to survive and many of them are rare or uncommon, for example the beetle *Claviger testaceus*. Donisthorpe (1915, 1927) lists many such species. Many of the aphid species associated with the ants also have a very close relationship with them (Nixon 1951, Way 1963), the ants providing protection for the aphids, and in return receiving honeydew.

Elimination of, or reductions in, the ant populations, for example by ploughing up grassland, could well lead to decreases in the populations of some of these bird species. If management of grasslands results in the ant population remaining healthy then the benefits would obviously be widespread.

3.11. Lasius flavus and agriculture.

The impact of *L. flavus* on agriculture led Moore (1966 p. 78) to describe it as a pest species.......

> " In the midlands the yellow mound ant *Lasius flavus* may reduce the yield and edibility of the

> herbage on large acreages of grassland. The ants do not feed on the herbage but their tunnelling activities and the hills of soil so formed cut off essential water supplies from the grass roots. Moreover, several species of aphids may live in an anthill, and unlike the ants actually feed on the grass roots. Affected grassland needs to be drastically harrowed using spiked implements which will tear out the ant hills and spread the soil. This treatment must be followed by a suitable application of fertilizers to feed the grass and encourage the remaining plants to fill up and knit together, to form a turf again. In very severe cases reseeding may be necessary."

Moore (1966) does not give the source of his information, but this is clearly a problem which has been with farmers for a long time. Duffey et al (1974) state that ant-hills were a serious nuisance on many grasslands, with the example being given of a report on agriculture in Rutland (Crutchley 1794). Here the spreading of the contents of the hills over the sward on light soils was recommended as a valuable top dressing. However, on heavy soils (unlike chalk), the complete removal of the debris was suggested.

We can contrast this position with that of King (1977a) who concluded the ants had little if any direct effect on grassland plants. It is also clear that modern intensive grassland farming methods are inimical to the establishment of populations of L. flavus, and nature reserves need to be managed correctly to encourage stable populations of this ant.

3.12. The importance of **L. flavus** in its habitats

The information presented above illustrates how L. flavus is widely linked with other organisms and the environment. Knowledge of the biology of this species can be related to that of many other species of animal and plant and may not only contribute to the conservation of the ant itself but to the many other species with which it is associated and thus the general species richness of the environments which it inhabits. In the light of the perceived abundance of this ant in many areas and the relationships it has with many other species of plant and animal, it appears that it has a major role in many habitats. For example, the variety of plants to be found in a habitat can be increased (section 3.7) and the amount of soil turnover can be substantial (Grubb et al 1969, Woodell and King 1990).

Furthermore, the energy flow through the ants would appear to be quite substantial. Pontin (1978) estimated that colonies of L. flavus could easily take in up to 10 Kcal per day in honeydew. Using this figure King (1981b) estimated that up to 310 KJ/m^2/year passed through ants in lowland grassland ecosystems.

There can be no doubt of the importance of L. flavus not only by virtue of its large and often dense populations but also because of the substantial effect it has on the fauna and flora of the ecosystems in which it is found. Its absence would lead to a considerable impoverishment of its characteristic habitats. Conservation management of chalk grassland should take note of the particular requirements for the maintainance of L. flavus.

CHAPTER FOUR

The hypotheses to be tested.

4.1. Introduction.

Having discussed the aims of the project and the background information to it, we can ask the question, what are the hypotheses that we are seeking to test? In its most fundamental form the null hypothesis of this whole project can be stated as follows.

4.2. The null hypothesis, H:0.

The characteristics of *Lasius flavus* populations on chalk grasslands are not significantly affected by variation in:

1) management procedures,

2) the physical environment,

3) the biological environment.

4.3. The alternative hypothesis, H:1.

The characteristics of *L. flavus* populations on chalk grassland are significantly affected by variation in:

1) management procedures,

2) the physical environment,

3) the biological environment.

4.4. The characteristics of the ant populations.

The characteristics of the *L. flavus* populations that have been used in testing this hypothesis are:

1) the size of the earth mounds produced by those colonies, as measured by; a) the diameter of the mounds,

b) the height of the mounds,

c) the above ground volume of the mounds,

d) the area covered by the mounds,

2) the density of mounds present,

3) the spatial distribution of the mounds,

4) the worker populations of the colonies,

5) the sexual production of the colonies as described by;

   a) the total productivity,

   b) the investment ratio.

4.5. The management procedures.

Management was considered on the basis of:

1) past procedures,

2) present procedures ie,

   a) grazing, mainly by sheep,

   b) mowing and scrub cutting.

4.6. The physical environment.

Those attributes of the physical environment which were considered likely to be important in determining the characteristics of the *L. flavus* populations were:

1) the aspect of the habitat,

2) the slope of the habitat,

3) the altitude of the habitat,

4) the temperature regime of the habitat,

5) the soil depth,

6) the soil density,

7) the soil water contents,

8) the soil pH.

4.7. The biological environment.

Those attributes of the biological environment which were considered likely to be important in determining the characteristics of the *L. flavus* populations were:

1) the flora of the habitat,

2) rabbit grazing in the habitat,

3) the soil invertebrates of the habitat, in particular the root aphids associated with the ants.

PART THREE

THE METHODS

CHAPTER FIVE

The study sites.

5.1. The selection of suitable study areas.

Field sites that could be used in this project had to fulfill certain criteria which are listed below.

1) They should be chalk grassland.

2) They should have large populations of the ant *L. flavus*.

3) The owners of the sites should be willing to allow work to take place on their land.

4) There should be areas with differing management regimes and environmental conditions.

5) The past history of these areas should be relatively well known.

6) The areas should not be subject to excessive public disturbance, particularly in view of some of the later work involving marking of individual colonies.

5.2. The selection of the major sites.

Many well known areas of chalk grassland do not fulfill these criteria, Box Hill for example would suffer from excessive public disturbance. Many other areas do not have well documented past histories and are not subject to a controlled mangement system. It was felt that the best locations were likely to be those under control of a conservation body, employing full-time wardens, such as those under the jurisdiction of the Nature Conservancy Council (NCC). The NCC is the government body which promotes nature conservation in Great Britain. It gives advice on nature conservation to government and to other interested parties. It is also responsible for selecting, establishing and managing a series of National Nature Reserves (NNRs) (Ratcliffe 1977, Jones 1987). It is also keen to encourage research work on its reserves.

The NCC were thus approached and asked to suggest suitable areas in which they would be willing to allow field work. Three sites were suggested by the NCC, all NNRs, Old Winchester Hill and Martin Down in Hampshire, and Aston Rowant in Oxfordshire. These sites, or at least areas within these sites, fulfilled all the criteria required of the field work sites.

5.3. The advantages of the selected sites. On these reserves current and past management has been as far as possible accurately recorded and such records as exist on management prior to the establishment of the areas as NNRs, have also been collated. This enables the researcher to quickly determine the management characteristics of many areas.

One of the problems of a project such as this, is that an experimental test of the effect of management on ant populations would require many years to carry out, it being necessary to establish and consistently manage experimental areas until results could be observed. This is beyond the scope of a Ph.D. study because of the time limitations. The next best thing is to observe the results of controlled management regimes which have been set up as part of other projects. In effect the researcher is collecting the results of someone elses experiment. Because management has been accurately recorded on each of these study sites it is possible to do this in certain areas on each of the reserves.

5.4. Descriptions of the study sites

Figure 5.1 shows the location of the three reserves, and a map of each is also shown, (Figures 5.2, 5.3 and 5.5). In addition to these three major sites one minor site was also used, St. Catherines' Hill,

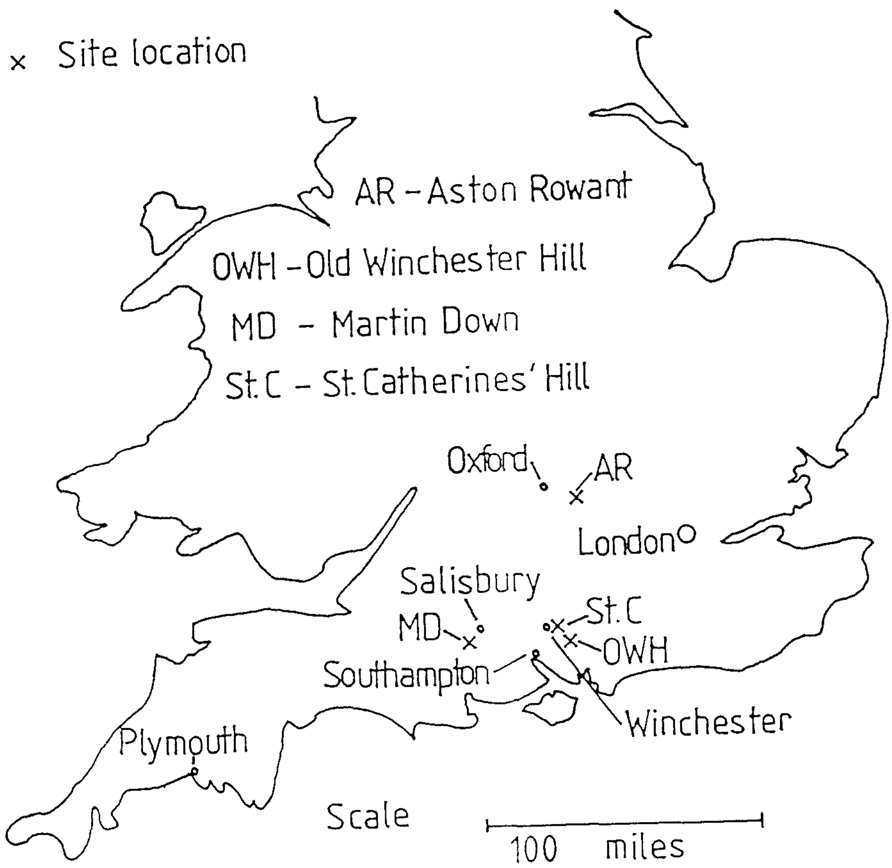


Figure 5.1.

<u>The Location of the study sites.</u>

near Winchester in Hampshire.

5.4.1. Old Winchester Hill. (Grid reference SU 642 210)

This reserve can be seen on the Ordnance Survey 1:25,000 map SU 62/72 (Petersfield and East Meon).

5.4.1.1. General description. This reserve was established as an NNR in 1954, preserving one of the remnants of chalk vegetation on the South Downs. The reserve covers over 60 hectares and is situated in eastern Hampshire overlooking the Meon Valley. It was classified as Grade 1 grassland by Ratcliffe (1977). Old chalk grassland, still in good condition is now rare in Hampshire but aside from this, Old Winchester Hill is of special interest because of its geographical position. It lies in the middle of a range of decreasing oceanicity from the west to the east across England. The reserve is important for its botanically interesting grazed chalk grassland, areas of ungrazed chalk, mixed chalk scrub, yew (*Taxus baccata*) woodland and mature deciduous woodland. Important plants found include the Round Headed Rampion *Phyteuma orbiculare* which gives a spectacular display in July, and Juniper, *Juniperus communis* (see Figure 1.1). It is also rich in orchids, and butterflies (38 species recorded). The eastern part of the reserve was once the site of an Iron age fort and the ancient earthworks are still clearly visible.

Most of the grassland is dominated by *Festuca ovina*. On the south facing slopes an interesting short and diverse thermophilous community of plants has developed which is in contrast to the vegetation on the north facing slopes and coombes, which is rich in mosses and liverworts (Thomas 1960, 1963, Watson 1960).

A nature trail has been constructed around the main parts of the reserve and controlled public access is encouraged. For example it was

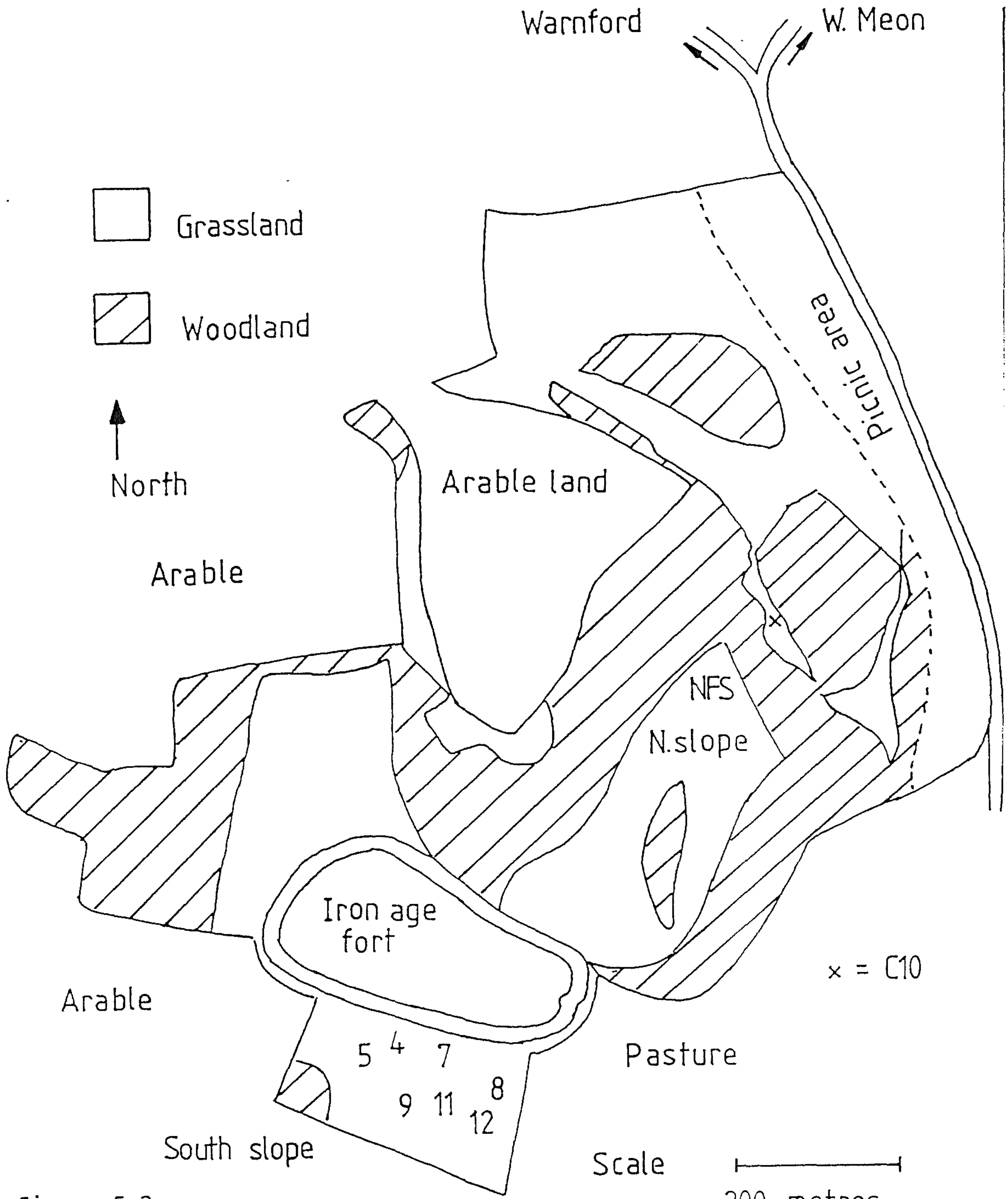


Figure 5.2.

Map of Old Winchester Hill NNR.

The positions of areas on the reserve whose ant populations were examined (see Chapter Ten) are indicated by numbers or letters (eg. 5, 12, NFS).

estimated that 60,000 people visited the reserve in 1977 (NCC 1977). An information centre has also been set up and is opened for most of the summer months.

There is one particular problem encountered at Old Winchester Hill which is uncommon in ecological research. During the Second World War the reserve was used by the Army as a practice mortar range. Unexploded devices are still found on the reserve and some areas are cordoned off because of this. Any digging or putting in of posts etc. has to be preceded by an examination of the area with a metal detector to check that an unexploded mortar bomb is not in the way.

On the Ordnance Survey (1974) map of rainfall in England and Wales, 1941-1970 this reserve lies between the mean annual rainfall contours of 950 and 1,000 millimetres. The annual mean amount of bright sunshine per day, 1941 to 1970, is 4 to 4.5 hours per day (DOE 1975-). The mean January temperature was between 3.5 and 4^{o}C and the mean July temperature between 16.5 and 17^{o}C in 1941 to 1970 (DOE 1975-). The predominant winds are south westerly DOE 1975-).

5.4.1.2. Previous research work at Old Winchester Hill. Thomas (1960, 1963) used this reserve as one of the major sites for his work on monitoring the effects of the decline in the rabbit population, induced by the spread of myxomatosis, on the flora of chalk grasslands. A transect, which no longer exists, was set up across the reserve and the flora monitored for many years. Watson (1960), in association with Thomas' work, also monitored the bryophytes on the reserve.

5.4.1.3. Management policy and history on the reserve Current management on this reserve is aimed at producing a range of long, medium and short grass areas in which the maximum variety of both plants and invertebrates can be fostered. In common with most other downlands the area was extensively rabbit grazed until the outbreak of myxomatosis, which occurred in 1954 on this reserve (Thomas 1960). There was little rabbit grazing until 1957, since when a fluctuating population of rabbits has existed, depending on new outbreaks and recovery from the virus. In 1957 there was an extensive attempt to clear much of the danger from unexploded mortar bombs on the reserve. This resulted in some disruption which Thomas (1960) comments on as causing severe damage to the population of Juniper on the south slope of the reserve.

From 1957 to 1961 there was some cattle grazing with winter grazing of sheep. Throughout the 1960's there was only spasmodic sheep grazing which was not fully effective in the maintainance of the grassland. In the 1970's cattle grazing was restarted but led to erosion problems in some places. In 1979 sheep grazing, under a specific management plan, was begun and has continued ever since. There may be, though, the occasional use of light cattle grazing on some places on the reserve, as for example in winter 1989 on the western part of the reserve. The grazing tends to be of a rotational nature, rather than every year.

5.4.2. **Aston Rowant** (Grid reference SU 740 975)

This reserve can be seen on the Ordnance Survey 1:25,000 map SU 69/79 (Watlington and Stokenchurch).

5.4.2.1. General description. This reserve was established in 1958, conserving a fine example of chalk downland, scrubland and beech woodland. The reserve covers 146 hectares of the Chiltern Hills in Oxfordshire. It is situated to the south east of Oxford, and the M40 motorway cuts straight through the middle of it (see Figures 5.3. and

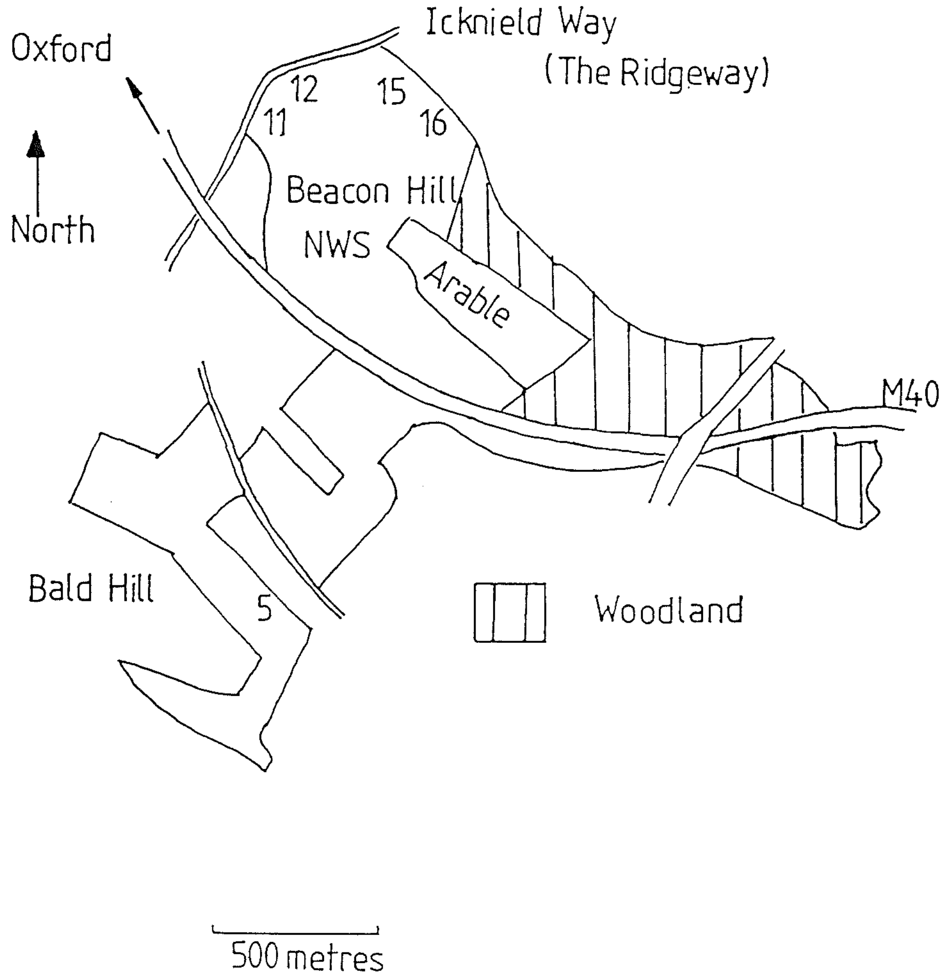


Figure 5.3.

Map of Aston Rowant NNR.

The positions of areas on the reserve whose ant populations were examined (see Chapter Ten) are indicated by numbers or letters (eg. 5, 11, NWS).

5.4.) providing excellent access for visitors via junctions at Stokenchurch, just to the south, and Lewknor at the north end of the reserve. It was rated by Ratcliffe (1977) as a grade 1 site for grasslands with grade 2 woodland also present. It is one of the very few protected areas, left in Oxfordshire. The grasslands are important for their Juniper (on the western side of the reserve), and several rare plant species are found; Iberis amara, Gentianella germanica and Vulpia unilateralis An uncommon Avenula pratensis grassland has developed on the North slope adjacent to Beacon Hill.

The public are encouraged to visit the reserve and a nature trail has been created on and around Beacon Hill to observe some of its variety. There is also a standing display area and wild flower garden established at the beginning of the nature trail.

The reserve lies in an area which received a mean annual rainfall of between 750 and 800 millimetres from 1941 to 1970 (Ordnance Survey 1974). The mean number of bright sunshine hours per day was between 4 and 4.5, the mean January temperature 3.5 to 4^{o}C and the mean July temperature 17 to 17.5^{o}c (DOE 1975-). The winds are predominantly south westerly (DOE 1975-).

5.4.2.2. Previous research work at Aston Rowant. The site has long been used for field research. King (1972, 1977a,b,c) conducted an extensive program of research into the floras of ant mounds (of L. flavus), contrasting them to the surrounding grassland. Thomas (1960, 1963) used the reserve as one the locations for his study of the effects of the decline in rabbit populations, due to myxomatosis, on the chalk grassland flora. Watson (1960) examined the bryophytes on the reserve.

5.4.2.3. Management policy and history on Aston Rowant. The reserve

Figure 5.4.

<u>M40 motorway running through Aston Rowant.</u>

The motorway runs through the centre of the reserve in a large chalk cutting seen on the right of this picture.

contains a great variety of habitats and management is varied to suit the interest of each area. The grasslands have been sheep grazed for many years, with organised grazing being maintained at least since the 1960's. An area on the western side of the reserve was ploughed up by the army from 1939 to 1945. Areas alongside the M40 have also been disturbed, with excess soil from the building of the motorway being dumped on them.

5.4.3. Martin Down. (Grid reference SU 050 200)

The reserve can be seen on the Ordnance Survey 1:25,000 map SU 01/11 (Fordingbridge).

5.4.3.1. General description. This reserve was established in 1978, when the large tract of land, 249 hectares (since extended to 336 hectares) was acquired jointly by the N.C.C. and Hampshire County Council. It lies on the eastern end of the Dorset Downs only a short distance from both Salisbury and the New Forest. It is just within the Hampshire border with both Dorset and Wiltshire. The reserve is registered common land and is subject to sheep grazing rights held by local land owners. The western boundary of the reserve is marked by a Bronze Age earthwork, the Bokerley Dyke, which is also the County Boundary. Ratcliffe (1977) describes it as a Grade 1 grassland in the Nature Conservation Review.

Most of the chalk grassland represented within N.N.R.s in England occurs on scarp faces. Relatively flat areas of grassland, such as much of Martin Down is, are rare and often not managed in an ideal manner (eg. the Porton Ranges).

The reserve has varying areas of downland, ranging from ancient herb rich sites such as on the dyke, grassland last ploughed 400 years ago, to grassland ploughed in the second World War and which is much

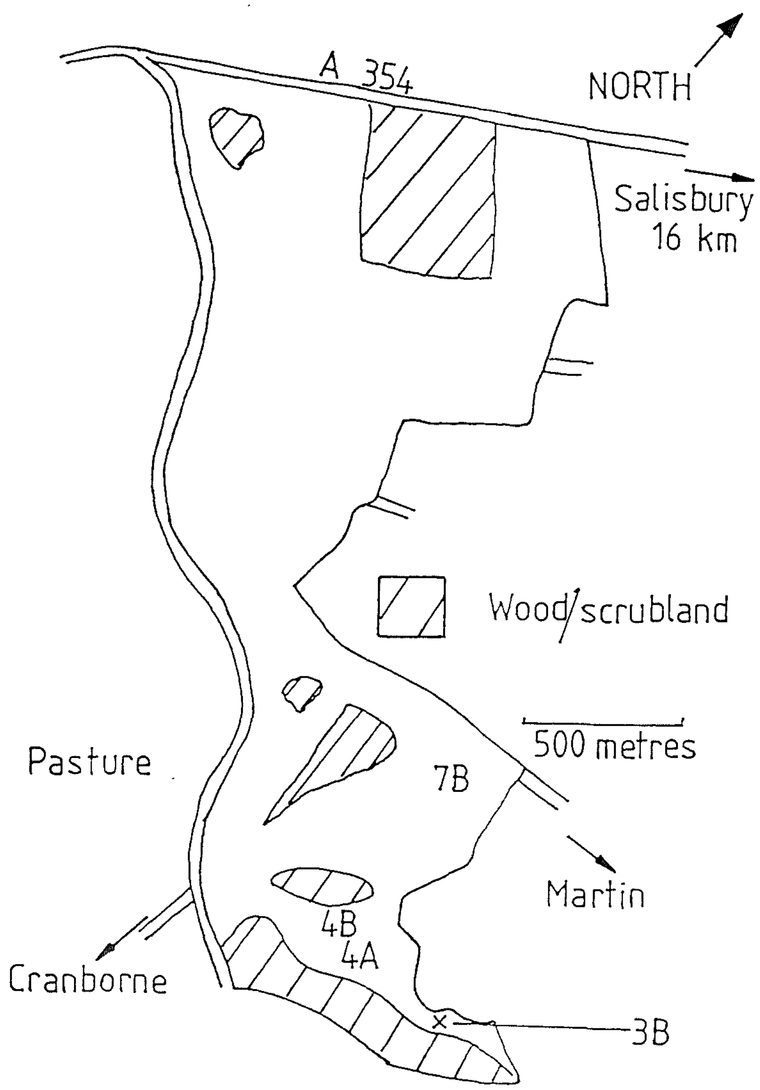


Figure 5.5.

Map of Martin Down NNR.

The positions of areas on the reserve whose ant populations were examined (see Chapter Ten) are indicated by numbers and letters (eg. 4A, 7B).

impoverished as a result. There are also scrub areas and some chalk heath. The reserve can be roughly divided into two halves, the northern half ploughed during the second world war with a relatively poor flora and fauna, although improving under the correct management procedures and the southern half, not recently ploughed and supporting a much more rich flora and fauna.

The reserve is particularly rich in butterflies, with 39 species so far recorded, and also in orchids, with the Green-winged, Orchis morio and Burnt-tip, Orchis ustulata occurring for example, both increasingly rare species.

The reserve also supports a variety of interesting birds, both breeding and visitors. During the course of this project for example Sparrowhawk (Accipiter nisus), Hen Harrier (Circus cyaneus), Barn Owl (Tyto alba), Stone Curlew (Burbinus oedicnimus), Turtle Dove (Streptopelia turtur) and Quail (Coturnix coturnix) were seen. There are many other important plants and animals to be found on the reserve in addition to those named above.

The reserve received between 900 and 950 millimetres of rainfall as a mean annual amount between 1941 and 1970 (Ordnance Survey 1974). The mean number of bright sunshine hours was between 4 and 4.5, the mean January temperature between 4 and 4.5^{o}C and the mean July temperature 16.5 to 17^{o}C (DOE 1975-). The winds are predominantly south westerlies (DOE 1975-).

5.4.3.2. Previous research work at Martin Down. This reserve has had no recorded research carried out on it. The work reported in this thesis is as far as is known by the reserve Warden the only extensive project carried out on it, despite his encouragement. This may be due partially to its location.

5.4.3.3. Management policy and history on Martin Down. Until the 1930's the reserve was grazed by commoners' sheep flocks, which were sufficient to keep the grassland areas free from scrub. During the Second World War the northern half of the reserve was ploughed, although since then it has gradually been reverting to a more typical species rich chalk grassland. After this, grazing became much reduced and sporadic and since the myxomatosis epidemic in the mid 1950's much of the rich grassland became dominated by Upright Brome, *Bromus erectus* and was becoming colonised by scrub. Throughout this period sheep grazing was only spasmodic, with no organised management plan, at the whim of graziers with rights to the area. Since 1978, though, organised grazing by sheep has been reintroduced and the succession has been stopped. The Warden has introduced a management plan giving areas of short, medium and longer grass, with scrub in some areas. This is intended to firstly enable the overgrown parts of the reserve to be recovered and secondly to give a variety of conditions for both flora and fauna.

5.4.4. St. Catherines' Hill. (Grid reference SU 490 280)

This reserve can be found on the Ordnance Survey 1:25,000 map SU 42/52 (Winchester south and Chandler's Ford).

This site did not fulfill all of the criteria stated in 5.1. St Catherines' Hill is a Local Nature Reserve managed by the Hampshire and Isle of Wight Naturalists Trust. This is a reserve heavily used by local people for recreation purposes (walking etc.) and it is only lightly grazed by a few cattle each year. It thus provides some contrast to the other reserves on which sheep grazing dominates.

The reserve lies in an area receiving a mean annual rainfall of between 800 and 850 millimetres (1941 to 1970), (Ordnance Survey 1974). On average between 1941 and 1971 it received between 4 and 4.5 hours of bright sunshine per day, the mean January temperature was 3.5 to 4^{o}C and the mean July temperature 16.5 to 17^{o}C. The predominant winds were again south westerly (DOE 1975-).

CHAPTER SIX

The examination of the sample areas.

6.1. Selection of the sample areas.

The exact location of the areas on the three main study sites whose ant populations were to be sampled was decided by a detailed examination of each reserve and consultation with the reserve wardens. These were selected in order to encompass a range of both management and environmental variables so that the hypotheses described in Chapter four could be investigated. Each sample area consists of a unit of chalk grassland which is managed as one block.

In total 9 sample areas were selected on Old Winchester Hill (OWH), 6 at Aston Rowant (AR) and 4 at Martin Down (MD). A further single area was selected on St. Catherines' Hill (ST.C.).

The methods employed to examine the sample areas are described in 2 sections consisting of,

a) those basic methods used to describe all of the sample areas and

b) a set of methods which were much more labour intensive, so that in practice it was only possible to use them in a selected subset of the sample areas.

In the remainder of this chapter the methods associated with a) will be described.

At the end of Chapter Seven a summary is given of which methods were employed in which sample areas.

6.2. What type of sample to examine?

It was not possible to examine all of the ant mounds within all of the sample areas as the sample areas were much too large. A representative sample had to be taken in each sample area. Typical sampling methods for the examination of the characteristics of an area are transects and quadrats (Southwood 1978). A transect across the sample area was judged to be unsuitable for this study as it would be likely to cover a range of environmental variables such as aspect or slope. A number of small sample quadrats within the sample area would suffer from the same problem. Thus it was necesary to use a sample area which concentrates on a minimal distance around a centre point, ie. a circle or square area.

Southwood (1978), referring to the work of Seber (1973), states that use of a circular sampling area minimises possible edge effect bias to the sample. A square sample area will have a large edge effect. Hexagons lie intermediate to these extremes. Edge effects are proportional to the ratio of the boundary length of the sample to its area.

In practice, a square area is much simpler to use, as a coordinate system can simply be used to pinpoint the location of any object within it. With a large sample area, such as envisaged in this study, the edge effects are reduced. Southwood (1978) states that when using a square quadrat, by using the convention of only counting members of the population that lie on the top and left-hand boundaries and not those that lie on the bottom and right-hand boundaries, edge effects are much reduced. This simple convention was adopted for this study and a square quadrat area used.

6.3. What size of sample quadrat to use?

Clapham (1936) quite clearly pointed out how varying the sample size can affect the results obtained from the sample. It was not the intention of this study to take a large number of small samples, but to take single large samples from each of the populations of interest. The larger a sample is, then the more accurately it should represent the population it derives from, assuming a uniform population. It was necessary to determine how large the sample needed to be to adequately represent the population and also what the minimum sufficient size was, in order to minimise the 'cost' of sampling.

In order to establish what the optimum size was likely to be, two sets of trial samplings were conducted in the Winter of 1983/4. The ants were, therefore, not active and no attempt was made to distinguish between occupied and unoccupied mounds. Also, in this set of samplings some of the small young colonies could easily have been missed because of the lack of soil thrown up at this time of year. In spite of these sources of inaccuracy, it was felt that this was an adequate method of determining a suitable size for the quadrats.

The first trial was conducted on chalk grassland at Box Hill (Grid reference TQ 185 530) where the population and distribution of mounds did not seem to differ radically from that seen later in the chosen sample areas. The layout of the sample quadrat that was examined is shown in Figure 6.1. The sample quadrat was carefully searched and all mounds were located and mapped, firstly in the centre 10 x 10 quadrat, then the 15 x 15 quadrat and finally the 20 x 20 metre quadrat.

The second trial was at Aston Rowant N.N.R. The layout is shown in Figure 6.2. Again, all mounds were located and mapped in each of the sub-quadrats marked in Figure 6.2a. and 6.2b.

In both of the sample areas nearest neighbour analyses were carried out on the sub-quadrats and whole quadrats. The basic method of Clark and Evans (1954) was used to calculate R, the Index of Dispersion. This method is described in great detail in Chapter Fourteen. For the purposes of this examination it gave another basic variable, beside the density of the mounds, that the quadrat size might affect. When R = 1

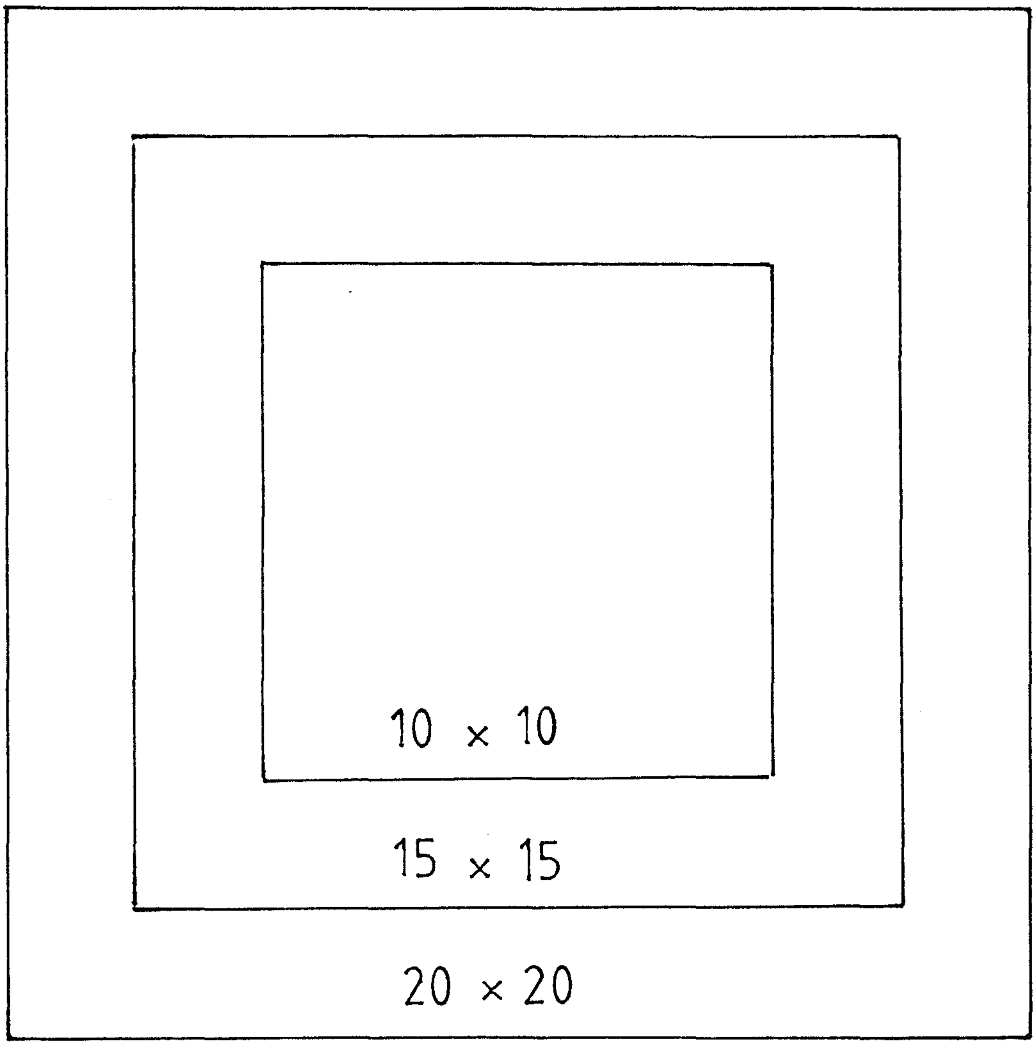


Figure 6.1.

Layout of the trial quadrat at Box Hill.

All of the ant mounds within firstly the central 10 x 10 metre quadrat, then the 15 x 15 metre quadrat and finally the 20 x 20 metre quadrat, were located and mapped. The results from each of the quadrats were analysed to look at the effect of sample size on measuring the characteristics of the ant mound population.

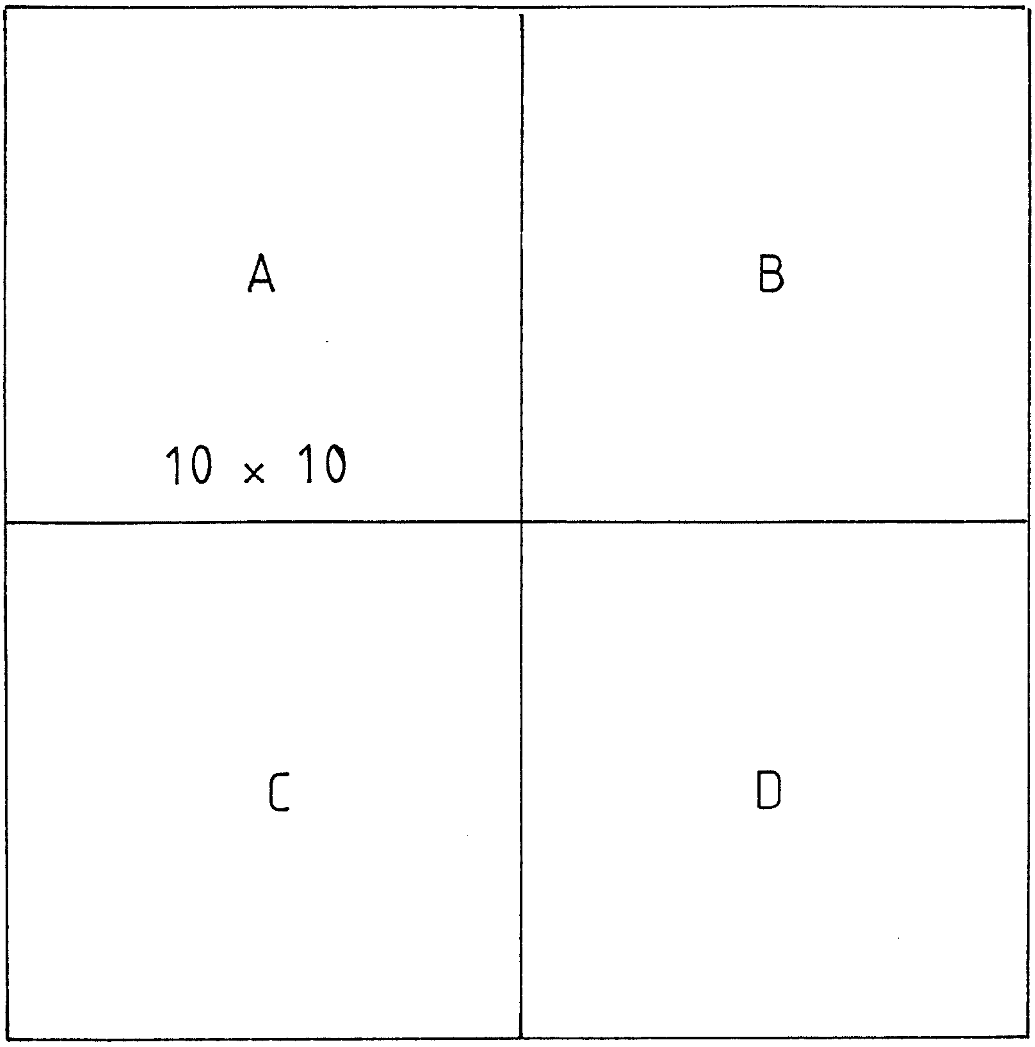


Figure 6.2a.

Layout of the trial quadrat at Aston Rowant.

All of the ant mounds within each of the 10 x 10 metre sub-quadrats shown in this figure, and each of the sub-quadrats shown in part b of this figure, were located and mapped. The results from each of the sub-quadrats were analysed to look at the effect of sample size on measuring the characteristics of the ant mound population.

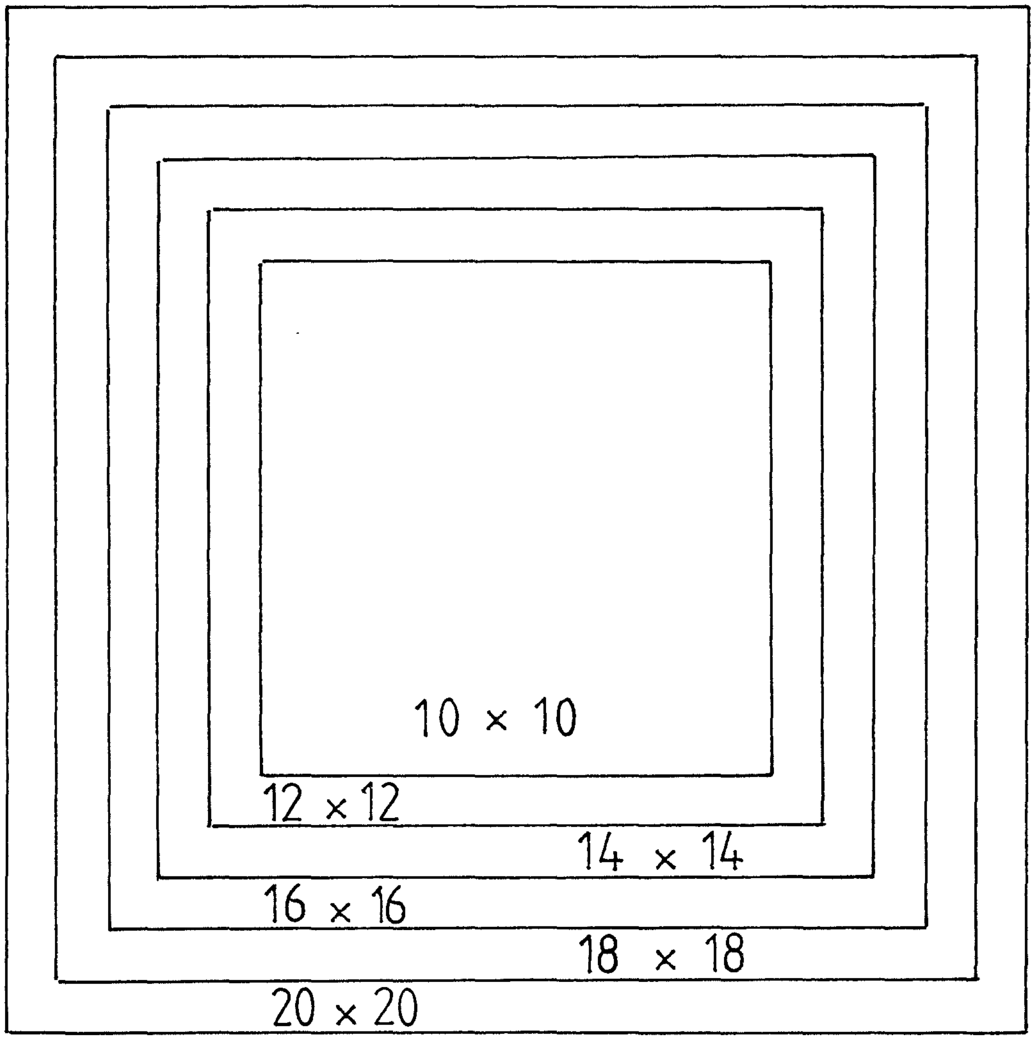


Figure 6.2b.

Layout of the trial quadrat at Aston Rowant.

All of the ant mounds within each of the sub-quadrats shown in this figure, and each of the 10 x 10 metre sub-quadrats shown in part a of this figure, were located and mapped. The results from each of the sub-quadrats were analysed to look at the effect of sample size on measuring the characteristics of the ant mound population.

All measurements are in metres.

the mounds are randomly dispersed, when $R < 1$ the mounds are aggregated and when $R > 1$ the mounds are overdispersed or regular in distribution. Sample size is an important factor in the accurate measuring of the spatial distribution of a population.

6.4. The position of the sample quadrat within the sample area.

This was subjectively decided on. The main criterion for the position of the sample quadrat was for it to be in a part of the sample area that was representative of the typical conditions. Patches of scrub or clearly different vegetation, pathways and other disturbed areas were avoided as far as possible. All of the sample quadrats were placed with the eastern and western sides aligned on a north-south axis, which was positioned using a compass.

6.5. The management and past land use of the sample areas.

The past and present management of each of the sample areas was determined in three ways.

a) Firstly by discussion with the reserve Wardens whose knowledge of the areas they manage is particularly important for details of the reserve history and past management.

b) Secondly by detailed examinations of reserve records, in the form of event cards, both by the author and the reserve Wardens. The event cards list the details of when an area was grazed, for how long, and at what stocking density. Events cards also list other important events such as scrub cutting and mowing in the sample areas. The use of these methods enabled estimates of the intensity of grazing (in terms of the number of sheep grazing days/hectare/year) to be established in most of the sample areas for at least the previous three years, and in some cases much further back.

c) By examination of the research literature relevant to each site.

Where previous researchers have carried out research on the reserves they have often recorded useful information.

6.6. Methods used to examine the characteristics of the ant populations.

6.6.1. Preliminary studies. Before proceeding with the examination of the quadrats a number of questions had to be answered. *L. flavus* is thought to be a monodomous ant, one colony inhabiting a single nest mound. Well established colonies of *L. flavus* are usually easily identified because of the large soil mounds resulting from their repeated excavations of soil over many years (see section 3.5.). Some mounds present problems though.

6.6.1.1. Unoccupied mounds. Some mounds are unoccupied by colonies of ants, the colony having died out. Such mounds can be identified by brief investigation. Mounds containing ants frequently have freshly excavated soil on their surfaces. When this is absent scratching at the surface of the mound often brings worker ants to the surface. A more extensive excavation may occasionally be necessary, for example when conditions are very dry. Older unoccupied mounds can then be easily identified because they are often very solid and hard in comparison to active mounds, and they often have not so modified a flora as occupied mounds (see section 3.7.)

However, it is generally a straightforward process to see if a mound is occupied by a colony. In the mapping of the sample areas unoccupied mounds were not included.

6.6.1.2. Young colonies. In young colonies the mound is not so obvious and during the Spring, Summer and Autumn, the location of the colony may only be marked by a small area of freshly excavated earth. During preliminary surveys it became clear that, particularly in some areas, such small patches of freshly excavated earth could be found in close proximity to (ie. within 1 metre) existing large mounds, as well as in more isolated positions. The question arose as to whether these were newly founded colonies or perhaps the external signs of galleries originating from the mound of the large established colony or even small satellite nests/mounds of the main colony.

In order to investigate this question, in September 1984, 10 such small patches of freshly excavated soil were located, dug up and returned to the laboratory for examination. All of the soil in a radius of 15 to 20 cm. from the centre of the patch and down to the solid chalk subsoil was removed. The patches were located in the quadrat which will later be called AR 12, where there were a large number of such questionable colonies. In the laboratory the soil dug up was thoroughly examined and all of the ants found within it extracted. For each patch the number of worker ants present was counted. The presence and abundance of brood, and the presence of queen/s was also determined. In addition the headwidths of a sample of thirty of the workers from each patch of activity were measured. Headwidth was measured across the eyes of the ants, using an eyepiece graticule in a monocular microscope.

6.6.2. <u>Measurements made on the mounds in the sample quadrats.</u> Having decided from the above preliminary studies the size of the sample quadrat to employ in each of the sample areas and the exact position of the sample quadrat, the following measurements were made on the ant mounds in each of the sample quadrats. All of the sample quadrats were examined between May and September 1984, except for that at St. Catherines' Hill, which was examined in 1985.

6.6.2.1. <u>The location of the mounds.</u> The sample quadrat was carefully searched, initially in approximately two metre wide strips. All the mounds that fulfilled the criteria determined from the investigations described above, were located and marked with a bamboo cane, placed in the geometrical centre of the mound (see Figure 6.3.). The search for the mounds was literally a hands and knees one, in order not to miss small colonies.

When the whole quadrat had been examined the position of each of the mounds in the sample quadrat was recorded by measuring two coordinates, relating the position of this cane relative to the two sides of the square quadrat. The south west corner of the sample quadrat was taken as the origin. The Y axis ran to the north of this origin, the X axis to the east. The position of the cane was measured to the nearest centimetre on the X and Y axes.

The coordinates (and sizes of the mounds) were also measured in two metre wide strips. As this involved going over the quadrat again, it gave a second opportunity to find any of the mounds missed on the first search.

As noted in section 6.2. mounds whose centre lay on the bottom or right hand boundaries of the quadrat were not included.

6.6.2.2. The size of the mounds in the sample quadrat. To measure the size of the mounds the maximum horizontal and vertical measurements of each was recorded to the nearest centimetre. These will hereafter be called the maximum diameter and maximum height of the mounds. Ant soil mounds are seldom circular in shape (see Figure 6.4). If the diameter was recorded on a constant axis position for each mound (eg. a north-south line) it could underestimate the size of some mounds in relation to others. Thus if the mound is considered as an oval it was the major axis distance that was recorded. The height measured was that

Figure 6.3.

Mapping the mounds in a sample quadrat.

Each of the small canes with a numbered flag on top, marks the position of a mound. The tape running in front of the canes marks one of the boundaries of the sample quadrat. The large pole on the far right marks one of the corners of the sample quadrat.

The patches of tall vegetation are groups of Majorum plants, (Origanum vulgare) which often occurred around the ant mounds in this sample area (AR 16).

Figure 6.4.

An oval shaped mound of *L. flavus*.

This mound was approximately 70 cm. along the long axis and 40 cm. on the axis at 90° to this. It would have been recorded as a mound of 70 cm. maximum diameter.

On this mound much more soil is being heaped on the south east corner. This movement of soil mainly to one side of the mound results eventually in the irregular shape of the mound.

from the level of the surrounding ground to the highest point of the mound.

The volume of each mound was calculated as the volume of a half ellipsoid, with the diameter as the major axis and the height as the minor axis.

The percentage area of the sample quadrat covered by the mounds was calculated by treating the mounds as circles with a diameter equal to the measured maximum diameter. The area covered by all of the mounds was calculated and expressed as a percentage of the sample quadrat area.

6.6.2.3. The spatial distribution of the mounds. This was investigated using the nearest neighbour technique.

In all of the sample areas the distances to the 1st nearest neighbour of each mound were measured to the nearest centimetre. This was done at the same time as the recording of the numbers and sizes of the mounds. The distance measured was that between the canes placed in the centres of the sample mound and that of its nearest neighbour. It was usually clear which mound was nearest but if there was any doubt, the distance to a number of near nests was measured and the smallest distance recorded. If the nearest neighbour to a mound lay outside of the quadrat the distance measured was that to the mound outside of the quadrat, and not that to a mound further away but inside the quadrat. This was as recommended by Clark and Evans (1954).

6.7. The physical environment of the sample areas.

6.7.1. The altitude of the sample areas. The altitude of each of the areas was determined from the Ordnance survey 1:25,000 maps of each site referred to in Chapter Five. Contours on these maps are either 5 metres or 25 feet contours.

6.7.2. The aspect of the sample areas. The direction in which the sample areas faced (if they were not on level ground) was measured with a standard geographers compass.

6.7.3. The slope of the sample areas. This was assessed by measuring the distance apart of contours on the Ordnance Survey 1:25,000 maps of the sample areas referred to in Chapter Five.

6.7.4. The soil pH. Soil samples were collected from the sample areas in the form of soil cores. Samples of 10 g. of dried soil (taken from 5 to 15 cm. depth) were mixed with 20 ml. of deionised water. The pH was measured to the nearest 0.05 of a unit with a Pye-Unicam model 292 pH meter.

6.7.5. The soil depth. A metal probe was inserted into the ground 10 times on a diagonal walk across the sample quadrat in each sample area. The depth the probe reached before hitting the bedrock chalk or any other obstruction was recorded to the nearest 1 cm.

6.8. The biological environment.

6.8.1. The flora of the sample areas. The flora of the sample areas was described generally by making a complete list of the plants found in each area. However, to analyse the differences in order to test the hypotheses posed in Chapter Four, two phytosociological methods, recommended by Mueller-Dombois and Ellenberg (1974) were used.

Mueller-Dombois and Ellenberg (1974) concluded that two types of sampling were necessary for such analyses of vegetation. The first type was a large minimal area quadrat for sampling the species which are representative of a vegetation. Within this sample area species are simply recorded as being present or absent. The second was for a number of small quadrats in which the abundance of different plants could be assessed using a cover abundance scale such as the Domin-Krajina, Braun-Blanquet or Dobenmire scales (see Mueller-Dombois and Ellenberg 1974).The second approach was much more labour intensive and was only used in a limited number of the sample areas (see Table II) and is discussed in the following Chapter.

One of the problems with both of these types of analysis is knowing what size of sample quadrat to use. The minimal area concept has been frequently discussed in works on the practice of vegetation analysis (Cain and Castro 1959, Shimwell 1971, Moore and Chapman 1986, for example). Basically this concept refers to the area of quadrat necessary to gain an adequate representation of the plants to be found in a vegetation type. In a small quadrat (25 x 25 cm. for example) in an area of chalk grassland, perhaps only 10 species of plant may be recorded as being present, in a larger (1 x 1 metre) quadrat perhaps 15 will be found. As the quadrat size increases more plant species are likely to be found. However, as the quadrat size increases beyond a certain value the effort involved in searching a larger quadrat will yield fewer new species. This is graphically represented in Figure 6.5. As the line first tends to become horizontal the minimal sample area is deemed to have been reached.

Minimal areas for the first type of analysis tried, ie. the simple recording of presence and absence data are discussed by Mueller-Dombois and Ellenberg (1974), who suggest that for different types of grassland between 10 and 100m^2 should be used and also by Moore and Chapman (1986), who suggest that for calcareous grassland the minimal area should be at least 10 to 50m^2. Goldsmith et al (1986) suggest that for the purposes of vegetation analysis the sample area used should in fact be slightly greater than the minimal area.

In order to achieve this the whole of the sample quadrats were used

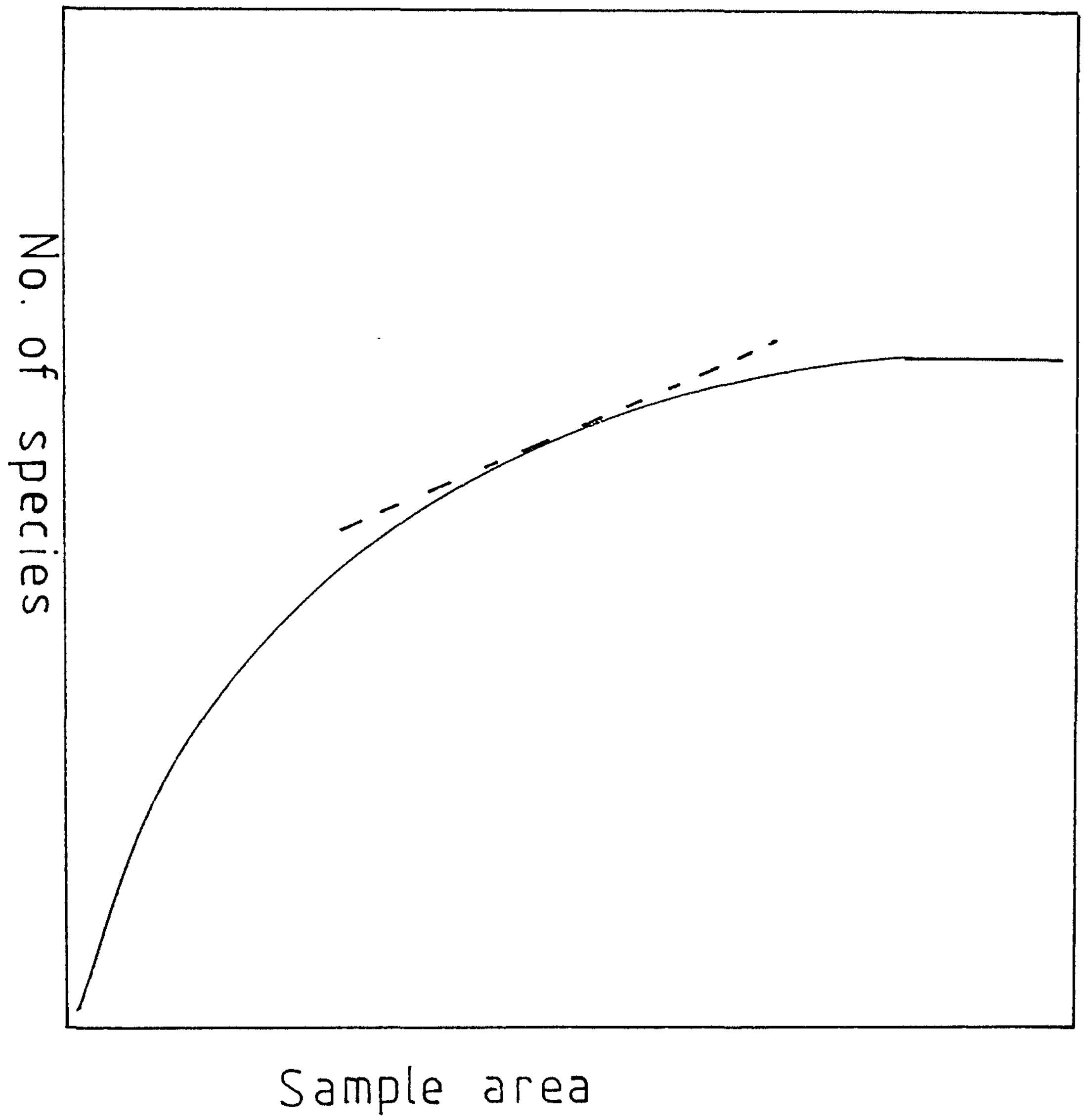


Figure 6.5.

A species-area curve.

This figure shows a typical species-area relationship. As the sample area increases the number of species found in it also increases. The curve initially rises steeply and then levels off. The point at which the curve levels off is considered to be the minimal area necessary to describe the community adequately. Alternatively the minimal area can be considered to occur at a predetermined gradient (Hopkins 1955) as shown by the tangent on the line.

thus giving an area of $400m^2$, well above the minimum necessary area and more than adequate to gain a representative view of the sample areas. This also removed the need to lay out further sample quadrats.

A list of the plants found in each quadrat was compiled. Each of the sample areas was examined throughout the year and as far as possible a complete list of the plants found in each area made. angiosperms, bryophytes and lichens were recorded. The frequency of each species within the sample area was assessed subjectively on a three point scale to provide a more realistic view of the flora.

1 = rare,

2 = scattered, or in local patches,

3 = common,

A few plants were recorded under separate categories, eg. S, which indicated that the species was growing on one of the stone sample slates which were placed in the sample areas or J, which indicated the species was growing as an epiphyte on a Juniper plant within the sample area. Plants found within the sample area, but not in the sample quadrat were recorded as present, but not included in the analysis. The full list of categories in given in Appendix Nine together with the full results.

6.8.2. Rabbit grazing in the sample areas. It was not possible to observe grazing as it occurred. This would have been extremely difficult (rabbits are easily disturbed) and time consuming (observations would be necessary over quite a long period at difficult times of the day to enable enough consistent data to be obtained).

The extent of rabbit grazing in the sample areas was thus estimated by periodic examinations of the density of droppings. The observation of the density of droppings is extremely simple and can be carried out at any time. It is a recognised method of establishing numbers of animals present (Neff 1968, Bailey and Putman 1981) and of estimating the intensity of grazing pressure (De Leeuw and Bakker 1986).

Ant mounds have been described as rabbit "lavatories" (Elton 1966). Droppings are certainly found in large numbers on the tops of the mounds. Thus in order to look at the density of droppings present, droppings were recorded separately both on the mounds and on the ground between the mounds. The method used was straightforward.

On a diagonal walk across the sample quadrat, beginning at the south-west corner (the coordinate origin), 10 mounds were randomly selected. A 25 x 25 cm. quadrat was placed in the centre of the selected mound and the number of rabbit droppings within it recorded. On the same walk the quadrat was thrown in a random direction 10 times and the number of droppings in the quadrat recorded for the area between the mounds on which the quadrat came to rest. If the quadrat came to rest on, or partially on a mound, the throw was retaken.

It was not possible to count the rabbit droppings in quadrats that had been recently grazed by sheep as rabbit pellets could not be satisfactorily distinguished from broken up sheep faeces which are also in the form of small pellets.

Observations on the density of droppings were made between February 1989 and February 1990.

6.8.3. Other animal influences. The presence of fewmets (deer droppings) in a quadrat was noted if seen, as was the presence of Green Woodpecker droppings, these being easily distinguished (small cylindrical brown droppings, 2-3 cm. long, about the width of a pencil and with a white tipped end).

CHAPTER SEVEN

Methods used in a subset of the sample areas.

7.1. Selection of a subset of sample areas.

The sample areas that were selected to be used for the more labour intensive methods described in this Chapter were selected in order to still encompass a range of environmental and management characteristics, but also on the basis of the results from the first section of methods described in the previous chapter. Seven sample areas were selected on which to concentrate work, three from Old Winchester Hill, two from Aston Rowant and two from Martin Down. However, where possible, other sample areas were also used.

7.2. The characteristics of the ant populations.

7.2.1. The collection of ants from colonies in the field. As *L. flavus* is an underground ant species it was not possible to collect ants, (workers, brood or sexuals) without accessing the galleries in the nest mound which they occupy. This could have been done by digging into the mound on each occasion a sample was required but this would have caused excessive disruption and damage to the mound and colony, and would have provided messy samples, contaminated with large amounts of loose soil.

7.2.1.1. The use of stone slates. In order to collect samples in a non-disruptive, simple manner it was necessary to place stone slates on the colonies from which samples were required. A large stone slate (25 x 25 x 2.5 cm.) was positioned on the top of each of the mounds (see Figure 7.1.) The workers excavate galleries directly underneath the slates in order to take advantage of the enhanced temperature regime, the slates warming up more quickly in the morning than the vegetated surface of the mound, and retaining heat for longer periods.

Figure 7.1.

Slate in position on top of an ant mound.

The slate measures 25 x 25 x 2.5 centimetres. The ants build galleries underneath the slate in order to take advantage of the enhanced temperature regime that the stone slate provides.

Worker ants, brood and adult sexuals all collect in the galleries underneath the slates, when the temperature is suitable (see Figure 7.2.). This method of collecting ants has been used by several authors before (Pontin 1961, Boomsma et al 1982 for example).

7.2.1.2. When to put the slates down. The slates were positioned in the Autumn of the year before the first samples were taken, in order to allow the galleries to be fully excavated by the workers. The digging occurred particularly during the following Spring, when activity was at its greatest. It was found that when slates were positioned on mounds early in the year, ie. mid-Winter, when samples were required in the Spring, not enough time had elapsed for the workers to excavate adequate galleries under the slates.

7.2.1.3. Sampling the ants from underneath a slate. When a sample of ants was required it was a simple matter of lifting the slate and collecting the ants from underneath it. Workers and sexuals could be gathered using an aspirator (see Figure 7.3.) but a large sample could often be collected by simply brushing the ants off of the underside of the slate, with a soft 1 inch wide paintbrush, into a container.

7.2.1.4. Times of day at which ants can be collected. The time at which samples can be collected from underneath the slates depends on environmental conditions. The ants will not congregate under the slates if it is too hot or too cold. The ants gather under the slate as it warms up in the morning and will remain there if the temperature does not rise too far. Under these conditions, for example in overcast weather, samples may be taken at any time. However, if the temperature under the slate becomes too high the workers will move further down into the nest (it was found in practice that above 19^{o}C the

Figure 7.2.

Workers, brood and sexuals as seen on lifting a slate on a sample colony.

Worker ants build galleries underneath the slate to take advantage of the enhanced temperature regime it provides. When temperatures are suitable, the workers will bring the brood to these surface galleries, where they can be easily collected. See section 6.2.1. for further details.

Figure 7.3.

Collection of an ant sample from beneath a slate, using an aspirator.

Here a standard aspirator is being used. Filters can be used to prevent excessive breathing in of formic acid. However, this reduces the suction power considerably. Battery operated aspirators are available, but are easily blocked when collecting large ant samples.

Large home made aspirators were found to be most suitable for collection of big samples of L. flavus workers and sexuals. Ants can also be brushed from the underside of the slate directly into a container.

The large icebox behind the author was used to carry ant samples in the field. Ants could be kept cool and out of direct sunlight.

galleries directly underneath the slates were abandoned. On hot and sunny days, sampling can only take place in the early morning and later in the day when the temperature has fallen again. On such days the time that the ants remain in large numbers under the slates could be very limited, as little as 30 minutes, before it becomes too hot. This means that the period when sampling is possible can be extremely limited. After being disturbed during sampling the ants will not immediately return to the underside of the slate. Thus samples cannot be taken soon after each other. In practice, one morning and one evening sample only, is possible from each slate on each day. On overcast days when the temperature under the slates does not go above 12°C very few ants will collect there.

7.2.2. The estimation of worker ant populations in the field. Two different methods were used to estimate colony sizes and one to estimate the relative density of foraging *L. flavus* workers. These are as follows.

7.2.2.1. Mark-release-recapture estimates of colony sizes. This section of work is discussed in full in Chapter Eight. It was used to estimate colony sizes for the same colonies in which the sexual production was measured (see Table II).

7.2.2.2. Digging up colonies. Mounds were dug up and the number of workers counted. This was done to examine the accuracy of the mark-release-recapture estimates. Five mounds were dug up in three sample areas. Mounds were dug up in January 1986. A spade was used to dig around the edge of the whole mound. This was then levered up and placed in a large dustbin bag, together with loose soil from the hole, for removal back to the laboratory. In the laboratory all the mound material was carefully examined and the ants extracted and counted.

7.2.2.3. The collection of workers from core samples. The core samples collected in order to investigate the biological environment of the sample areas also contained worker ants which were extracted along with the other invertebrates. This gave a measure of foraging worker ant density in the sample areas. The method is discussed in full in section 7.3.

7.2.3. The measurement of the sexual production of colonies.

7.2.3.1. Limitations to the sampling of colonies. Ideally it would have been better to take large samples of colonies from each of the chosen subset of sample areas. However, because of:

a) the locations of the sample sites and the of the sample areas within the sample sites, and

b) the limited time in which sampling of the ants from underneath the slates was possible during the day, this was not possible.

Consideration of the methods to be used suggested that a sample of 5 colonies from each of the selected areas was the maximum that it was possible to collect sexuals from adequately.

7.2.3.2. The choice of colonies to sample. In each of the chosen sample areas a set of 5 mounds was selected by stratified random sampling within the sample quadrat. Each quadrat was divided into 5 equal strips. The nearest nest mound to a random coordinate in each strip was selected. Very small mounds were not considered for inclusion (assuming these were young colonies they were unlikely to have reached maturity and therefore be producing sexuals). If the nearest mound to the random coordinate was a very small one (under 20 cm. maximum diameter) then the next nearest larger mound was selected. The selected mounds were in the mid-range of the mound sizes in each quadrat. (see Figures in Chapter Ten and Appendix Three.)

7.2.3.3. <u>The collection of the sexuals.</u> The sexual production of the individual colonies was simply measured by collecting from each colony all of the males and gynes produced. Pupal gynes could have been collected but it was not possible to be sure that all of them would survive to maturity. Pupal males would not have been as easy to collect as they are sometimes difficult to distinguish from pupal workers and so for this reason also only adult males were collected.

Collections were begun as soon as adult sexuals appeared under the slates and continued until no more were found. Checks on the colonies were continued up to and indeed past the sexual flight time as some males can be left in the colony. The numbers of males and gynes were counted at each collection and summed to give final figures for each colony.

Sexuals were collected in 1985, 1986 and 1987 in the chosen sample areas (see Table II) except in MD 4A when they were collected only in 1987.

7.2.3.4. <u>Further measurements on the sexuals.</u> In 1985, the head-width (across the eyes) of a sample of 10 gynes and 10 males was measured for each colony. The total dry weights of 10 gynes and 20 males were measured after drying for 7 days at 105^{o}C.

The males maintain their dry weight at a reasonably constant level after eclosion (cf. Boomsma et al 1982, Peakin 1972) and so the samples of males for weighing were collected at any time. The gynes in contrast gain weight after eclosion, up to the mating flight, and so the samples of gynes for weighing were from those collected as close as possible to the flight, in order to get an estimate as close as possible to the flying weight.

7.2.3.5. <u>Energy contents of ants.</u> The energy content of samples of dried gynes and workers was estimated using a Gallenkamp ballistic bomb calorimeter.

The calibration of the bomb calorimeter. This was done using benzoic acid tablets of known weights and energetic contents. Four strands of gun cotton were used to ignite the test material. The results are shown in Table I.

The ant samples. The following ant samples were tested.

1) A set of freshly collected worker ants from a colony at Aston Rowant. The number of individual ants was not counted.

2) A set of 718 worker ants collected from a colony at Martin Down. These had been kept in a fridge in the laboratory for 4 monthes prior to being killed and dried.

3) A set of 563 workers from the same colony which were fed with sugar solution 1 day prior to being killed.

4) A set of 942 worker ants from a different colony at Martin Down collected at the same time. Half of the ants had been fed and half not.

5) A set of males from the collections made in 1985 which had been weighed but not counted.

6) Another set of males from the same collection.

7) A set of 39 gynes from collections made in 1985, collected as near to the nuptial flight time as possible.

8) Another set of 50 gynes from collections made in 1985.

7.2.3.6. The phenology of sexual production. In 1986 records were made of the observed state of advancement of the sexual brood at each of a large number of visits to the sample areas. The first appearance of eggs, sexual larvae and pupae was noted.

7.2.3.7. The sexual flight. A sexual flight was observed in detail in 1989 at Old Winchester Hill. Timings of other sexual flights both

Table I.

Calibration of the bomb calorimeter.

SAMPLE TYPE	WEIGHT (g)	DEFLECTION	CORRECTED DEFLECTION
Blank, wick + pot only	-	0.5	-
Benzoic acid	0.3031	23.2	22.7
Benzoic acid	0.3396	25.3	24.8

The deflection measured is the number of units on a galvanometer scale. Each unit represents 1% of the full scale deflection.

From these the following calculation was made.

1g Benzoic acid = 26.45 KJ

For the two standards:

1) 22.7 units = 0.3031 * 26.45 KJ
22.7 units = 8.017 KJ
1 unit = 0.353 KJ

2) 24.8 units = 0.3396 * 26.45 KJ
24.8 units = 8.982 KJ
1 unit = 0.362 KJ

On average 1 unit = 0.358 KJ

for the sample areas and other sites were recorded as far as possible.

7.3. The physical environment.

7.3.1. The soil cores The soil cores were collected primarily to get some information on the invertebrates associated with the populations of the ant in the different areas (see section 7.3.1). However, they were also used to provide data on the physical environment of the areas.

7.3.1.1. The collection of the cores in the field. Cores were extracted using a corer of 6.5 cm. diameter, an area of 33.2 cm^2. Cores were collected on each visit to the sample areas selected, from March 1989 to January 1990. The cores were always collected at a distance of 1 metre to the north of an ant mound within the sample quadrat. The major limitation on the number of cores that could be collected for examination was the availability of Tullgren funnels to extract the invertebrates.

The corer was always inserted to the maximum possible depth, ie. up to 16.5 cm. Frequently, due to the thin and stoney nature of chalk soils it was not possible to attain this maximum depth. On removal from the corer the cores were placed in sealed plastic bags and transported as soon as possible to the laboratory.

7.3.1.2. Laboratory procedure with the cores. Once in the laboratory the cores were weighed to the nearest 0.1g and their length measured to the nearest 0.5cm. After the invertebrates had been extracted the cores were dried to constant weight by placing them in an oven at 50^{o}C for a further 48 hours.

There was a small amount of soil lost from the cores during the extraction of the invertebrates (disturbed by the invertebrates and falling into the collection tube in the funnels). In order to see if this was significant a duplicate sample of cores were collected at Old Winchester Hill on 10/4/89 and at Martin Down on 29/3/89. These cores were directly dried without placing in the Tullgren funnels.

7.3.1.3. Water contents of the cores. The initial fresh weight measurements and the final dry weight measurement enabled a calculation of the percentage water content of each of the cores.

7.3.1.4. The soil core density. This was measured by dividing the dry weight of the core by its volume.

7.3.2. Temperature measurements in the sample areas.

7.3.2.1. The thermometer. The temperatures were measured using a Whatman Temp-u-Sensor calibrated in degreees centigrade. This has a metal probe which can be inserted up to 12 cm. depth into the soil.

7.3.2.2. The timing of measurements. Visits were only made to one major study area (ie. Old Winchester Hill, Aston Rowant and Martin Down) on one day. All of the chosen subset of sample areas on this site (see Table II) were examined on that day.

Visits were made to the sample sites between March 1989 and January 1990. More frequent visits were made during the period April to September, when the peak of ant activity occurs. In each sample area temperatures were measured at 4 times during the day, these being 9.00AM, 12.00NOON, 3.00PM and 6.00PM BST.

7.3.2.3. The measurements taken. Five replicated sets of measurements were usually made. Each set of measurements consisted of six temperatures as follows.

1) The temperature in the top 1cm. of soil of the south facing side of an ant mound.

2) The temperature at a depth of 10 cm. in the same location on the

ant mound.

3) The temperature in the top 1cm. of soil of the north facing side of the same ant mound.

4) The temperature at a depth of 10cm. in the same location on the ant mound.

5) The temperature in the top 1cm. of soil in the ground surrounding the ant mound.

6) The temperature at a depth of 10 cm. in the same location.

The air temperature, at 1 metre height, was also measured for each sample area at each time.

Thus for each sample area there were 6 x 5 ground temperatures recorded plus 1 air temperature at each time. Therefore a total of 124 temperatures were recorded for each sample area during the day.

7.3.2.4. The sample points. The mounds in which temperatures were measured were selected at random in the sample area. The same mounds were not used at each day or each time. The mounds were selected on a diagonal walk across the sample quadrat (not necessarily the same diagonal on each occasion). A mound was selected and the first 4 temperatures measured on it. Then a location in the surrounding ground within 1 to 2 metres of the mound was selected for the fifth and sixth measurements of each set. Very small mounds (ie. under 20 cm. diameter) were not selected.

7.4. The biological environment.

7.4.1. The soil cores. The principal purpose for collecting soil cores was to assess the numbers of root aphids and other invertebrates associated with the ants, extracting them by use of the Tullgren funnel method.

7.4.1.1. The Tullgren funnels. These were standard funnels as described by Southwood (1978). A 40 watt light bulb was used as a heat and light source, placed 20 cm. above the grid on which the cores were placed. The cores were placed on their sides on the grid, their small width meant that they would not stand upright on the grids which were 12 cm. in diamter.

They were kept in the funnels for 7 days. Early observations indicated that more time in the funnels did not produce any more invertebrates. The invertebrates extracted fell into 70% alcohol and were kept in this for later examination.

7.4.1.2. The examination of the invertebrates. The invertebrates extracted from the cores were examined under a binocular microscope. Barring Nematodes and Enchytraeids, the visible invertebrates were sorted into categories and counted.

7.4.1.3. The root aphids. Members of this important group (see Section 3.9) were given special attention. Root aphids were removed and prepared for identification. Several methods can used to prepare aphids for identification (see Van Emden 1972) but in this case one of the most simple was used. The aphids were cleared and fixed by placing in drops of polyvinyl lactophenol on microscope slides. Cover slips were added and the slides placed in an oven at 50°C for 48 hours. After cooling, the cover slips were ringed with nail varnish. This provided a semi-permanent preparation which could be examined at leisure. Cavity slides were used for the larger specimens. Ordinary flat slides were adequate for small 1st instar specimens.

The aphids were identified as far as possible using the key of Paul (1978).

7.4.1.4. Other invertebrates. Some of the more interesting species of invertebrates (subjective decision) were also identified to species level (eg. the pseudoscorpions and other ant species). Reserve wardens are always interested in species lists of invertebrates from their reserves, as they add to the other indicators of the conservation value of areas and some of the categories examined in this work are unlikely to have been previously investigated. Any such identifications are thus valuable.

7.4.2. The flora of the sample areas, part 2.

7.4.2.1. Cover-abundance analysis. This was the second part of the floral analysis described in section 6.8. To gain the detailed data on cover abundance of plant species requires an adequate sample size, this size being much smaller than needed for the simple presence and data described in the previous chapter. The required sizes have also been investigated by workers in vegetation analysis, notably by Cain and Castro (1959). They recommend a small sample quadrat area of 1 to $2m^2$ for herb layers such as in grasslands. In this study $1m^2$ was used.

Four of the $1m^2$ sample quadrats were laid out in each sample area. One was placed in each quarter of the sample quadrat in the sample area. The $1m^2$ quadrats were positioned so as not to cover any ant mounds and thus the assessment was of the flora of the ground surrounding the ant mounds. Cover-abundance of all plant species present was assessed subjectively using the Domin scale (see Appendix Nine). All of the chosen sample areas were examined between 7/6/89 and 22/6/89.

7.4.3. Miscellaneous observations on the flora. A number of such observations on various aspects of the flora of the sample areas were made.

7.5. Summary of the methods used in each sample area.

This is summarised in Table II.

Table II.

Summary of the methods employed in each sample area.

QUADRAT	1	2	3	4	5	6	7	8	9	10
OWH SS 4	y	y	y		y	y	y	y	y	y
SS 5	y				y	y			y	
SS 7	y				y	y			y	
SS 8	y				y	y			y	
SS 9	y				y	y			y	
SS11	y	y	y		y	y	y	y	y	y
SS12	y				y	y			y	
NFS	y				y	y	y		y	y
C10	y	y	y		y	y	y	y	y	y
AR 11	y				y	y			y	
12	y				y	y			y	
15	y	y	y	y	y	y	y	y	y	y
16	y	y	y	y	y	y	y	y	y	y
5	y				y	y			y	
NWS	y				y	y			y	
MD 7B	y	y	y	y	y	y	y	y	y	y
4A	y		y		y	y	y	y	y	y
4B	y	y	y		y	y	y	y	y	
3B	y				y	y	y		y	y
ST. C	y				y					

y = method was employed in the sample area.

1 - Mapping and measurement of ant mounds, spatial analysis.
2 - Mark-release-recapture estimates of colony size.
3 - Collection of sexuals.
4 - Digging up of mounds, counting of worker population.
5 - Altitude, slope and aspect of the sample area measured.
6 - Soil depth and soil pH of the sample area measured.
7 - Temperature measurements.
8 - Cores collected, soil core densities, water contents, extraction of invertebrates.
9 - Flora 1, complete list of plant species made, rabbit dropping densities measured.
10 - Flora 2, cover-abundance assessments.

CHAPTER EIGHT

The estimation of the worker population of individual colonies

8.1. Methods of estimating the populations of ant colonies

8.1.1. Digging up the colony. In this method part or all of the nest containing the ants is dug up and all of the ants counted. This however is extremely time consuming, tedious and worse is destructive to the nest, which means that further study of the same colony in its original condition is impossible. Further it cannot be assured that all workers are within the dug up portions of the nest, particularly in summer, when many may be foraging away from the central mound.

8.1.2. Removal sampling. This has been described by Ballard and Pruess (1980). As many ants as possible are removed from the colony in a sample. This is repeated several times (necessitating great disturbance) and the numbers removed at each successive sample enable an estimate of the total numbers in the nest to be made. Ballard and Pruess (1980) used this method to estimate the colony sizes of *Lasius neoniger*, *Myrmica americana* and *Pogonomyrmex occidentalis*. It was, though, only partially successful, some estimates being inaccurate. Use of this method would also entail removing large numbers of worker ants from colonies of *L. flavus* over quite a long period of time and would thus disrupt the colony's normal activity considerably.

8.1.3. Mark-release-recapture estimation of the population. With this method a minimum of two population samples only are needed, resulting in less disruption to the colony and less visits to the chosen sample sites.

8.2. Reasons for choosing mark-release-recapture.

The mark-recapture technique is the only possible technique for the type of studies needed in this project because of the intention to look at the sexual production of the same colonies. The minimum of disruption to the sample colonies was desired, so that the production of sexuals would take place as far as possible completely normally. Thus it was decided to use a mark-release-recapture technique. This required that the worker ants had to be suitably marked.

8.3. The marking of worker ants.

A large number of methods have been used to mark invertebrate organisms (Southwood 1978) but ants can be considered to present special difficulties. It is known that ants, along with many other social insects, are not easy to mark.

8.3.1. External paints and dyes. The application of external paints and dyes to individual ants is both difficult and time consuming (Waloff and Blackith 1962, Ayre 1962) and is often far from permanent (Chew 1959). The marks can be removed by the ants themselves in personal and mutual "grooming" (Brian et al 1967). Most of the marking techniques can be shown to have derived from the early work of Karl von Frisch (1923, 1965) who first applied the so called "bee spot code" to workers of the Honey bee *Apis mellifera* (Rooum 1989).

These techniques have become more successful as better dyes and paints have been developed, for example Porter and Jorgenson (1980) sprayed workers of *Pogonomyrmex owyheei* with a fluorescent ink spray and Bhatkar and Vinson (1987) used adhesive spray paints to mark very large numbers of workers of the small pest species *Solenopsis invicta*. Several researchers have managed to successfully apply paint marks to individual larger ants, such as the wood ants, *Formica* spp., for example Holt (1955) marked individual workers of

Formica rufa with nitrocellulose paint. Fowler (1983) marked workers of Formica pallidefulva with coloured nail varnish in order to study their foraging behaviour. As a variation of this Ayre (1962) used a standard laboratory marker pen (Techpen) to mark individuals of Formica exsectoides, Camponotus herculeanus and Formica fusca. Much smaller ants have been successfully marked, for example Franks and Scovell (1983) marked the slave-making ant Harpagoxenus americanus using the a technique described by Porter and Jorgenson (1980).

Chew (1959) found that such marks could be rapidly removed by the ants. He used "Testors coloured dope" to mark individuals of the ant species Novomessor cockerelli, Myrmecocystus mimicus and Pogonomyrmex occidentalis. Population estimates using mark-release-recapture tended to gradually increase with time as the ants removed the marks on them. Kruk-de Bruin et al (1977) also found this a problem when they marked workers of Formica polyctena with "Testor's pla enamel paint".

However, L. flavus is very small to easily paint and will rapidly remove most paint marks (J. Pontin pers. comm.) although Waloff and Blackith (1962) reported some success using aluminium paint marks.

8.3.2. Internal dyes. Another method of marking is to use an internal dye. The ants are fed a dye in sugar solution (or another suitable foodstuff) and this then shows through the abdominal wall. Such methods were tested by Goldberg et al (1983) to mark worker termites of the Reticulitermes genus (Rhinotermitinae). They found a range of suitable dyes. More recently, Grace and Abdally (1989) successfully marked workers of Reticulitermes flavipes with the dye Sudan red 7B. Unfortunately a suitable dye for L. flavus is not yet known. A brief laboratory trial with neutral red was unsuccessfull.

Another method is to mark the ants by removing a portion of their anatomy. For example the epinotal spine of species of Myrmica was used by (Brian 1951, 1971) and an antenna by (Stradling 1970). One of the problems with such operations (particularly the latter) on the worker ants is that it can considerably modify ant behaviour (Sudd 1967). It is also again difficult to apply on the large scale required by mark-release-recapture studies.

8.3.3. External tags on ants. Another set of methods that have been used is to attach identifiable objects to the bodies of the insect being studied. Such methods have frequently been used to mark large social insects like honey bees, where it has proved possible to attatch small discs to the bees, each disc bearing an individual number (Smith 1972, Gary 1971, Robinson et al 1984). Otto (1985) describes a primitive version of such commercial tags that were used on workers of Formica rufa. Small paper tags were cut from a road atlas and stuck to the back of worker ants. Each tag bore a small number, part of a grid reference in the atlas. Thus the tags did not contain a set of numbers but rather whatever letters and numbers happened to be available. Later Fresneau and Charpin (1977) used a specific set of photographically reduced numbers for this purpose and succesfully marked both honey bees and a variety of ant species.

Kruk-de Bruin et al (1977) used small small fine copper wires to mark individuals of the ant Formica polyctena as part of a mark-release-recapture procedure. Individuals had to be anaesthetized with carbon dioxide and then individual rings of metal tied around the petiolus. Other workers have also used this technique. Bonavita and Poveda (1970) marked individuals of the primitive ant Mesoponera caffraria as part of a behavioural study. For the same reason Dobrzanski (1966) marked individuals of the small ant Leptothorax acervorum. Provost (1983) marked individuals of L. lichtensteini with wires of different colours and in different positions on the ants, such that he could individually identify up to 240 workers. Stuart (1988) managed to tie coloured polyester fibres around Leptothoracine workers. All of these methods suffer from being again time consuming and difficult to apply and certainly not suitable for large scale studies on a small ant species.

8.3.4. Radioactive marks. Perhaps one of the most usefull techniques over the last 30 years for the purpose of mark-release-recapture experiments, has been to mark ants with a chemical or element that can be identified by means of its output of radiation (alpha, beta or gamma radiation). Two methods were originally used to mark worker ants.

8.3.4.1. Radioactive metal wires. Firstly small pieces of radioactive metal were attached to the workers. Sanders and Baldwin (1969) cemented small pieces of wire containng Iridium 192 (a gamma emitter) to the abdomens of workers of ants of the genus Camponotus. This enabled them to track individuals as they moved through their subterranean tunnels. This was a modification of techniques used on other insect species (Baldwin and Cowper (1969) on Rhodnius for example).

8.3.4.2. Soluble isotopes. For the purposes of mark-release-recapture experiments dipping techniques were initially used to mark worker ants. Large numbers of workers were dipped in solutions of the radio-isotope. A number of different isotopes have been used. Medlar and Wagner (1964) marked workers of Formica cinerea with Gold 198, Iodine 131 and Phosphorus 32 (P32), concluding that P32 was the best isotope to use because its ease of application and suitable half life. Odum and Pontin (1961) dipped worker ants into a solution containing P32 to mark them as part of a mark-release-recapture estimate of colony sizes in L. flavus.

8.3.5. Advantages and disadvantages of soluble isotope marks. Such marks were easily applied and generally long lasting. There were, however, problems with the dipping method of application. Medlar and Wagner (1964) were unable to use the marks they applied for the purposes of a mark-release-recapture estimate of colony size, because of the massive contamination of non-marked workers due to the practices of mutual grooming and trophallactic feeding adopted by most ant species. In contrast, Odum and Pontin (1961) did not report this as a problem.

8.3.6. The solution to the problem.

8.3.6.1. Internal radioactive marks. In an effort to overcome the problems of contamination, internal application of radioactive marks in sugar solution was tried. Other researchers had used isotopes fed in sugar solution to determine the spread of food throughout a colony of ants (Gosswald and Kloft 1963 for example, who also investigated some termite species, and Eisner and Wilson 1958). Isotopes in sugar solution were also fed to ants to mark individuals in colonies of Camponotus by Riordan (1960) who used Iodine 131 and by Kloft, Holldobler and Haisch (1960) who also used Iodine 131 to mark ants of the species Camponotus herculeanus and C. ligniperda. The spread of the mark around a colony by trophallactic feeding was still a problem in these studies and was highlighted by Erickson (1972) who marked workers of the genus Pogonomyrmex with P32.

8.3.6.2. The use of a starvation period. To prevent this spread a variation on the technique was developed for the purposes of mark-release-recapture estimates. A period of starvation and isolation after feeding the sugar solution was introduced. After the radioactively marked sugar has passed through the proventriculus of the gut it cannot be passed on to other ants by trophallaxis. Internal marking of the ants, in this manner with P32 fed to the ants in sugar solution, was first described by Brian et al (1965) based on work with the ant Tetramorium caespitum and later further developed by Stradling (1970) on a number of British ant species. Breen (1979) has more recently used the technique on an Irish population of the ant Formica lugubris.

8.3.7. Another variation. Boomsma et al (1982) used a minor variation on this method which avoided the release of radioactive material into the environment. They used the rare earth element Europium (fed in sugar solution) to internally mark workers of Lasius niger. While this element is not itself radioactive it can be subjected to neutron bombardment and the resulting products are radioactive and thus identifiable. This technique of neutron activation analysis does of course require a lot of specialised equipment, not the least a strong source of neutrons.

8.4. The method chosen for this study.

The use of an internally applied radio-isotope mark appeared to be the most profitable line to follow in order to mark workers of L. flavus. Large numbers of workers could be collected and marked quite easily. However, while Stradling (1970) demonstrated that L. flavus could be marked in this manner he did not apply the technique to population estimation. It was therefore necessary to conduct some preliminary laboratory experiments to determine the details of the method, before using it to estimate field populations.

8.5. Steps in the use of the chosen technique.

The basic technique of mark-release-recapture using P32 can be divided into the following parts.

1) The collection of a satisfactory sample of the population.

2) The feeding to the ants of sugar solution marked with P32.

3) An isolation period when the ants are starved so that the sugar passes through the proventriculus of the gut and cannot then be transmitted through trophallaxis to unmarked ants.

4) The release of the marked sample back into the population.

5) The collection of the second sample after a time period sufficient to allow thorough mixing of marked and unmarked ants.

6) The examination of the second sample for the number of 'tagged' ants.

8.6. The preliminary experiment.

8.6.1. Points it was necessary to clarify. Initially a laboratory study was undertaken to look at the following points.

1) The use of a brief period of starvation prior to feeding with P32 (1 day only) in order to enhance the pickup of the mark.

2) The amount of P32 to feed the ants so that a satisfactory mark was obtained. Was the amount of P32 used by Stradling (1970) adequate for the purpose of this study?

3) The necessary length of the starvation period.

4) The length of time for which the mark was distinguishable. Would the mark be discernable for long enough for the recaptured ants to be easily identified?

5) Whether any significant mortality was caused by the use of P32, or any other aspects of the technique.

8.6.2. Details of the experiment. The experiment was conducted at

Queen Mary College, Department of Biology, where the necessary facilities for the handling of radioactive isotopes were available.

8.6.2.1. The ants used in the experiment. Two sets of worker ants were used in the experiments. Set A had been collected 1 month previously and kept at around 5^{o}C and fed on sucrose solution. Set B had been collected 1 week before the experiment began. From each of these sets groups of 100 ants were placed in sealed petri dishes, with pieces of moist sponge as a water source. These were then subjected to the different experimental procedures.

8.6.2.2. Details of the treatments. The experimental treatments are summarised in Figure 8.1. In treatments 1 to 3 ants were fed with a small amount of sugar solution the day before the start of the experiment to see if this affected the subsequent pickup of the mark. In treatments 4 to 11 this was not done.

Treatment 1 and 4 were then control treatments with no feeding after the start of the experiment, in order to assess the background mortality levels.

In the other treatments (excepting treatments 3, 5 and 11) the worker ants were fed the P32 in sugar solution. The P32 used was obtained from Amersham International (5mCi of carrier-free orthophosphate in 'acid free' aqueous solution, pH 4-7). A dilution of 1mCi/5ml of 10% sucrose solution was prepared and administered impregnated onto a small cotton wool ball, as proposed by Stradling (1970). Each set of 100 worker ants was given 0.1 ml (0.02 mCi) of the isotope solution, again the dose used by Stradling (1970). The ants in treatment 11 were given only half of this amount. The ants in treatments 3 and 5 were control treatments and were fed sugar solution without the P32 in it with mortality subdequently assessed for the

Figure 8.1.
Summary of treatments in laboratory experiments on the mark release recapture technique.

	TREATMENT NUMBER										
DAY	1	2	3	4	5	6	7	8	9	10	11
-1	FEED ANTS DAY BEFORE			DO NOT FEED ANTS ON THE DAY BEFORE							
1	DO NOT FEED	FEED + P32	FEED - P32	DO NOT FEED	FEED - P32	FEED + P32					FEED 1/2 P32
2	REMOVE ALL FOODS					REMOVE ALL FOODS					
3	STARVE ALL ANTS					STARVE ALL ANTS					
4	STARVE ALL ANTS					STARVE ALL ANTS					
5		CHECK MARK				MIX			CHECK MARK		CHECK MARK
6						CHECK MARK	MIX				
7						CHECK MARK	CHECK MARK	MIX			
8		CHECK MARK				CHECK MARK	CHECK MARK	CHECK MARK	CHECK MARK		CHECK MARK
9						CHECK MARK	CHECK MARK	CHECK MARK			
10		CHECK MARK				CHECK MARK	CHECK MARK	CHECK MARK	CHECK MARK		CHECK MARK
11							CHECK MARK	CHECK MARK			
12								CHECK MARK			

Explainations to legends

1) Day -1, the legends refer to whether the ants were fed a small amount of sugar solution or not, the day before feeding with the P32 in sugar solution was to take place.
2) Day 1, ants were fed with either P32 in sugar solution (FEED + P32), or sugar solution only (FEED - P32). FEED 1/2 P32 refers to a group fed half the concentration of P32 in sugar solution.
3) The MIX procedure; here the ants from each group were mixed with an equal number of unmarked ants from the same nest.
4) CHECK MARK; marks were generally measured on 20 individual ants from each group, except treatments 6, 7 and 8 where 30 were tested.

rest of the course of the experiment.

Feeding took place on day 1 of the experiment. All foodstuffs were removed on day 2. No further feeding took place in any treatment.

Treatments 2, 9 and 11 were then used to assess the level of the mark and its loss with time. The mark was checked on days 5, 8 and 10. To check the mark (dose level of an ant), 20 ants were removed and killed in 80% alcohol. These were then individually assessed for dose using a hand held Geiger-Muller probe. All dose levels were measured in counts per minute, (c.p.m.).

The remaining treatments, numbers 6, 7 and 8 were used to examine whether a period of isolation and starvation of 3, 4 or 5 days was sufficient to prevent trophallactic transfer of the isotope to unmarked worker ants. Thus in treatment 6 the worker ants were mixed on day 5 (after 3 days isolation and starvation) with 100 fresh unmarked ants from the same nest. In treatment 7 the isolation period was 4 days and in treatment 8, 5 days. Marks were checked in 30 ants from each treatment for the 5 days following the mixing procedure.

Mortality was checked in all treatments at the completion of each experimental procedure.

8.7. Laboratory estimates of known populations.

In a further set of experiments the accuracy of the estimate of populations using the mark-release-recapture method was tested. The technique used was that decided on from the experiments described in Section 8.6.

8.7.1. The Lincoln Index. The mark-release-recapture method uses the Lincoln Index formula to estimate population size.

The standard Lincoln Index formula is:

$$N = \frac{an}{r} \qquad (1)$$

N = estimated population
a = number marked and released
n = number in second sample
r = number of marked individuals in second sample

The variance of the estimate is given by Var(N) where:

$$Var(N) = \frac{a^2\, n(n-r)}{r^3} \qquad (2)$$

However when r is small it is usual to adapt the formula:

$$N = \frac{a(n+1)}{r+1} \qquad (3) \qquad\qquad Var(N) = \frac{a^2\,(n+1)(n-r)}{(r+1)^2\,(r+2)} \qquad (4)$$

This has been found to give better population estimates when r is less than 20 (Bailey 1951, 1952).

The conditions which need to be met for the formulae to be valid and the formulae themselves are summarised by Southwood (1978). Many modifications of the basic method can be used (Southwood 1978, Blower et al 1981), but because of the logistical problems of applying these methods to *L. flavus.* colonies selected, it was only possible to use the simple basic method.

8.7.2. The experimental estimates.

Five sets of ants with different, known populations were set up in small jars with a moist sponge as a water source. The first sample was taken from these and marked using the procedure determined by the experiments decribed in section 8.6., except that in sets 4 and 5 a half dilution of P32 was used (0.01 mCi per 100 ants). The marked ants were returned to the population and two days were allowed to elapse before the second samples were taken. A variety of second sample sizes were taken and the number of marked ants that were recaptured recorded.

8.8. The field estimates

8.8.1. Assumptions about the use of a mark-release-recapture technique. The use of a mark-release-recapture technique involves certain assumptions about the population whose size is being estimated (see Southwood 1978 for example). These are essentially that the population is:

a) a closed and stable one, with no immigration, emigration, births or deaths during the sampling period, (or that these are estimated),

b) that all individuals have an equal chance of being captured on all occasions, and

c) that marking does not affect behaviour.

8.8.2. Colonies of ***L. flavus*** and the assumptions. A colony of *L. flavus* is thought to be closed, with no mixing with other colonies and thus no immigration or emigration. The period between the two samples is so brief that it is likely that mortality will not be significant. The production of new workers can be observed as these callow workers have a distinctly pale coloration compared to older ones. They can thus be left out of consideration in the second sample. Thus assumption a) appears to be a valid one.

Assumption b) is more difficult to assess. The method of sampling, colection of ants from underneath the slates, appears to enable a random sample of workers to be taken. This assumes, though, that the workers assembled in the galleries under the slate are a random sample of the colony. Division of labour amongst workers of *L. flavus* has not been investigated. It is possible that some ants may specialise in brood care and others in foraging as is commonn in other social insects (Wilson 1971). However, as the galleries underneath the slate constitute the centre point of activity of the mound (brood, pupae, eggs and workers accumulate here) it is likely for example that foragers would be constantly passing through in order to "deliver" food and would thus be represented in the population under the slate.

The time period allowed for mixing of the marked individuals with the rest of the colony was assumed to be sufficient to ensure that the chances of a biased catch for the second sample were eliminated. Odum and Pontin (1961) concluded that 4 days were sufficient for this.

As far as assumption c) goes no changes in behaviour were observed for marked ants in the laboratory, but clearly it was not possible to assess this in the field.

8.8.3. Timing of the field estimates. Two sets of estimates were made on the same colonies, the first set in July/August 1985, the second in September/October 1985. The full dates and sampling details are given in Appendix Two.

This meant that the first set of estimates were made before the major production of new adult workers and the second estimate afterwards.

PART FOUR

THE RESULTS

CHAPTER NINE

Results and conclusions of preliminary investigations.

9.1. Introduction.

In this Chapter the results of a number of different investigations, carried out to determine the methodology and sampling procedure for the examination of the characteristics of the ant populations and their environments are presented and conclusions drawn.

9.2. What size of quadrat to use? The trial quadrats.

9.2.1. Results. The results of the trial quadrat analyses are summarised in Tables III and IV.

9.2.2. Interpretation of the results of the trial quadrats.

9.2.2.1. Box Hill. At Box Hill the density of the mounds did not vary with the increasing sample size, indicating perhaps that any of the sizes would be adequate to measure the density of ant mounds present. This was not true for the measurement of spatial distribution. The value of R for the whole quadrat showed a significant departure from 1 towards overdispersion, as did the middle 15 x 15 metre quadrat. The smallest did not, suggesting that a quadrat of 10 x 10 metres was too small to provide an accurate estimate of the distribution of the mounds.

9.2.2.2. Aston Rowant. The more complex analysis at Aston Rowant confirmed that a 10 x 10 metre quadrat size was not representative of the population. In these quadrats it was evident that there was considerable local variation in the density of mounds present, from 0.1 to 0.2 mounds/m^2 and in their spatial distribution. The values of density recorded from the larger quadrat sizes were much more consistent. The values of R for the enlarging quadrats increased asymptotically to around 1.21 to 1.22.

Table III.

Results of the trial quadrat at Box Hill.

Quadrat size in metres	No. of mounds located	Density in mounds/sq. metre	R	Sig.
10 x 10	28	0.28	1.113	N.S.
15 x 15	66	0.29	1.184	1%
20 x 20	112	0.28	1.166	1%

R is the Index of Dispersion from a Clark and Evans (1954) nearest neighbour analysis.
Sig. is the significance of the departure from a random distribution.
N.S. indicates no significant difference.

Table IV.

Results of the trial quadrat at Aston Rowant.

Quadrat size in metres	No. of mounds located	Density in mounds/sq. metre	R	Sig.
10 x 10 cent	10	0.10	0.970	N.S.
10 x 10 a	20	0.20	1.045	N.S.
10 x 10 b	16	0.16	1.102	N.S.
10 x 10 c	20	0.20	1.415	1%
10 x 10 d	15	0.15	1.271	5%
12 x 12	20	0.14	1.090	N.S.
14 x 14	29	0.15	1.191	N.S.
16 x 16	37	0.15	1.217	5%
18 x 18	51	0.16	1.215	1%
20 x 20	71	0.18	1.206	1%

In both of the trial samplings it was clear that the best representation of the characteristics of the population was given by the largest 20 x 20 metre quadrat size. The asymptotic nature of the increase in R and probably the density recorded indicated that larger sample sizes would not yield any greater benefit, in terms of accurracy, and would thus not be 'cost effective'.

9.2.3. Conclusions from the trial quadrats. Taking these results into account it was decided to use a 20 x 20 metre quadrat as the sample size for future work. This would ensure a representative sample, while any larger would have involved far more work for apparently little benefit. The trial quadrats had demonstrated that a 20 x 20 metre quadrat could be surveyed in a reasonable amount of time. As long as the sample area was carefully chosen as representative of the population as a whole, no problems were envisaged.

9.3. Laying out a 20 x 20 metre quadrat in the field.

Having selected the exact area in which to position the quadrat, a 20 metre line was measured out on a north-south compass bearing. The second line measured out was 20 metres long, at a right angle to first line. To check the accuracy of this positioning, the diagonal of the quadrat was measured. For a perfect right angled triangle with two sides of 20 metres the hypotenuse should be 28.28 metres long. Having established that this was correct, two 20 metre lines were then measured from the corners of the triangle, thus establishing the position of the fourth corner of the quadrat. The diagonal from that corner to the origin, also 28.28 metres was then checked. Using this system it was possible to set up the 20 x 20 metre quadrat to an accuracy of under 5 cm., a maximum error of 0.25%.

9.4. The examination of young colonies.

9.4.1. Characteristics of colonies of *L. flavus* that may indicate their status.

A colony of *L. flavus* would be expected to contain a queen, a large population of worker ants and brood. However, when digging up and examining colonies of *Lasius* ants it is often difficult to find the queens (c.f. Anderson 1970, Duckett 1975), and thus the absence of a queen can not be taken as conclusive evidence as to whether a colony is queenright or not. Even when a queen is found in a colonies' nest it may not be an active, egg laying queen. At the time of year these patches were dug up, gynes from the sexual brood may still have been present in colonies, having missed the sexual flight. It is possible that such gynes could lose their wings, and thus be indistinguishable from young egg laying queens. When winged gynes were kept in the laboratory for long periods there was quite a high frequency of wing loss observed. Thus, the presence or absence of queens cannot provide incontravertible evidence of the status of the contents of such a patch of freshly excavated earth.

A better guide to the status of these areas may be the presence of eggs, larvae and pupae. These indicate the presence of an active, egg laying queen. It is still possible that larvae could be moved away from the large central mound of a colony, for example to be closer to a food source, such as a colony of root aphids. Worker ants will excavate galleries around aphids clustered on the roots of suitable plants, and the soil thrown up from such 'feeding galleries' may produce a patch of excavated soil on the surface, similar to those observed. The movement of eggs and pupae seems less likely.

Another indicator is the size of worker ants, measured by head width. The size is known to correlate with the overall worker size, which increases as colonies get older (Brian and Brian 1951, Elmes and Wardlaw 1982).

9.4.2. Results of the examinations. The results are summarised in Table V.

Queens were only found in 2 of the 10 patches, (numbers 7 and 8) and in both of these there was more than one queen. It is known that young colonies of L. flavus may have more than one queen, (Donisthorpe 1915, Waloff 1958, Pontin 1960, Anderson 1970). Both of these patches also had large numbers of brood, in all stages. There were quite large numbers of workers present (2,000 to 4,000) and the worker head widths were also at the smaller end of the range of the ten patches. All of this evidence taken together indicated that these patches were the sites of real, small young colonies of L. flavus.

In four of the patches no queens or brood were found, and the workers were larger. The numbers of worker ants found was under 2,000 in each of the patches. Numbers 9 and 10 had been chosen as patches of activity next to larger mounds, and in both cases there were small numbers of relatively large workers only, and no brood or queen found. Both appear to be patches of activity of worker ants away from the main colony mound, possibly around a food source. A large number of root aphids were noted in the other two patches without brood, numbers 2 and 6. No queens were found and the workers measured were medium sized. There is no evidence to suggest that these were small young colonies in their own right. It seems likely that these two patches also represented soil excavated around local feeding 'stations' of large nearby colonies.

In patch 5, another isolated area, there were small number of very small workers with a small amount of brood present. No queen was found

Table V.

Results of the AR 12 patch excavations.

Patch	Type	Workers	Brood	Queens	Head width
1	Chosen as probable real nest. Digging ~ 20 cm. across.	5722	V. many All stages	None found	0.770 +\- 0.057 mm.
2	10-15 cm. digging. Adjacent to nest no. 1	1783	0	None found	0.708 +\- 0.067 mm.
3	15 cm. digging next to large mound.	6522	~ 30 2nd. instar	None found	0.716 +\- 0.084 mm.
4	Next to 3. Small digging between two mounds. 15-20 cm. across	3053	Quite a lot.All stages	None found	0.704 +\- 0.053 mm.
5	Small digging 10 cm. across.	1514	20-30 eggs+ brood	None found	0.658 +\- 0.039 mm.
6	Small digging (~10 cm.) around a thistle.	851	0	None found	0.720 +\- 0.055mm.
7	Small soil working 12-15 cm. across.	2270	Many, all stages	Yes 3	0.694 +\- 0.050 mm.
8	Small digging (5-10 cm.) around a thistle, between two large mounds.	3750	Many, all stages	Yes 2	0.621 +\- 0.027 mm.
9	Thought to be a patch of digging next to a large mound	666	0	None found	0.719 +\- 0.049 mm.
10	Digging ~15 cm. across next to large mound.	371	0	None found	0.770 +\- 0.063 mm.

Due to difficulty in telling small colonies from satellite galleries of larger colonies on surface features alone, 10 areas where small amounts of soil had been thrown up, were dug up and the ants present examined. Results confirmed that both small colonies and satellite galleries appeared very similar on surface features alone, and that excavation of an area like this, to look for the presence of brood was necessary to classify it properly.

but eggs were. Peakin (pers. comm.) has suggested that queens of L. flavus are seldom found far from their eggs and this would suggest that this patch may represent a true small colony.

However, with the other three patches it is more difficult to come to any firm conclusion. All had brood present, although in very different numbers. The mean sizes of the workers varied considerably, from the second smallest out of the ten to the largest, but no queens were found. Patch 1 was chosen as looking like a young colony. It was not located near to any large mound of which it could be a satellite. A large number of workers were extracted as well as a lot of brood. These characteristics would suggest that this was a real young colony. In contrast, no queen was found (although the importance of this character has already been suggested to be relatively minor), but the workers were amongst the largest found. Possibly, this was in fact quite a well established young colony (5,722 workers) in which worker size was already quite large. Little is known of the early growth of L. flavus colonies and at what stage they start to build the characteristic mounds. Perhaps extensive mound building does not go ahead until the colony is quite large. A tentative conclusion would be that this was an entire growing colony and not the satellite of a larger established colony. Patch 2 lay adjacent to patch 1 but it is unlikely that it represented a satellite of it. There was a large and significant ($P<0.01$, $t = 3.98$) discrepancy between the sizes of the workers from each. Patch 2 is likely to have been a satellite of other nearby larger colonies.

Patch 3 was deliberately selected as being likely to be the satellite of an established colony. It was located within 50 cm. of a large established mound. The workers were of a moderate size only, but there were a lot of them, this patch containing more workers than any other (6,522). No queen was found but there was a very small amount of brood present. It does not seem likely that a large colony would allow the establishment of a rival colony so close to it. The tentative conclusion here would be that this was a satellite of the main colony and that a few brood had been moved from the central mound, possibly ~~to~~ to a food source.

In patch 4 there were quite a lot (3,053) of medium range sized workers with a lot of brood present. No queen was found but otherwise this has the characteristics of a small colony. However, this patch was located between two other large mounds and next to patch 3. The worker sizes of the two patches are not significantly different ($t = 0.56$, $P>0.05$). It is difficult to come to a conclusion as to the status of this patch.

9.4.3. Conclusions from the examinations. The difficulties in determining the status of some of these patches has been clearly demonstrated by the examination of the samples. The difficulty in distinguishing between small real colonies and more temporary activity, on surface features alone was clearly shown. For example, patches 6 and 8 were identical on the surface, but patch 6 was apparently not a true colony, while patch 8 was demonstrated be a young colony of *L. flavus.* It proved impossible to determine the status of some of these patches despite completely digging them up.

In practice, during the mapping of the sample quadrats, observations of the position of a suspect nest, in relation to larger mounds, were taken into account. If the patch was near (under 1 metre) to a large mound it was deemed likely to be a satellite of the large colony. A brief investigation of the area under the surface was also made, with the size of the worker ants examined and presence of brood looked for. Small worker ants and presence of brood were taken as indicating the patch was a young colony and not a satellite.

In most of the areas that were later examined the determination of the status of such patches of activity did not prove to be a problem. They tended to be very rare. In the few cases where they were common it was hoped that the approach adopted to them was a reasonable one and would not lead to any large errors. The presence of such satellite areas appears to have been disregarded by other authors (Waloff and Blackith 1966, Pontin 1963, 1969 for example).

9.5. The results of the preliminary mark-release-recapture experiments.

9.5.1. The effect of pre-starvation on the mark level. Treatments 2 and 9 were designed to check the effects of prestarvation on the acquisition of a mark. The results are set out in Table VI. In this Table the mark levels in counts per minute for the two groups are presented for 4, 7 and 9 days after feeding on marked sugar solution.

In set B, ants starved the day before treatment had a clearly higher mark level than the ants fed sugar solution. In set A ants there was no clear increase in the mark level. The differences in group B ants were significant for the 4 and 9 day ants but not for the 7 day ants. In group A the differences were not significant between the two groups, except in the 7 day ants (see Table VI).

Since prestarvation had enhanced the amount of P32 in sugar solution eaten by the group B worker ants, this practice was subsequently undertaken in all experiments.

9.5.2. The amount of sugar and P32 solution fed to the ants.

The treatment 11 ants, fed the half concentration of P32, were

Table VI.

The effect of pre-starvation on dose level.

Dose level in counts per minute with standard errors.

GROUP	A		B	
TREATMENT	2	9	2	9
+ 4 DAYS	>>100	168+/-13	16+/-3	47+/-6
+ 7 DAYS	139+/- 4	116+/- 7	16+/-4	25+/-4
+ 9 DAYS	129+/- 7	114+/- 5	10+/-1	22+/-5

20 ants were assessed in each group.

Ants in treatment 2 were starved for 24 hours before feeding with sugar solution containg P32. Ants in treatment 9 were fed sugar solution without P32, 24 hours before feeding with the P32 in sugar solution. Ants in group A, treatment 2 at day +4 were only recorded as all being greater than 100 cpm.

The significance of the differences between the prestarved and the and non-prestarved ants was tested with a series of t-tests. The t values were as follows.

	Group A	Group B
+ 4 days	---	3.51**
+ 7 days	2.67*	1.47
+ 9 days	1.69	2.30*

* Significant difference at the 5% level.
* Significant difference at the 1% level.

found to be inadequately marked, and only the use of a more sensitive radiation probe enabled them to be satisfactorally distinguished from unmarked ants.

In all other treatments, where ants were fed the full dose of P32, the dose level attained was sufficient to distinguish marked ants from unmarked ants. Even in set B ants, which generally failed to attain a high dose level, it was still possible to distinguish the marked ants after 7 days.

9.5.3. The length of the isolation period This was tested using set A ants only, in treatments 6, 7 and 8. The results proved conclusively that the isolation period had achieved the desired effect. In all cases the ants fell into 2 groups, one group with high level doses, the original marked ants, and one group of ants with no mark or a little contamination. There was no overlap between the groups in any case.

Even in the group of ants that had been isolated for only 3 days it was possible to distinguish between marked and unmarked ants, which had been mixed with them (see Table VII). This indicated that there had been virtually no trophallactic transmission of P32 between the marked ants and the unmarked ants.

As an example of the actual dose levels of individual ants some results are given in full.

1) Isolated 3 days, mixed for 5 days.

10 15 250 40 150 45 25 175 30 20 25 200 40 25 200 25
25 260 20 170 200 200 150 200 200 195 25

2) Isolated 5 days, mixed for 4 days.

130 140 10 10 100 150 10 100 90 80 10 10 80 90 5 5
90 20 93 94 14 10 75 13 10 11 10 10 190 7 62 100

In group one, the marked ants had dose levels from 170 to 260, while

Table VII.

<u>Comparison of marked and non-marked ants, 1 to 5 days after the isolation period.</u>

Dose level in counts per minute with standard errors.

DAYS AFTER MIXING	STARVATION PERIOD 3 DAYS ISOLATION		4 DAYS ISOLATION		5 DAYS ISOLATION	
	MARKED	NON-MARKED	MARKED	NON-MARKED	MARKED	NON-MARKED
1	300.0+/-24.0	8.9+/-0.4	248.3+/-11.1	21.4+/-2.5	156.4+/-13.8	15.0+/-1.6
2	256.7+/-19.6	25.0+/-2.0	202.3+/-10.3	23.9+/-1.3	132.7+/-11.5	13.9+/-1.6
3	254.2+/-17.5	15.0+/-1.3	249.3+/-22.0	19.3+/-1.8	118.9+/-10.2	12.8+/-1.0
4	254.7+/-10.9	24.7+/-1.7	200.0+/-16.8	17.8+/-0.8	104.0+/- 8.2	10.3+/-0.9
5	196.2+/-11.3	26.4+/-2.7	186.5+/-18.6	15.5+/-1.2	106.5+/- 7.2	9.7+/-0.6

Ants that had been fed the P32 in sugar solution were starved for 3, 4 or 5 days. This allows the P32 to pass the proventriculus in the gut of the ants. it can then not be passed on to unmarked ants. after the isolation period the marked ant were mixed with equal numbers of unmarked ants. The doses of the groups were then monitored to establish the degree of contamination of non-marked ants. The experiment showed that the shortest isolation period tried (3 days) was adequate to prevent excessive contamination.

the unmarked ranged from 10 to 45. In group two the marked group ranged from 62 to 190, and the unmarked from 5 to 20. The rate at which the dose levels of the marked ants fell can be explained by the natural decay of P32 (half-life 14.2 days).

9.5.4. The length of time for which the mark is distinguishable. Treatments 2 and 9 demonstrated that the mark was easily distinguishable in set A ants for 10 days after feeding with P32. Mean counts were over 100 cpm for both treatments.

9.5.5. Mortality caused by the techniques used. The mortalities in the controls are shown in Table VIII. They were too high for satisfactory use in a mark-release-recapture estimate. The mortalities of group B were generally extremely high and much larger than that of group A. However, it was thought that the conditions under which the ants were kept, during the experiment, were not satisfactory and could be improved. *L. flavus* is a delicate species, susceptible to desiccation, waterlogging and other stresses. Stradling (1970) remarks on the susceptibility of the genus *Lasius* to its own production of formic acid when over excited. The treatments used involved repeated cooling to just above freezing point to reduce the activity of the ants and must have induced considerable stress on them.

In the subsequent laboratory experiments and field estimates greater care was taken in keeping and handling the ants and as a result mortality was kept below 10%.

9.5.6. Conclusions from the experiment.

1) A starvation period prior to feeding with P32 increased the dose level of the worker ants.

2) The concentration of P32 used, produced a clear mark.

3) The use of cotton wool balls impregnated with P32 was not

Table VIII.

Mortalities per 100 ants in the control treatments.

TREATMENT	1		3		4		5		10	
GROUP	A	B	A	B	A	B	A	B	A	B
DAY 2	0	4	2	0	1	3	2	1	5	1
DAY 5	3	22	2	1	1	26	4	7	7	8
DAY 7	4	22	5	3	2	33	2	10	7	15
DAY 9	10	32	11	11	1	>30	6	10	7	17
DAY 11	10	38	16	29	2	>50	16	17	7	19
DAY 12	14	38	15	>50	5	>50	25	19	13	20

Treatments given are as described in Figure 8.1.
Groups A and B were ants from different colonies. Group B, ants which showed higher mortalities, had been freshly collected one week before the experiment began. Group A ants had been kept in cool conditions for one month prior to the experiment. The mortalities were too high to use in a mark-release-recapture field estimate. However, the handling conditions of the ants were much improved for the field estimates and mortality was much lower.

successful. It was better to give the fluid in a small open container.

4) An isolation period of 3 days after feeding was adequate to prevent significant contamination of other unmarked ants.

5) The mark remained distinguishable for at least 10 days after feeding, more than enough for the mark-release-recapture technique to be completed.

6) Mortalities were high but were improved by better treatment of the ants and by better "housing" conditions.

9.6. Results of the estimates of laboratory populations.

9.6.1. The results. The results are shown in Figure 9.1.

9.6.2. Interpretation of the results. Accurate estimates of the population sizes were obtained in sets 1, 2 and 3. In set 4 where the size of the second sample was small the estimate was accurate, but surprisingly when the size was increased a low estimate was obtained. Set 5 produced a similar low estimate.

These latter results are difficult to explain, but in both of these sets the first sample was over 10% of the population size. Stradling (1970) achieved high levels of accuracy with his laboratory trials of the technique on *Myrmica rubra* His first sample sizes were also large, over 40% of the population. While it is generally recommended to attain large sample sizes for mark-release-recapture (Southwood 1978), it is difficult to achieve this with *L. flavus* in the field. Thus the large first sample sizes in sets 4 and 5 were unlikely to be repeated in the field estimates.

9.7. The application of the mark-release-recapture technique on colonies in the field.

Having taken into account the results of the two sets of experiments descibed above, the procedure for the estimation of colonies in the

Figure 9.1 **Results of the laboratory population estimates**

Set 1

Population size	= 1000 ants
Sample 1 size (the number marked)	= 100 ants
Sample 2 size	= 100 ants
Number of recaptures	= 7 ants
Population estimate (formula 3)	= 1267 +/- 412 ants

Set 2

Population size	= 1000 ants
Sample 1 size	= 100 ants
Sample 2 size	= 100 ants
Number of recaptures	= 7 ants
Population estimate (formula 3)	= 1267 +/- 412 ants

Set 3

Population size	= 1300 ants
Sample 1 size	= 100 ants

Sample 2 size	No. recaptures	Population estimate - formula 3
100	6	1443 +/- 492 ants
110	7	1388 +/- 448 ants
120	8	1344 +/- 411 ants
130	8	1456 +/- 444 ants
140	10	1282 +/- 355 ants
150	10	1373 +/- 381 ants

Set 4

Population size	= 1171 ants
Sample 1 size	= 188 ants

Sample 2 size	No. recaptures	Population estimate-formula 1	formula 3
40	6	1253+/-251	1101+/-189
50	9	1044+/-168	958+/-138
60	10	1128+/-173	1043+/-145
70	13	1012+/-135	953+/-117
80	16	940+/-112	895+/-100
90	19	891+/- 97	855+/- 88
100	22	855+/- 91	826+/- 79

Set 5

Population size	= 883 ants
Sample 1 size	= 100 ants
Sample 2 size	= 110 ants
Number of recaptures	= 21 ants
Population estimate (formula 1)	= 524 +/- 101 ants

field was as follows.

1) The first worker samples were collected. As many workers as possible were collected from a single visit to each slate.

2) These were then starved for 1 day.

3) Sample sizes were counted and fed the appropriate amount of phosphorus 32 in 10% sugar solution.

4) Any excess sugar solution was removed after 24 hours. Generally little, if any, was left.

5) The workers were then starved for a further 4 days.

6) They were then released back into the nests by simply lifting the slate and allowing them to enter the galleries beneath.

7) The tagged workers were allowed to mix with the rest of the population. On most occasions 4 days were allowed for mixing as recommended by Odum and Pontin (1961). On two occasions practical constraints limited this to 2 days.

8) Second samples of workers were taken from beneath the slates. Again as many as possible were collected in a single visit.

9) The number of ants in the second samples were counted, and the number of these that were marked noted.

10) The population estimate was made using the appropriate Lincoln Index Formula (see section 8.7.1)

For these estimates the workers were housed in larger containers, and were not repeatedly cooled to reduce their activity. This resulted in mortality being greatly reduced, generally to under 10%, and often much less.

The quadrats in which mark-release-recapture estimates were made are indicated in Table II at the end of Chapter Seven.

9.8. Energy contents of ants.

The results are shown in Table IX. From them we can calculate the mean energy contents per gram dry weight of ants.

workers	20.998 KJ/g
males	23.097 KJ/g
gynes	32.110 KJ/g

Gynes have a higher energy content per gram, because of the large amount of fat stored in their bodies prior to the nuptial flight.

From the dry weights of males previously measured there were about 3,125 males/g. The number of gynes, in the samples tested, was known. The number of workers per gram was known in three of the samples tested.

Therefore, 1 male is equivalent to about 7.4 J,

1 gyne is equivalent to about 360.8 J,

1 worker is equivalent to about 6.7 J.

There was little difference between the different groups of workers. Workers and males have similar energy contents and dry weights.

9.9. The soil cores.

Finally in this Chapter the differences between cores that had been through the Tullgren funnel extraction, and those that had not, is considered.

The percentage water contents of the two sets of cores are shown below. Each figure is the mean of the three cores collected from a sample area.

	Directly dried	Tullgren funnel invertebrate extraction first
OWH 1	44.11	42.21
2	45.39	43.27
3	51.28	54.12
MD 1	38.17	36.52
2	39.86	39.66
3	39.99	40.19

Table IX.

Energy contents of the samples of ants.

SAMPLE	WEIGHT (g)	CORRECTED DEFLECTION	TOTAL ENERGY CONTENT KJ	KJ/g SAMPLE
Workers 1	0.1620	10.4	3.720	22.962
Workers 2	0.2325	14.0	5.012	21.557
Workers 3	0.1928	9.9	3.544	18.382
Workers 4	0.2756	15.4	5.513	21.092
Males 1	0.0791	5.4	1.931	24.418
Males 2	0.1117	6.8	2.432	21.775
Gynes 1	0.3521	31.2	11.160	31.695
Gynes 2	0.4433	40.4	14.450	32.524

The calibration of the bomb calorimeter is shown in Table I.
Mean energy contents are as follows:

workers - 20.998 KJ/g
males - 23.097 KJ/g
gynes - 32.111 KJ/g

Four sets of cores show a lower percentage water content when subjected to the Tullgren funnel procedure, two sets of cores a higher percentage water content.

If the losses of soil were significant it would be expected that all the Tullgren funnel sets of cores would show a higher percentage water content, as the soil lost would be included as part of the water loss.

The differences are not consistent and indicate that with the natural variation in the water contents, the differences caused by the loss of small amounts of soil in the Tullgren funnels are not significant.

CHAPTER TEN

The results from the sample areas.

10.1. Introduction.

The results are presented in turn for each of the sample areas. The raw data for many of the results is contained in Appendices in volume two of this thesis as follows.

Appendix One contains the raw data from the mapping and measuring of the ant mounds in the quadrats.

Appendix Two contains the details of how the estimates of the colony sizes were obtained using mark-release-recapture.

Appendix Three contains the sizes and nearest neighbour distances of the mounds of the colonies from which mark-release-recapture estimates were made and the sexuals collected. The same information is also given for the mounds that were dug up.

Appendix Four contains the details of when the soil cores were collected, their physical characteristics and the numbers of the major invertebrate groups that were extracted from them.

Appendix Five contains the full details of the phenology of sexual production for each individual colony observed in 1986.

Appendix Six contains the individual measurements of soil depth in each sample area.

Appendix Seven contains the individual measurements of soil pH from each sample area.

Appendix Eight contains the raw data of the temperature measurements made in each sample area.

Appendix Nine contains the full lists of plants recorded in each sample quadrat and the details of the records from the small 1 m^2 sample quadrats examined in some of the sample areas.

Appendix Ten contains the raw data from the counts of rabbit droppings in each sample area.

10.2. The south slope at Old Winchester Hill.

10.2.1. General description. As seven sample areas were located on the south slope of this reserve some details of it are given here to avoid repetition. The slope faces almost directly due south and the Solent and Isle of Wight can be seen in the distance when standing on it It bears a rich thermophilous flora notable in particular for a large population of *Phyteuma orbiculare* a plant which grows in the south of England on very warm slopes such as this. Several species of orchis are also found on the slope, the most abundant being *Gymnadenia conopsea*, this being in contrast to the opposite side of the hill (see description of OWH NFS) on which the orchid *Dactylorhiza fuchsii* dominates. *Juniperus communis* is abundant on the lower half of the slope but the development of seedlings is closely monitored to observe the effects of grazing on them.

The grassland is generally dominated by *Festuca* spp. and *Avenula pubescens*. The turf is short over much of the slope but some areas have accumulated a thicker underlayer of grass and herbs. The sedges *Carex flacca* and *C. caryophyllea* are also abundant. Several plants such as the abundant *Hippocrepis commosa*, *Anthyllis vulneraria* and *Spiranthes spiralis* are indicative of the dry thin soils on the slope. Plants indicative of lower levels of grazing such as the coarse grasses *Brachypodium pinnatum* and *Arrhenatherum elatius* are in, contrast, much rarer on the slope.

Thus in summary the slope supports a short herb-rich flora indicating dry, warm, and well grazed conditions.

The soils of this slope were investigated by New (1969). The basal rock is middle chalk with a typically shallow soil overlying (the average depth is about 10 cm.). They are classified as shallow rendzinas and are considered typical of upper and middle chalk soils in lowland England. They lie within the Icknield series of soils (Avery 1964).

New (1969) also states that evidence from air photographs taken in 1957 suggests that the south slope was subject in the "distant past" to ploughing, as there is evidence of ridge and furrow plough marks being present.

10.2.2. Management of the south slope. The south slope has a total area of 15 hectares, which has been divided into 9 small plots, in which a nine year rotation of grazing is underway. The details of the rotation are shown in Figure 10.1. This rotation only began in 1981. It is only the use of flexi-netting fences which has enabled this rotation to be carried out. These fences, which can be set up anywhere and can be electrified with a small battery as a power source, have enabled grazing areas to be precisely delineated.

Before 1981 the grazing history was quite variable, with the whole area grazed as one unit. In common with many other downlands, the area was extensively rabbit grazed up until the outbreak of myxomatosis in 1954. There was spasmodic sheep grazing during the 1960's, but in the 1970's cattle grazing was started. This last occurred in 1976 when during September to October, 9 cattle grazed for a total of 531 cattle days an average of 35.4 cattle days per hectare. At this time it was recognised that the cattle were causing erosion problems, being much heavier on their feet than the sheep. The whole area was then left ungrazed for two years to recover. In 1979 sheep grazing was restarted. A total of 872 sheep days per hectare were grazed, followed

Figure 10.1.

Old Winchester Hill, south slope grazing plan.

OWH SS 4

1981 -
2 -
3 -
4 -
5 MAR - APR + S
6 MAY - JUN
7 MAY - JUN
8 JUL - SEP
9 OCT - DEC

OWH SS 5

1981 MAY - JUN
2 JUL - SEP
3 OCT - DEC
4 -
5 -
6 -
7 -
8 MAR - APR + S
9 MAY - JUN

OWH SS 7

1981 JUL - SEP
2 OCT - DEC
3 -
4 -
5 -
6 -
7 MAR - APR + S
8 MAY - JUN
9 MAY - JUN

OWH SS 8

1981 -
2 -
3 -
4 MAR - APR + S
5 MAY - JUN
6 MAY - JUN
7 JUL - SEP
8 OCT - DEC
9 -

OWH SS 9

1981 OCT - DEC
2 -
3 -
4 -
5 -
6 MAR - APR + S
7 MAY - JUN
8 MAY - JUN
9 JUL - SEP

OWH SS 11

1981 MAY - JUN
2 MAY - JUN
3 JUL - SEP
4 OCT - DEC
5 -
6 -
7 -
8 -
9 MAR - APR + S

OWH SS 12

1981 -
2 -
3 MAR - APR + S
4 MAY - JUN
5 MAY - JUN
6 JUL - SEP
7 OCT - DEC
8 -
9 -

S - scrub cut where necessary.

Each plot is grazed continuously for 5 years in the 9 year rotation, followed by 4 years with no grazing. Each grazing period corresponds to about 2,500 sheep days/hectare.

by 294 days per hectare in 1980. In the first year more grazing was needed to graze down the two years accumulated grass growth.

Since that time the rotation shown in Figure 10.1 has been followed. The grazing times indicate only the period in which grazing should take place in each area and not the actual length of time. In fact about two weeks is generally sufficient to graze down the grass tightly. Thus each grazing represents a short intense period, rather than a longer one of light grazing. Calculations from the grazing records, since the rotation began, show that, on average, each grazing period is equivalent to about 2,500 sheep days per hectare.

10.3. Quadrat 1, OWH SS 4.

Site - Old Winchester Hill (OWH).

Location - South Slope of the reserve (see Figure 5.2.).

The sample area in which this quadrat was positioned lies at the top of the slope, on its western side.

10.3.1. The characteristics of the ant population.

The ant mounds.

Number of mounds - 67
Mean diameter (D) - 40.8 +/- 1.69 cm.
Mean height (H) - 10.4 +/- 0.61 cm.
Ratio D/H - 3.9
Area of quadrat occupied by the mounds - 2.4%
Mean above ground volume of soil in the mounds - 12.2 litres.
Mean distance to nearest neighbour - 1.40 metres.

The distribution of the sizes of the mounds, as measured by the diameters, is shown in Figure 10.2.

The mounds in this quadrat had the smallest mean volume of those in any of the south slope quadrats.

Estimates of colony sizes and worker ant densities.

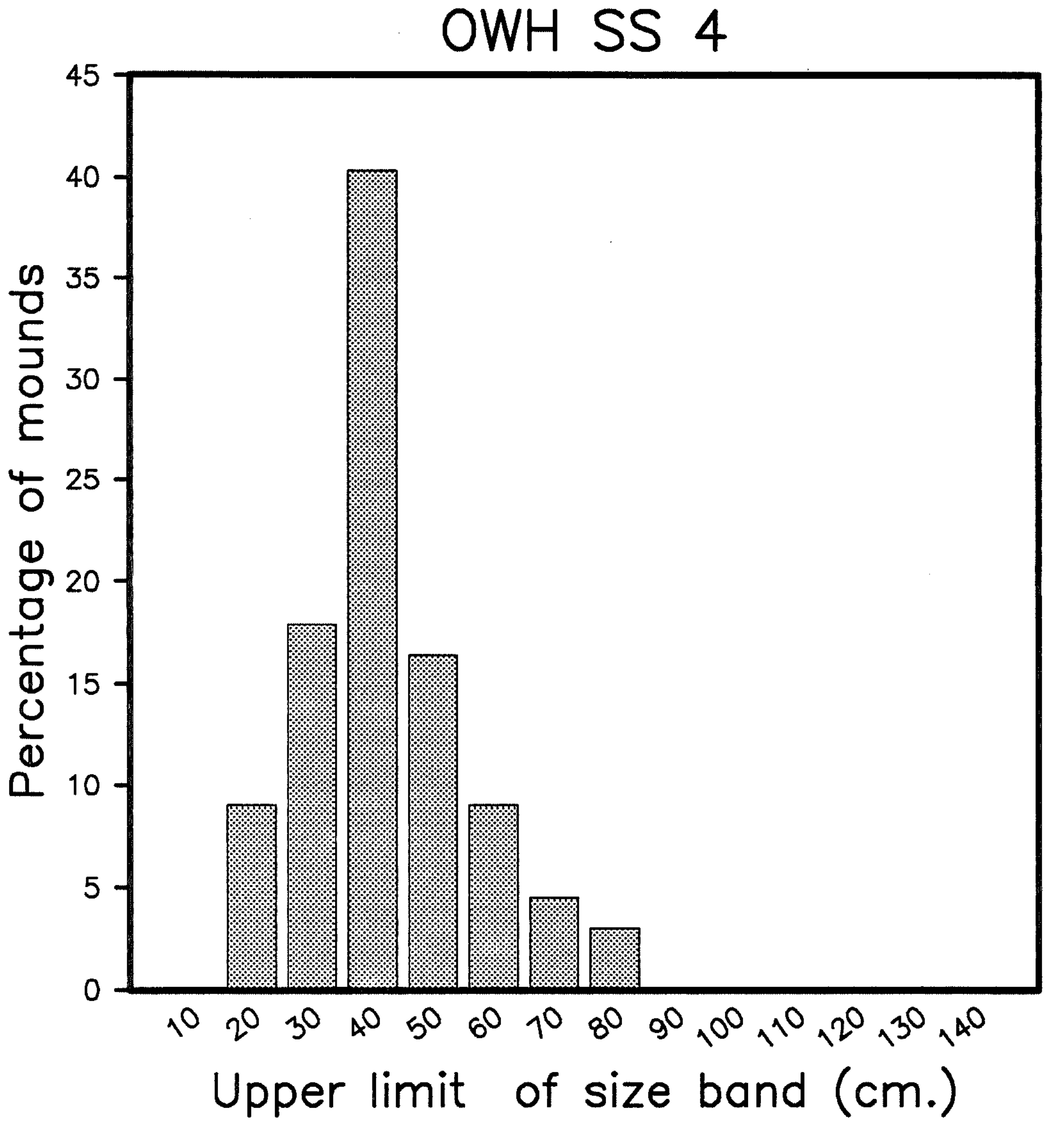
Mark-release-recapture estimates.

	Set 1. July/August 1985.	Set 2. September/October 1985.
Colony 1.	2,369 +/- 412	2,191 +/- 622
Colony 2.	6,590 +/- 1,799	4,913 +/- 947
Colony 3.	-	16,811 +/- 3,091
Colony 4.	-	2,024 +/- 402
Colony 5.	-	78,106 +/- 31,828
Mean	4,480	20,809 +/- 14,579

No recaptures of marked ants were made in colonies 3 - 5 in the first set of estimates. The value of 78,106 for colony 5 in the second set of estimates was the highest estimate for any colony. The mean of 4,480 for the first set of estimates, was the lowest of the sample areas in which population sizes were measured, although the sample size was only two colonies. In contrast, the mean of 20,809 was the

Figure 10.2.

The distribution of mound sizes in OWH SS 4.



A total of 67 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

highest of the second set of estimates.

Numbers of worker ants found in core samples.

In total 41 cores were collected. The mean number of worker ants extracted per core over the whole year was 8.49+/-2.41, exactly the same as in the other south slope quadrat in which cores were collected, OWH SS 11.

The sexual production of colonies.

The numbers of sexuals produced.

	1985		1986		1987	
	Gynes	Males	Gynes	Males	Gynes	Males
Colony 1.	59	862	33	2,476	0	137
Colony 2.	128	347	369	3	144	2,432
Colony 3.	40	104	339	940	246	1,464
Colony 4.	72	255	575	1,156	244	1,978
Colony 5.	136	537	511	3,565	324	2,573
Mean	87.0	421.0	365.4	1,628.0	191.6	1,716.8
SE	19.1	130.7	93.9	624.8	55.8	440.0

Sexual productivity in this sample area was consistently higher than in OWH SS 11, the other south slope sample area in which sexuals were collected.

Head widths of male and gyne samples. All measurements are in millimetres. The sample size for each colony is given in brackets. The final mean is the mean of the colony means.

	Males	Gynes
Colony 1.	0.67 +/- 0.008 (10)	1.41 +/- 0.010 (9)
Colony 2.	0.72 +/- 0.010 (10)	1.46 +/- 0.011 (10)
Colony 3.	0.70 +/- 0.010 (10)	1.45 +/- 0.011 (10)
Colony 4.	0.69 +/- 0.005 (10)	1.41 +/- 0.007 (10)
Colony 5.	0.71 +/- 0.009 (10)	1.44 +/- 0.014 (10)
Mean	0.70 +/- 0.009	1.43 +/- 0.010

Both mean male and gyne headwidths were of average sizes.

Dry weights of male and gyne samples. All measurements are in milligrams. The total dry weight of the whole sample of ants was measured. The number of ants in each sample is given in brackets.

	Males	Gynes
Colony 1.	0.250 (20)	9.87 (10)
Colony 2.	0.345 (20)	10.00 (10)
Colony 3.	0.300 (20)	4.18 (9)
Colony 4.	0.340 (20)	9.98 (10)
Colony 5.	0.345 (20)	10.09 (10)
Mean	0.316+/-0.019	8.82+/-1.16

The gynes from this sample area had the smallest mean dry weight of any of the sample areas in which sexuals were collected.

Dates at which stages were first observed in 1986.

The first small pupae were seen on 4/6, the first adult males on 17/7. The first gyne pupae were seen on 26/6 and the first adult gynes on 8/7.

10.3.2. Management. Grazing in this area followed the plan shown in Figure 10.1. Thus at the time of the recording of the ant mounds this area had not been grazed in the previous three years. After this the quadrat was grazed in March-April 1985, May-June 1986 and 1987, July-September 1988 and October-December 1989.

10.3.3. The physical environment.

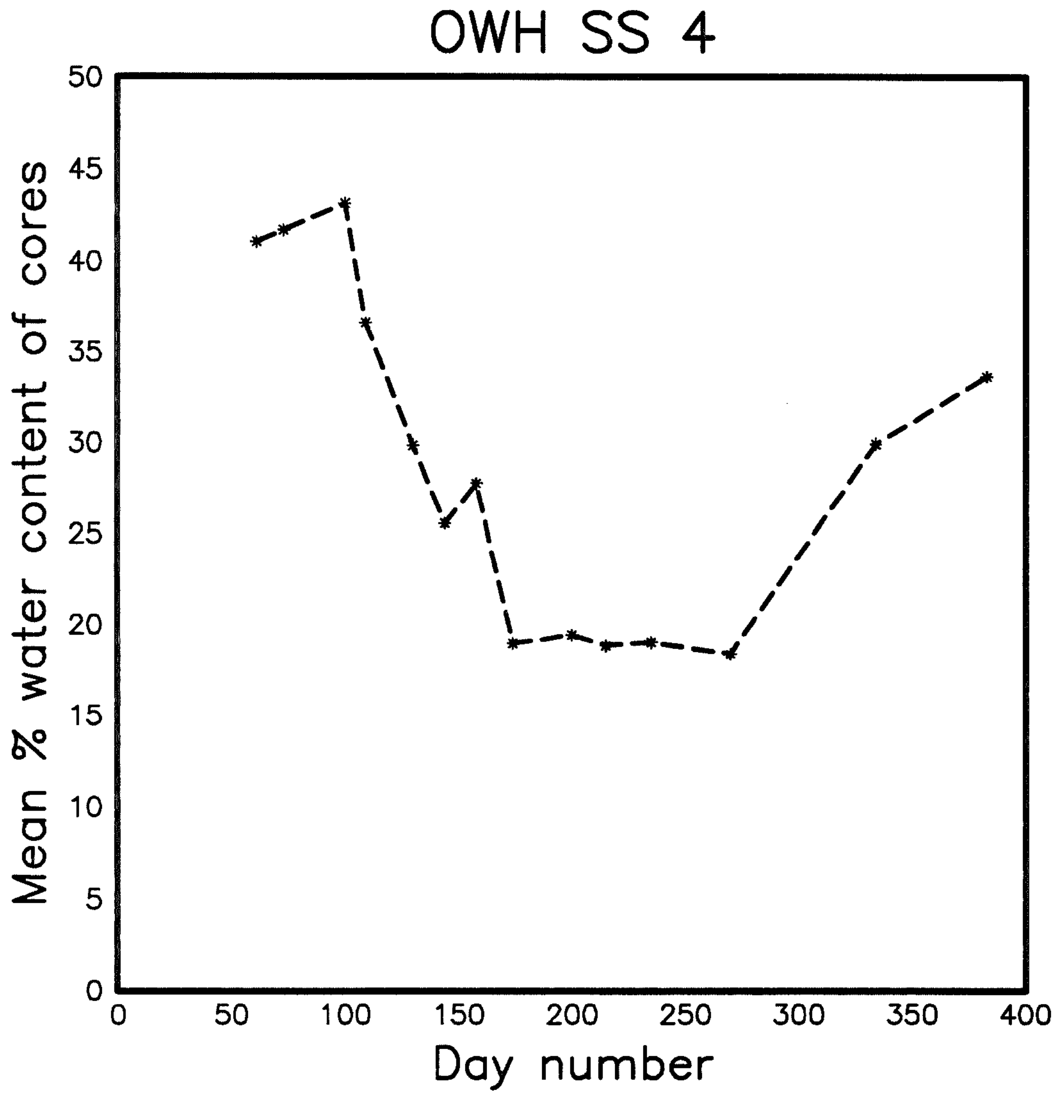
Altitude - 175 metres.
Slope - 22^{o}, facing 190^{o} (SSW).
Mean soil depth - 12.8 +/- 1.86 cm.
Mean soil pH - 7.42
Mean soil core density - 0.697+/-0.012 g/cm^{3}

This sample area had the deepest recorded soil depth of the south slope quadrats, although on the other reserves only AR 5 had a thinner soil.

The changes in water contents of the soil cores throughout the year are shown in Figure 10.3. The minimum mean water contents recorded were 18.8% on 3/8/89 and 18.4% on 27/9/89. The maximum was 44.1% on 10/4/89. Along with OWH SS 11 this was one of the driest of the sample areas that were examined, although the minimum water content measured did not reach as low a level as in some of the other sample areas.

Figure 10.3.

Water contents of soil cores collected in OWH SS 4.



Day number 1 = 1/1/89.

Each point represents the mean water content of a sample of cores collected on that day. The dates of sampling, sample size, mean water contents and standard errors are given in Appendix 4.

The annual mean temperatures are presented in Figure 10.4. Again, along with OWH SS 11, the other south slope quadrat, this area had the warmest mean soil temperatures of any of the quadrats in which temperatures were measured. The water contents and temperatures thus indicate that this was a hot dry area of chalk grassland.

10.3.4. The biological environment.

The flora. This quadrat had been grazed in the 4 years previous to the examination of the flora. As would be expected there was therefore a very short sward, with short herbs such as *Thymus serpyllum* and *Asperula cynanchica* abundant. The semi-parasitic plant *Euphrasia officinalis* and *Gentianella amarella* were also particularly common in this area, in contrast to the other south slope areas sampled.

Dense patches of both *Onionis repens* and *Hippocrepis commosa* were present in the area. In all 58 species of plant were recorded in this quadrat, the most of any of the quadrats on the south slope.

Rabbit droppings. The maximum mean number of droppings found on the mounds was 40.1 on 27/9, while the minimum was 2.0 on 15/3. Off the mounds the maximum mean number of droppings recorded was 2.2 on 27/9 and the minimum was 0 on 19/4 and 10/5. The full data is presented in graphical form in Figure 10.5. This quadrat was in the middle of the range of rabbit dropping densities recorded on the south slope quadrats.

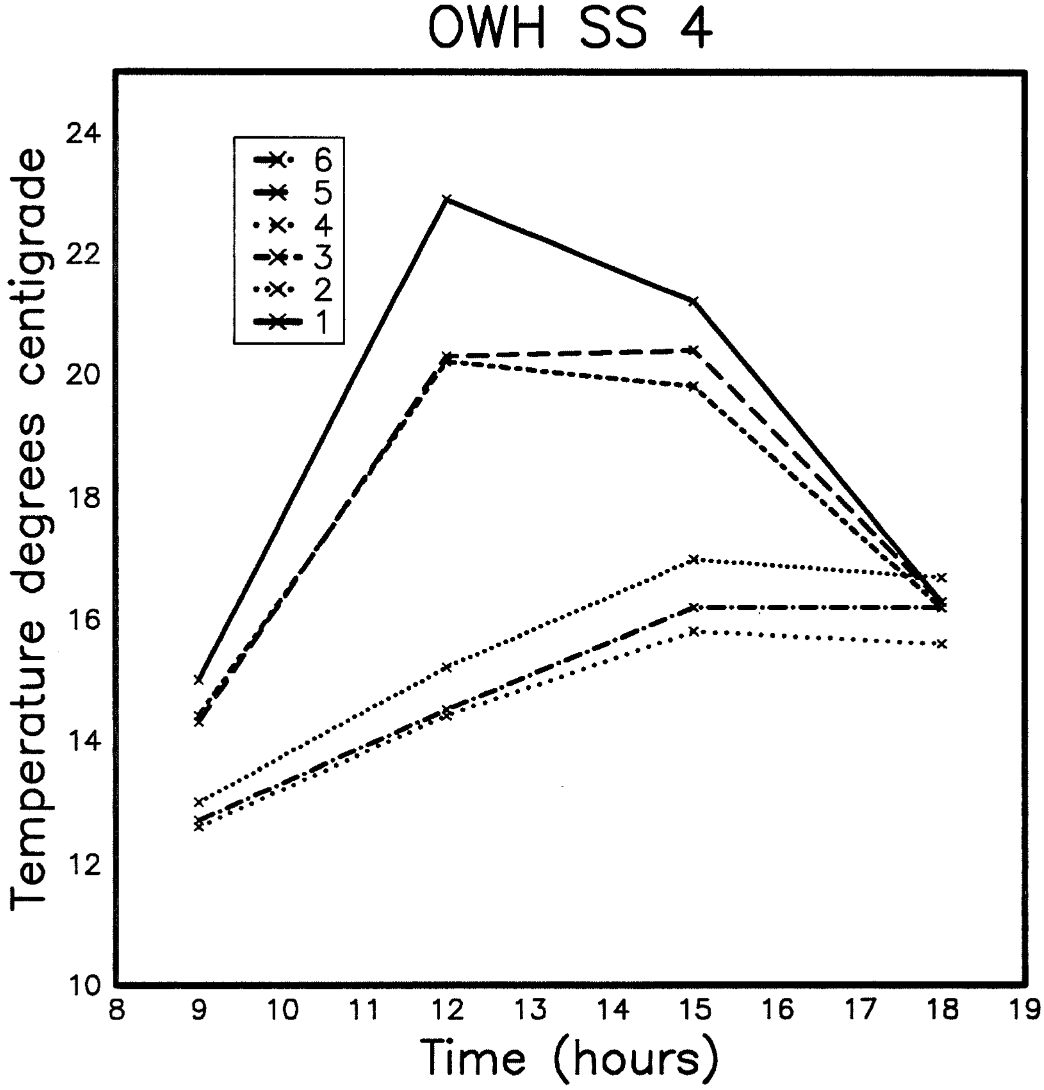
Root aphids and other invertebrates.

Root aphids. The overall mean number of root aphids extracted per core was 1.71 +/- 0.50.

Figure 10.4.

Summary of the annual mean temperatures in OWH SS 4.

The mean annual temperatures at four times of day are shown. Times are British Summer Time. In the table below the graph, the mean figures are shown, together with the mean annual air temperatures. 1 - 6 refer the locations as follows.
1, south side of mound, top 1 cm. of soil. 2, same location 10 cm. deep. 3, north side of mound top 1 cm. of soil. 4, same location 10 cm. deep. 5, ground, top 1 cm. of soil. 6, same location 10 cm. deep.

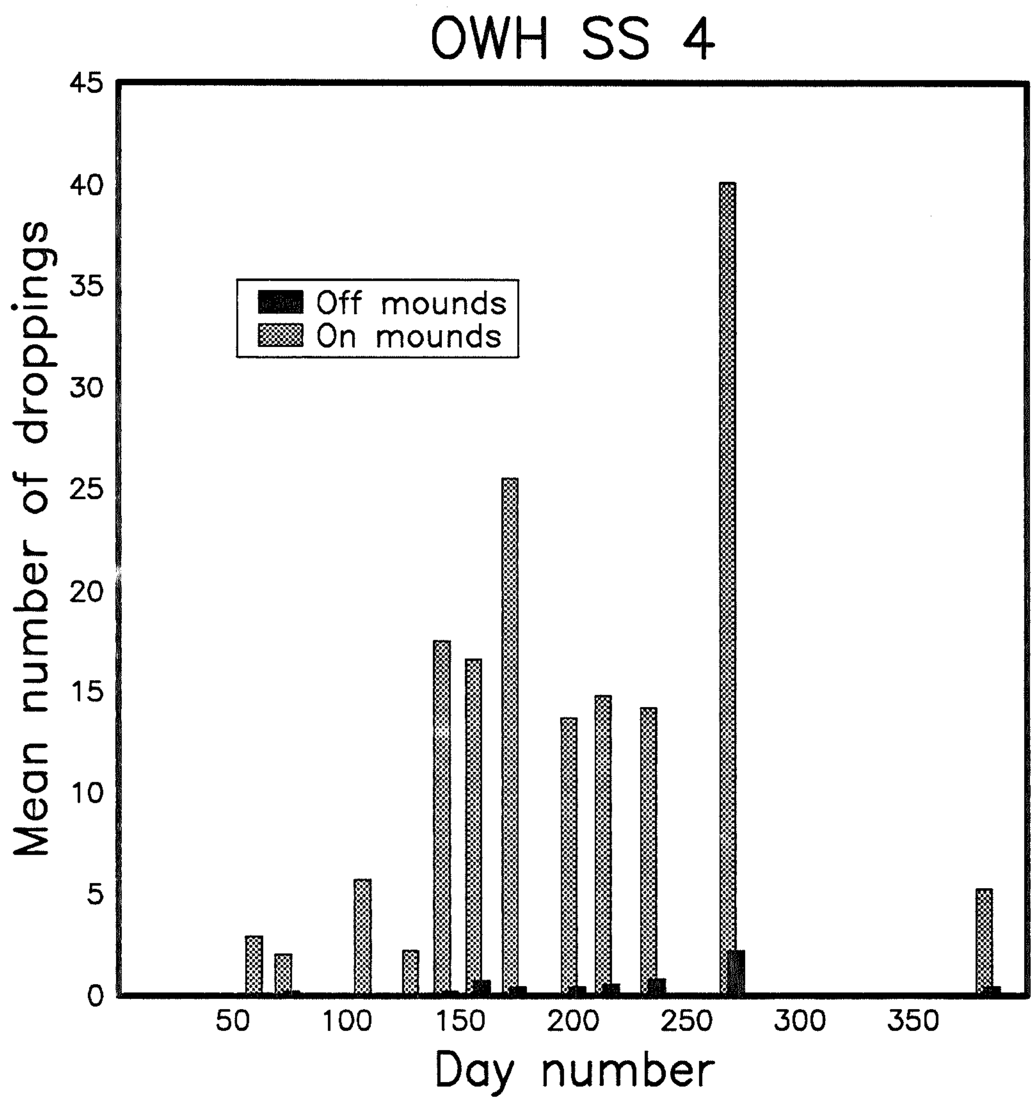


	1	2	3	4	5	6	AIR
9.00	15.0	13.0	14.4	12.6	14.3	12.7	13.0
12.00	22.9	15.2	20.2	14.4	20.3	14.5	16.0
15.00	21.2	17.0	19.8	15.8	20.4	16.2	15.9
18.00	16.3	16.7	16.2	15.6	16.3	16.2	13.8

The temperature raw data is given in Appendix Eight. The methods are further explained in section 7.3.2. Each point represents the mean of all the temperatures recorded in that location at that time throughout the year.

Figure 10.5.

Rabbit dropping densities in OWH SS 4.



Day number 1 = 1/1/89.

Each bar represents the mean number of droppings recorded in 10, 25 x 25 cm. quadrats. The dates of sampling and numbers of droppings recorded in each quadrat are given in Appendix 10.

This included confirmed records of the following species.

Brachycaudus spp.	5	(7.1%)
Forda formicaria	1	(1.4%)
Forda marginata	10	(14.3%)
Geoica eragrostidis	7	(10.0%)
Neanoecia corni	7	(10.0%)
Neanoecia zirnitsi	1	(1.4%)
Neotrama caudata	36	(51.4%)
Paracletus cimiciformis	1	(1.4%)
Unidentified	2	(2.9%)

Other invertebrates.

For the major groups of invertebrates the mean number extracted per core was:

Mites	129.27+/-13.45
Collembolans	35.34+/- 3.99
Platyarthrus hoffmanseggi	1.32+/- 0.60
Geophilomorph centipedes	0.66+/- 0.11
Beetle larvae	0.29+/- 0.12
Ants (excluding L. flavus)	1.63+/- 1.02

The ant species other than L. flavus recorded in this sample area was Mymica scabrinodis.

An elongate orange coloured coccid was extracted from cores collected on 16/3 and 7/6 when many were found. Identification of these is difficult but this coccid may have been Chnaurococcus subterraneous which has been previously found associated with ants, including L. flavus (Williams 1962).

The Tingids Campylosteira verna and Agramma laeta were also found in the core samples, with the latter being particularly abundant.

A parasitic mite of the genus Antennophorus was found in the sample colonies number 3, 4 and 5 in ant samples collected on 23/9/85.

The centipedes Schendyla nemorensis and Lithobius duboscqui were found in this area. L. duboscqui was on one occasion found in large numbers underneath the slate on a sample colony, apparently occupying the galleries built by the worker ants. It is not known whether there is any form of relationship between the ants and the centipedes.

The dipluran *Campodea staphylinus* was found on a few occasions in the core invertebrates.

10.4. Quadrat 2, OWH SS 5.

Site - Old Winchester Hill.

Location - South slope, of the reserve (see Figure 5.2.).

The sample area lies at the extreme western side of the slope, about half-way up.

10.4.1. The characteristics of the ant population.

The ant mounds.

No.of mounds - 64
Mean diameter of mounds (D) - 40.4 +/- 1.9
Mean height of mounds (H) - 9.3 +/- 0.8
Ratio D/H - 4.3
Area of quadrat occupied by the mounds - 2.3%
Mean above ground volume of soil in the mounds - 12.8 litres.
Mean distance to nearest neighbour - 1.50 metres.

In Figure 10.6 the percentage of mounds in each 10 cm. diameter band is shown. The mounds in this sample area had the smallest mean diameter and height of any of the south slope quadrats and the second smallest mean volume. The percentage area of the quadrat occupied by the mounds was also small, and was only lower in OWH SS 7 on the south slope, a quadrat with very few mounds in it.

10.4.2. Management. This is as outlined in Figure 10.1. This plot was grazed in May-June 1981, July-September 1982, October-December 1983, March-April 1988 and June 1989, as mentioned above. Thus at the time that the quadrats were examined it had had an estimated 7,500 sheep days per hectare in the previous 3 years.

10.5.4. The physical environment.

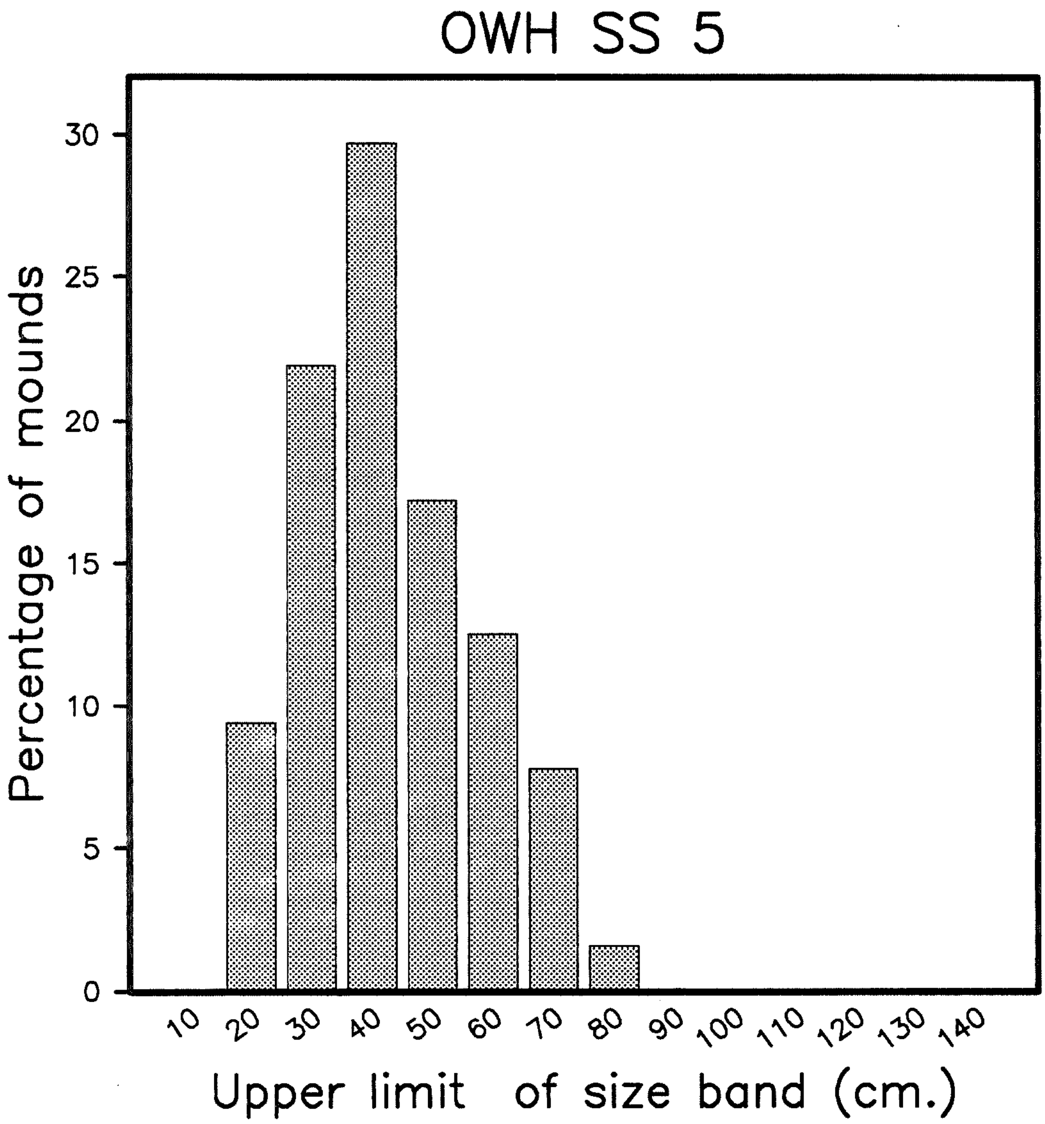
Altitude - 170 metres.
Slope - 16^{o}, facing 200^{o} (SSW).
Mean soil depth - 11.5 +/- 0.76 cm.
Mean soil pH - 7.55

10.4.5. The biological environment.

The flora. This quadrat was heavily grazed in June 1989 and as a

Figure 10.6.

The distribution of mound sizes in OWH SS 5.



A total of 64 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

result it is probable that several plant species that would have otherwise been recorded were missed. This is reflected in this quadrat having the fewest number of species recorded in it of all the quadrats (37).

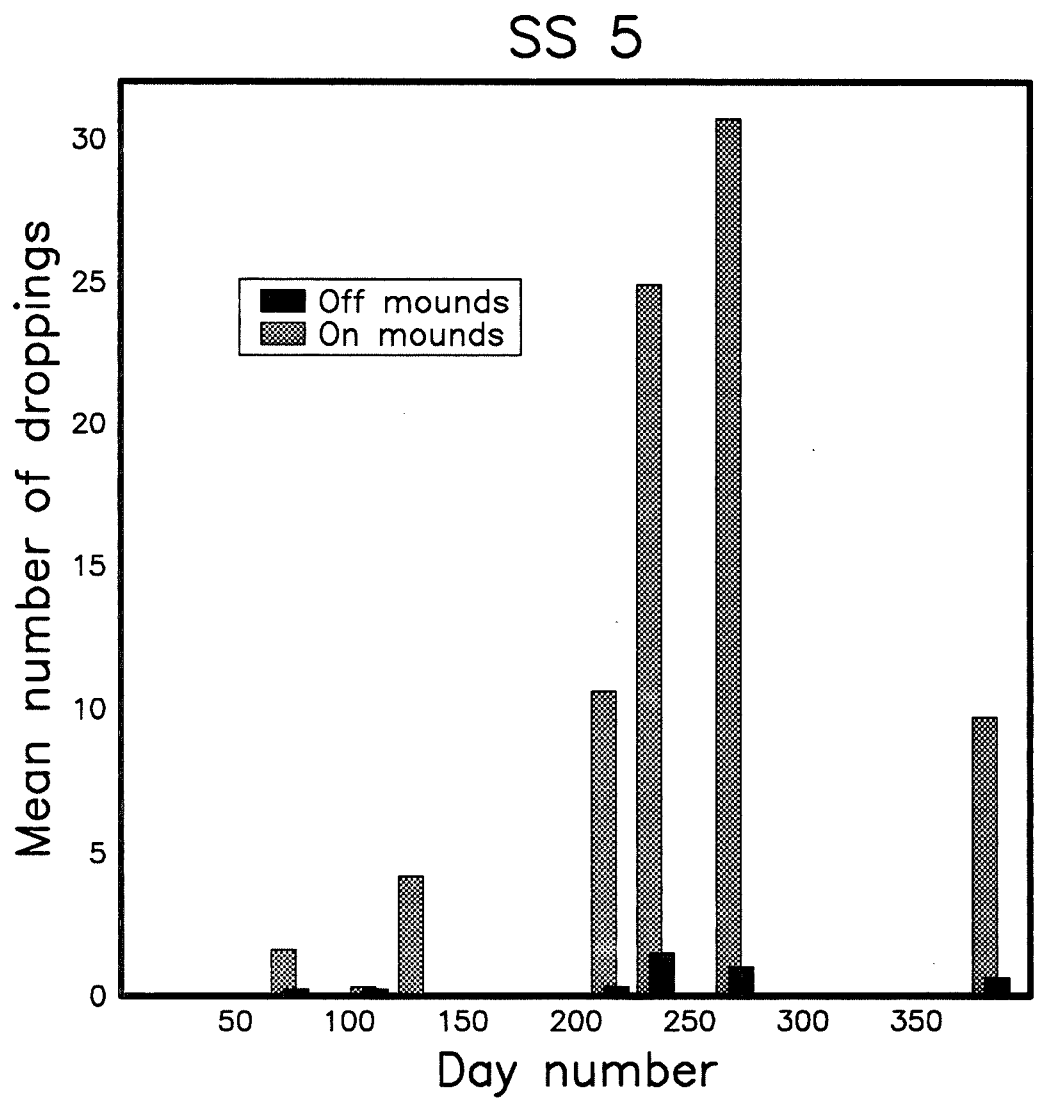
Carlina vulgaris was more abundant is this quadrat than the others on the south slope, but otherwise the quadrat seemed to support large populations of the typical chalk grassland plants as described by Tansley (1939) (see section 2.3.2.).

Rabbit droppings. The maximum mean number of rabbit droppings found on the mounds was 30.7 on 27/9 and the minimum was 0.3 on 3/8. Off the mounds the maximum was 1.5 on 23/8 and the minimum 0 on 10/5. The full data is presented in graphical form in Figure 10.7. Numbers of droppings were generally quite low compared to the other south slope quadrats.

Other invertebrates. Workers of the ant species Myrmica ruginodis were found in this quadrat.

Figure 10.7.

Rabbit dropping densities in OWH SS 5.



Day number 1 = 1/1/89.

Each bar represents the mean number of droppings recorded in 10, 25 x 25 cm. quadrats. The dates of sampling and numbers of droppings recorded in each quadrat are given in Appendix 10.

No data was collected between days 150-200 because of sheep grazing in the area.

10.5. Quadrat 3, OWH SS 7.

Site - Old Winchester Hill.

Location - South slope of the reserve (see Figure 5.2.).

This sample area is located at the top of the south slope, towards the eastern side of it.

10.5.1. The characteristics of the ant population.

The ant mounds.

No.of mounds - 8
Mean diameter of mounds (D) - 59.1 +/- 8.9
Mean height of mounds (H) - 17.9 +/- 4.3
Ratio D/H - 3.3
Area of quadrat occupied by the mounds - 0.6%
Mean above ground volume of soil in the mounds - 53.1 litres.
Mean distance to nearest neighbour - 3.40 metres.

In Figure 10.8. the distribution of the sizes of the mounds is shown.

This quadrat contained the fewest mounds of any quadrat examined. The few present were all of a large size, with the mean diameter, height and volume of the mounds only smaller than those in OWH C10. No small colonies were found. As a result of this, the area covered is the smallest of the sample quadrats and the mean distance to nearest neighbour is the largest.

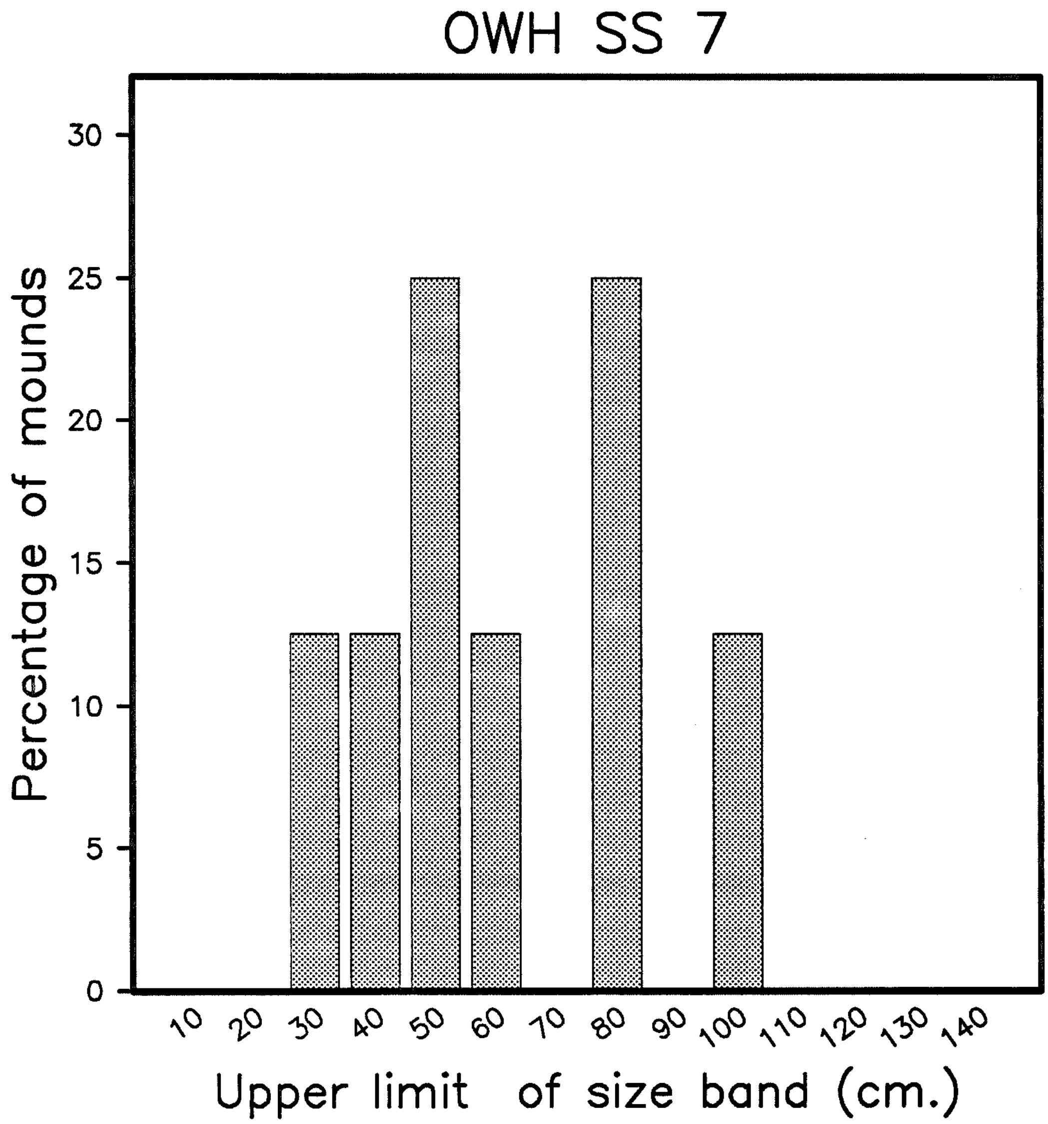
10.5.2. Management. This is as outlined in Figure 10.1. This plot was grazed in July-September 1981, October-December 1982, March-April 1987 and May-June 1988 and 1989, as mentioned above. Thus at the time that the quadrats were examined in 1984 it had had an estimated 5,000 sheep days per hectare in the previous 3 years.

10.5.3. The physical environment.

Altitude - 183 metres.
Slope - 11°, facing 200° (SSW).
Mean soil depth - 8.5 +/- 0.52 cm.
Mean soil pH - 7.31

Figure 10.8.

The distribution of mound sizes in OWH SS 7.



A total of 8 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

This area had the lowest soil pH and the thinnest soil of the south slope sample areas.

10.5.4. The biological environment.

The flora. At the time that the ant mounds were examined this sample area maintained a thick turf layer and dense grass growth. It was dominated by the grass *Tricetum flavescens*, unlike any of the other sample areas.

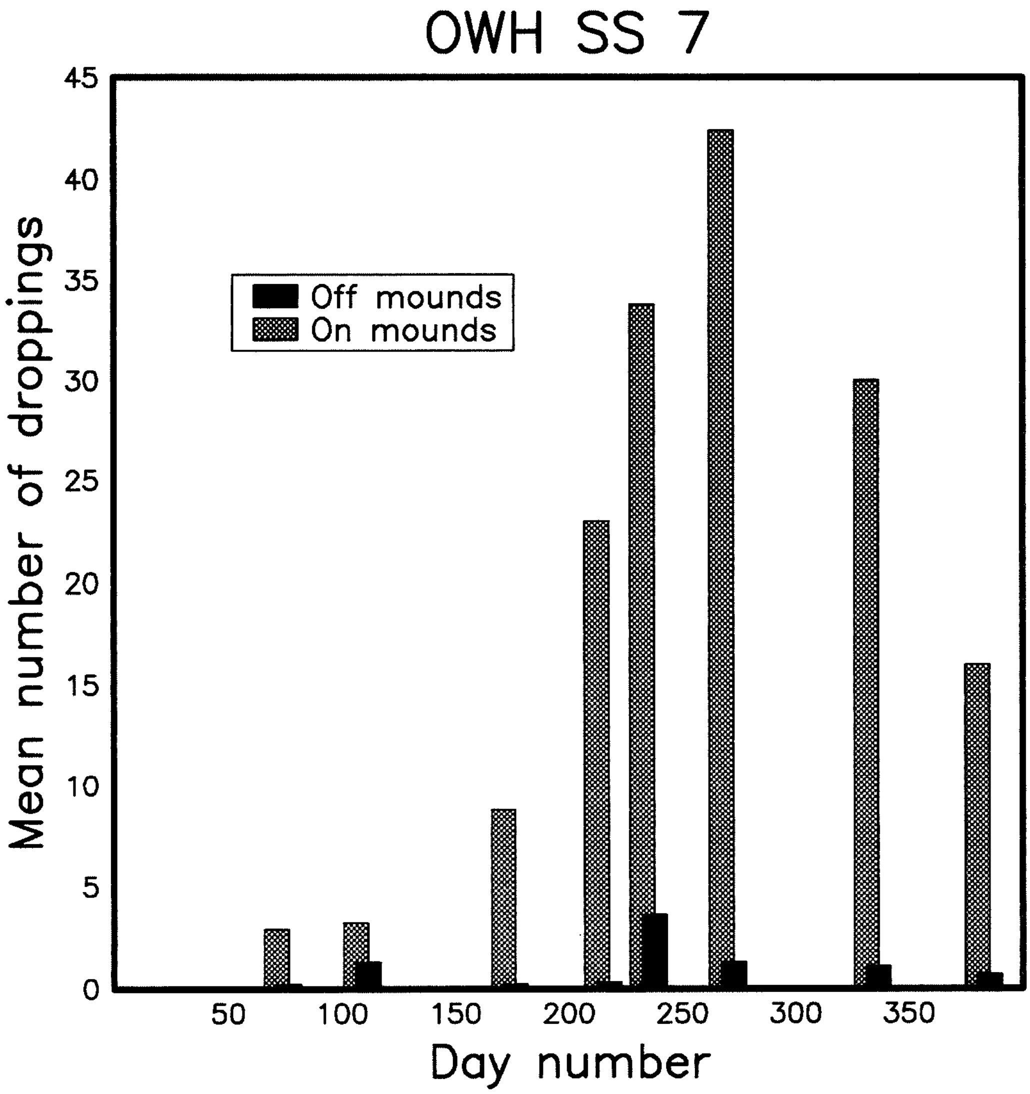
More recent grazing in 1987, 1988 and 1989 has reduced the standing vegetation but the area still appears to be relatively poor in short herbs compared to other areas, such as OWH SS 4 and 11. One indicator of this maybe that *Hieracium pilosella* was absent from this quadrat. This was the only quadrat in which the grass *Phleum pratense* was found on the south slope. Three species of moss found in this quadrat were not recorded elsewhere; *Phascum cuspidatum*, *Eurynchium swartzii* and a species of *Bryum*, possibly *B. bicolor*.

In all 42 species of plant were recorded in this quadrat.

Rabbit droppings. The maximum mean number of droppings found on the mounds was 42.4 on 27/9, the minimum 2.9 on 15/3. Off the mound the maximum was 3.6 on 23/8 and the minimum 0.2 on 15/3 and 23/6. The full data is presented in graphical form in Figure 10.9.

Figure 10.9.

Rabbit dropping densities in OWH SS 7.



Day number 1 = 1/1/89.

Each bar represents the mean number of droppings recorded in 10, 25 x 25 cm. quadrats. The dates of sampling and numbers of droppings recorded in each quadrat are given in Appendix 10.

This area was grazed in May 1989.

10.6. Quadrat 4, OWH SS 8.

Site - Old Winchester Hill.

Location - South slope of the reserve (see Figure 5.2.).

The sample area is located on the estern side of the reserve, north east of a small enclosure.

10.6.1. The characteristics of the ant population.

The ant mounds.

No.of mounds - 66
Mean diameter of mounds (D) - 46.9 +/- 2.2 cm.
Mean height of mounds (H) - 13.9 +/- 1.0 cm.
Ratio D/H - 3.4
Area of quadrat occupied by the mounds - 3.3%
Mean above ground volume of soil in the mounds - 23.4 litres.
Mean distance to nearest neighbour - 1.51 metres.

The distribution of the mound sizes is shown in Figure 10.10.

Aside from OWH SS 7, the mounds in this quadrat had the largest mean diameter and the highest mean volume of the any of the sample quadrats on the south slope.

10.6.2. Management. This is as outlined in Figure 10.1. This plot was grazed in March-April 1984, May-June 1985 and 1986, July-September 1987 and October-December 1988, as mentioned above. Thus at the time that the quadrats were examined it had had an estimated 2,500 sheep days per hectare in the previous 3 years.

10.6.3. The physical environment.

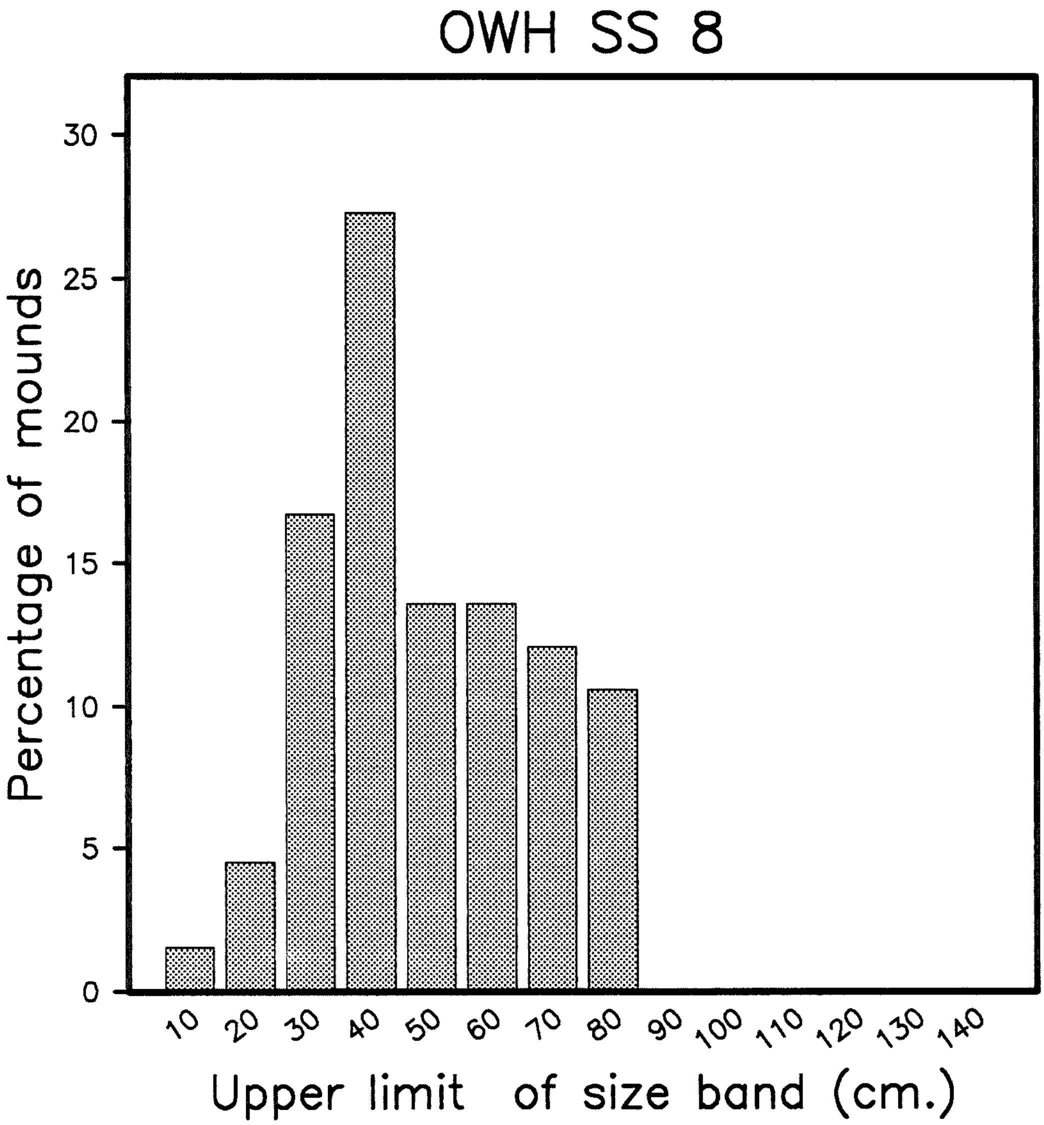
Altitude - 172 metres.
Slope - 16^{o}, facing 195^{o} (SSW).
Mean soil depth - 9.55 +/- 0.56 cm.
Mean soil pH - 7.54

10.6.4. The biological environment.

The flora. The flora of this area was quite rich but like OWH SS 7 there was a thick layer of vegetation built up. *Anthyllis vulneraria* was abundant as was *Phyteuma orbiculare* and the two *Gallium* species,

Figure 10.10.

The distribution of mound sizes in OWH SS 8.



A total of 66 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

verum and *mollugo*.

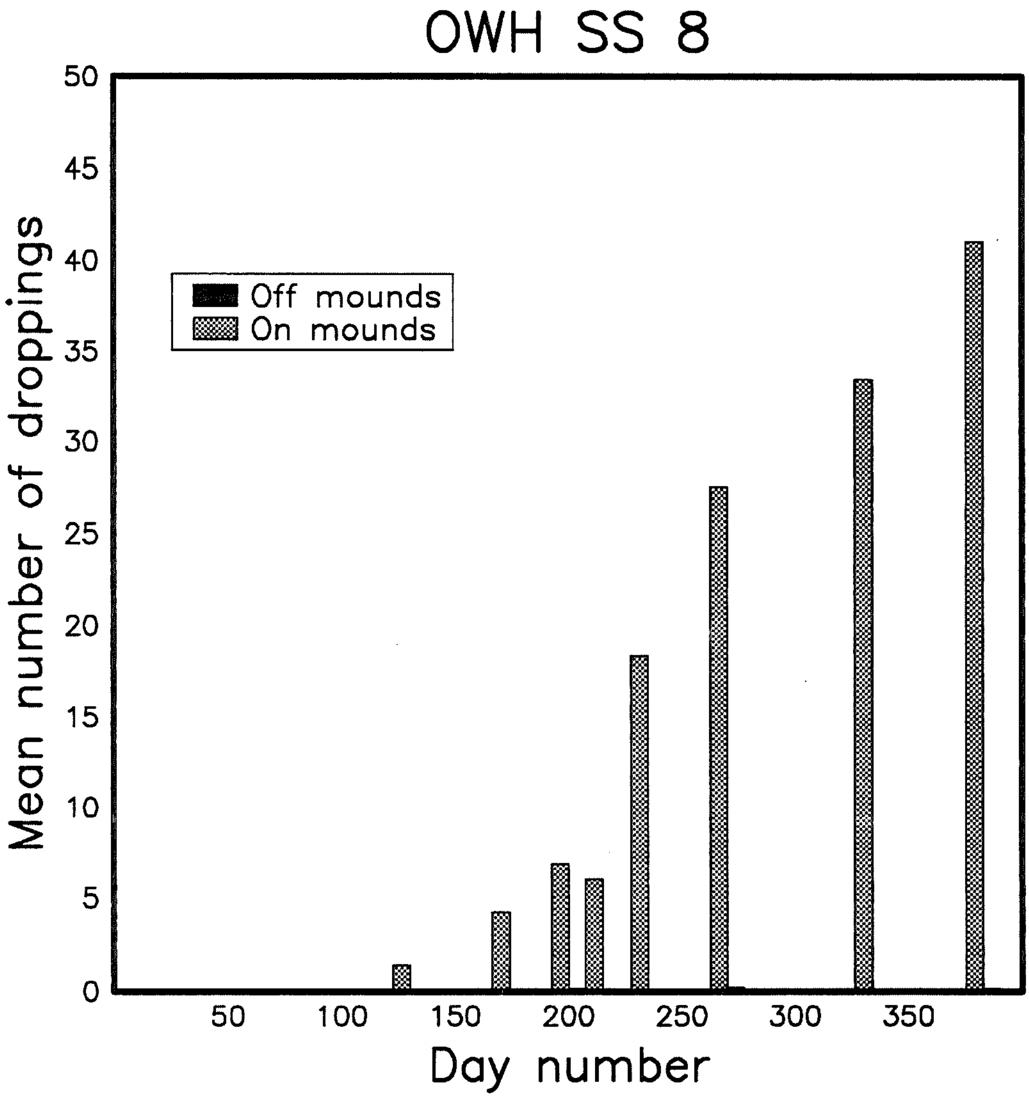
There was a small build up of scrub species such as *Cornus sanguinea* and *Ligustrum vulgare* and the tall grass *Arrhenatherum elatius* occured in small patches throughout the area. The coarse grass *Brachypodium pinnatum* was more abundant here than the other south slope quadrats. *Hieracium pilosella* was also absent from this quadrat.

In all 57 species of plant were recorded in this quadrat.

Rabbit droppings. On the mounds the maximum mean number of droppings recorded was 41.0 on 18/1/89 and the minimum 1.4 on 10/5. Off the mounds very few droppings were found, the maximum being 0.2 on 27/9 and the minimum 0 on several occasions. The full data is presented in graphical form in Figure 10.11.

Figure 10.11.

Rabbit dropping densities in OWH SS 8.



Day number 1 = 1/1/89.

Each bar represents the mean number of droppings recorded in 10, 25 x 25 cm. quadrats. The dates of sampling and numbers of droppings recorded in each quadrat are given in Appendix 10.

10.7. Quadrat 5, OWH SS 9.

Site - Old Winchester Hill.

Location - South slope of the reserve (see Figure 5.2.).

The quadrat was located in the centre of the south slope, approximately 10 metres west of OWH SS 11. A photograph of the area is shown in Figure 10.12.

10.7.1. The characteristics of the ant population.

The ant mounds.

No.of mounds - 99
Mean diameter of mounds (D) - 43.6 +/- 1.4 cm.
Mean height of mounds (H) - 15.8 +/- 0.7 cm.
Ratio D/H - 2.8
Area of quadrat occupied by the mounds - 4.1%
Mean above ground volume of soil in the mounds - 21.0 litres.
Mean distance to nearest neighbour - 1.28 metres.

In Figure 10.13. the percentage of mounds in each 10 cm. size band is shown.

This quadrat had the most ant mounds recorded in it of any of the south slope quadrats. The area covered by the mounds was also the highest on the slope. Aside from OWH SS 7, which can be considered a special case because of the limited numbers of mounds present, these were the tallest mounds on the south slope.

10.7.2. Management. This is as outlined in Figure 10.1. This area was grazed in October-December 1981, March-April 1986, May-June 1987 and 1988 and July-September 1989, as mentioned above. Thus at the time that the quadrats were examined, it had had an estimated total of 2,500 sheep days per hectare, in the previous 3 years.

10.7.3. The physical environment.

Altitude - 160 metres.
Slope - 16^{o}, facing 220^{o} (SW).
Mean soil depth - 10.1 +/- 0.85 cm.
Mean soil pH - 7.56

Figure 10.12.

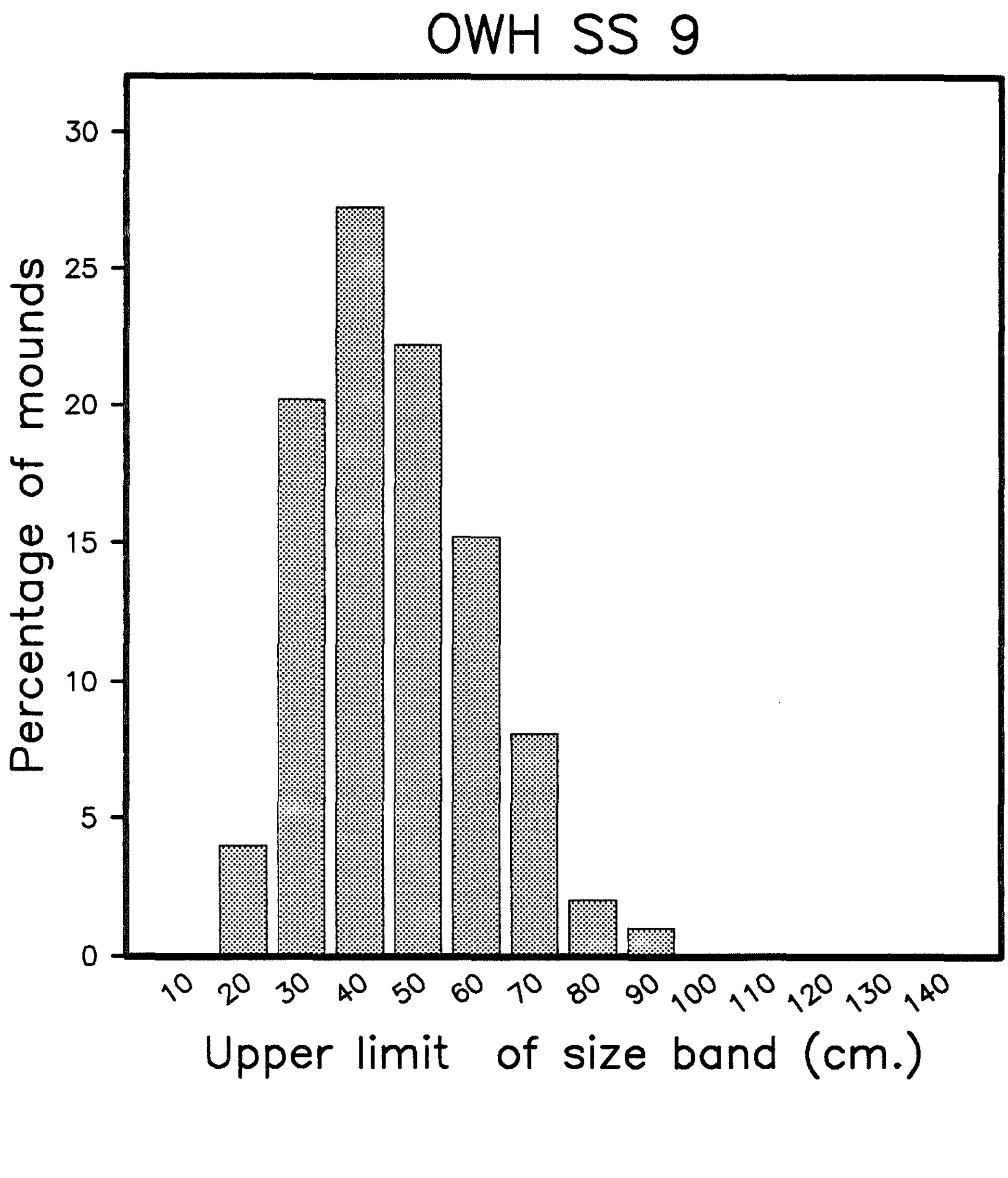
A view of quadrat 5, OWH SS 9.

Note the amount of Juniper growing in the area, more than any other of the south slope sample areas. Fragrant Orchids (Gymnadenia conopsea) can be seen in the foreground. The lushness of the vegetation was typical for this sample area.

The photograph was taken looking towards the south west.

Figure 10.13.

The distribution of mound sizes in OWH SS 9.



A total of 99 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

10.7.4. The biological environment.

The flora. This sample area was different from the others on the south slope, in that there was a much greater amount of *Juniperus communis* growing in it. The flora of this area was quite rich. It was the only sample area in which the Greater Butterfly Orchid (*Platanthera chloranthera*) was seen, although the 2 inflorescences disappeared (either picked or eaten by rabbits) before setting seed.

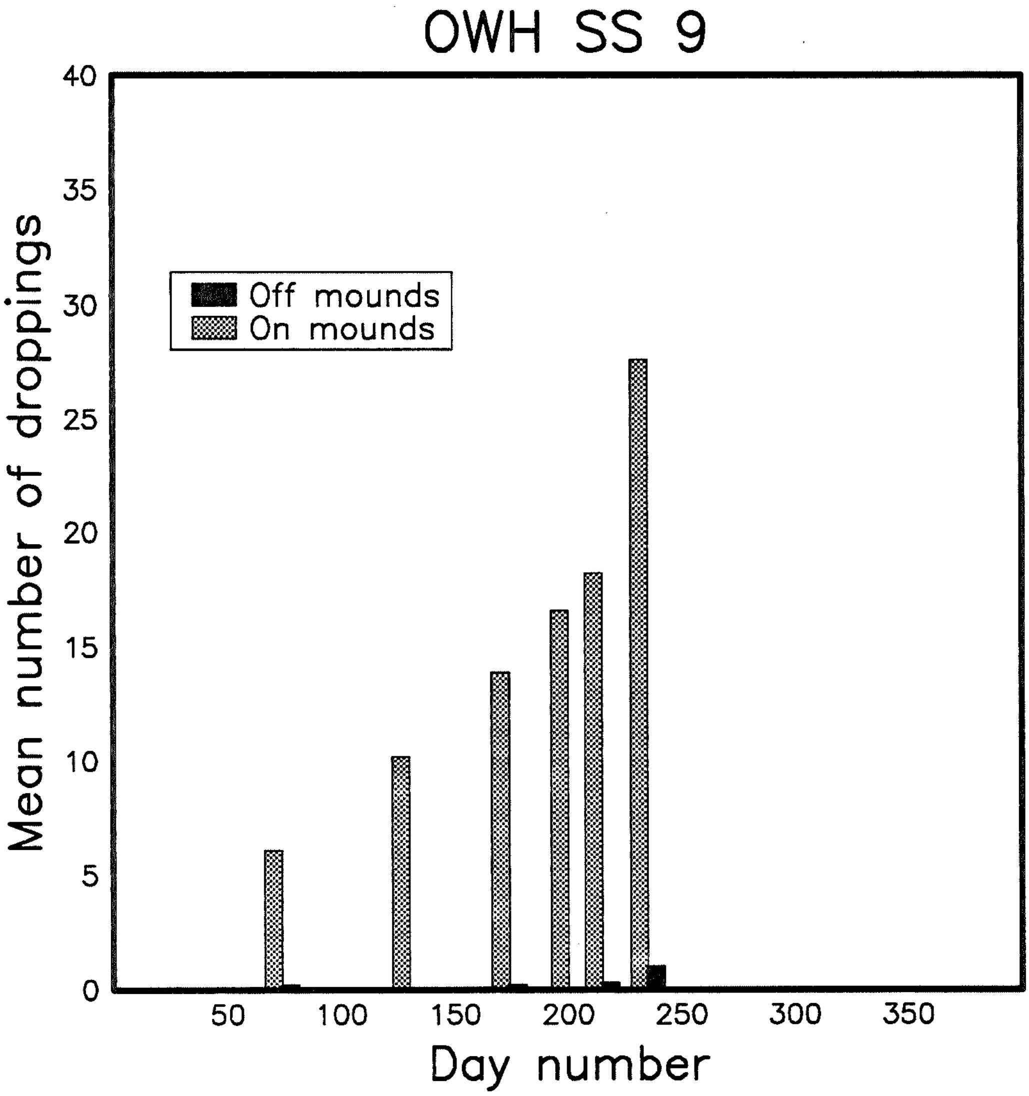
Grass growth appeared to be more luxurient here than in the other south slope quadrats and several plant species were more abundant in this area than on the rest of the south slope, notably the Juniper, *Leucanthemum vulgare* and *Pimpinella saxifraga*. Some species were only found in this area, *Reseda lutea*, *Sonchus oleraceous*, *Reseda lutea* and *Arenaria serpyllifolia*. The moss *Fissidens taraxifolius* was particularly common in this sample area.

In all 56 species of plant were recorded from this area.

Rabbit droppings. The maximum mean number of droppings found on the mounds was 27.6 on 23/8 the minimum 6.1 on 15/3. The maximum off the mounds was 1.0 on 23/8 and the minimum 0 on 10/5 and 19/7. The sheep grazing in this area in July-September 1989 disrupted the natural pattern of the droppings. The sheep deposited an extremely large number of pellets making it impossible to count rabbit droppings even as far after as, January 1990. The data collected is presented in graphical form in Figure 10.14.

Figure 10.14.

Rabbit dropping densities in OWH SS 9.



Day number 1 = 1/1/89.

Each bar represents the mean number of droppings recorded in 10, 25 x 25 cm. quadrats. The dates of sampling and numbers of droppings recorded in each quadrat are given in Appendix 10.

No records were made after day 250 because of sheep grazing in the area.

10.8. Quadrat 6, OWH SS 11.

Site - Old Winchester Hill (OWH).

Location - South Slope of the reserve (see Figure 5.2.).

The sample quadrat was positioned 1 metre west of a small enclosure on the western side of the south slope. The sample area lies between OWH SS 9 and 12.

10.8.1. The characteristics of the ant population.

The ant mounds.

Number of mounds - 57
Mean diameter (D) - 42.9 +/- 2.6 cm.
Mean height (H) - 9.6 +/- 0.8 cm.
Ratio D/H - 4.5
Area of quadrat occupied by the mounds - 2.5%
Mean above ground volume of soil in the mounds - 15.7 litres.
Mean distance to nearest neighbour - 1.59 +/- 0.03 metres.

The percentage of the mounds in each 10 cm. size band is shown in Figure 10.15.

This quadrat had the fewest mounds of any of the south slope quadrats, bar OWH SS 7. The ratio D/H was the highest of the south slope quadrats.

Estimates of colony sizes and worker ant densites.

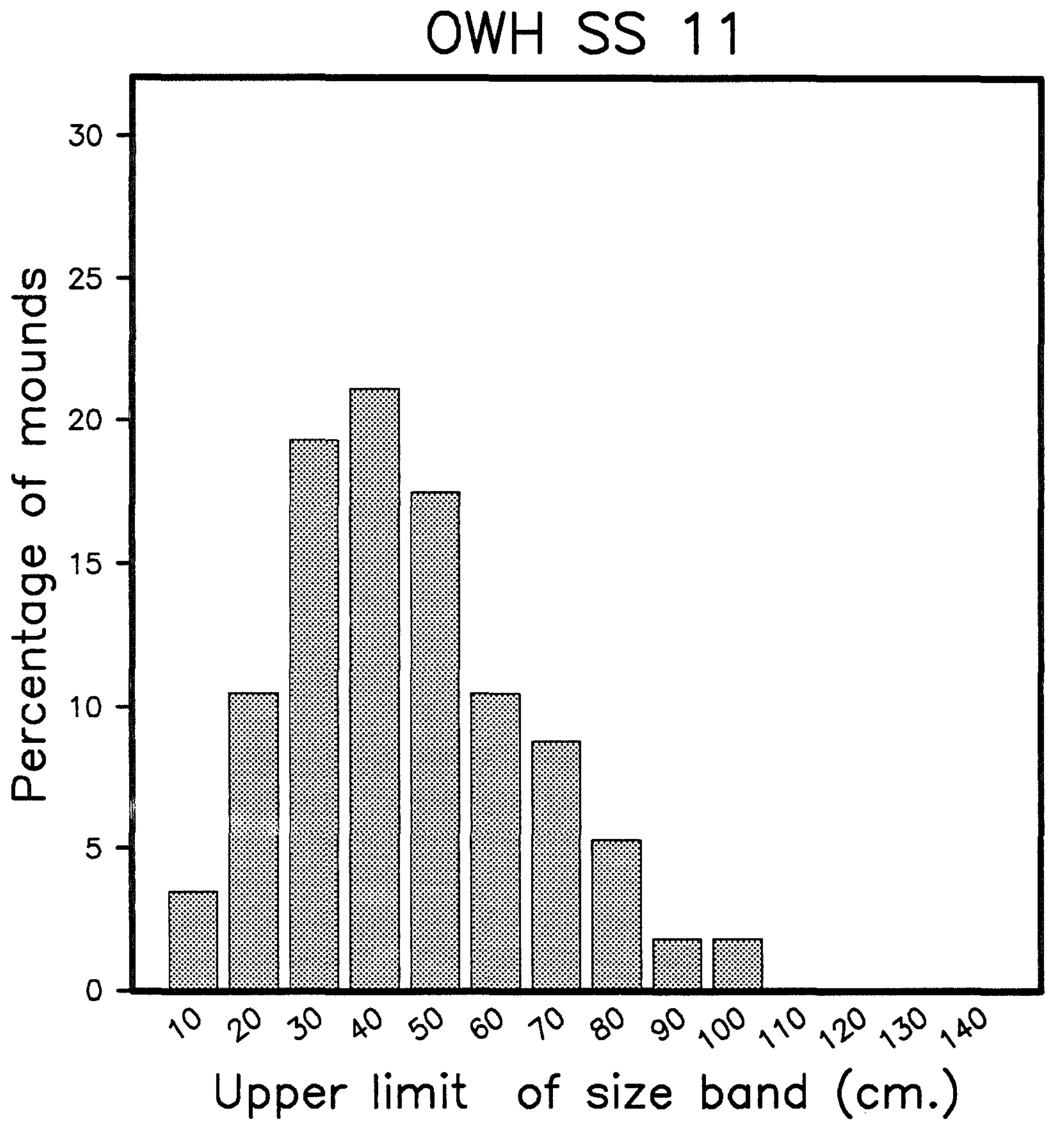
Mark-release-recapture estimates.

Set 1. July/August 1985.		Set 2. September/October 1985.	
Colony 1.	13,269 +/- 6,604	Colony 1.	5,700 +/- 2,068
Colony 2.	10,810 +/- 3,375	Colony 2.	5,129 +/- 1,700
Colony 3.	3,763 +/- 1,402	Colony 3.	10,859 +/- 1,630
Colony 4.	6,172 +/- 1,564	Colony 4.	16,640 +/- 3,968
Colony 5.	-	Colony 5.	-
Mean	8,503 +/- 4,318.	Mean	9,582 +/- 2,682

No marked ants were recaptured in colony 5 for the first or second set of estimates. For the first set of estimates, the mean colony size estimate was the second lowest of the sample area (only OWH SS 4 being lower) and the second estimates mean was in the mid-range of the sample areas.

Figure 10.15.

The distribution of mound sizes in OWH SS 11.



A total of 57 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

Numbers of worker ants found in core samples. The mean number of worker ants extracted per core over the whole year was 8.49 +/-2.73, exactly the same mean as OWH SS 4. In total 41 cores were collected.

The sexual production of colonies.

	1985		1986		1987	
	Gynes	Males	Gynes	Males	Gynes	Males
Colony 1.	87	1,476	186	1,793	0	0
Colony 2.	59	0	392	94	375	301
Colony 3.	0	255	186	462	220	608
Colony 4.	34	69	146	588	26	172
Colony 5.	0	0	30	0	0	11
Mean	36.0	360.0	188.0	587.4	124.2	218.4
SE	16.9	282.9	58.5	320.8	75.0	112.1

Over the three years this area had the lowest sexual productivity of the Old Winchester Hill sample quadrats in which sexuals were collected.

Head widths of male and gyne samples. All measurements are in millimetres.

	Males	Gynes
Colony 1.	0.69 +/- 0.008 (10)	1.40 +/- 0.009 (10)
Colony 2.	---	1.39 +/- 0.006 (9)
Colony 3.	0.70 +/- 0.004 (10)	---
Colony 4.	0.71 +/- 0.009 (10)	1.47 +/- 0.014 (10)
Colony 5.	---	---
Mean	0.70 +/- 0.006	1.42 +/- 0.025

Dry weights of male and gyne samples. All measurements are in milligrams. The mean dry weight of an individual ant is given together with the sample size.

	Males	Gynes
Colony 1.	0.300 (19)	9.84 (10)
Colony 2.	--	9.02 (9)
Colony 3.	0.267 (18)	--
Colony 4.	0.310 (20)	8.70 (10)
Colony 5.	--	--
Mean	0.292+/-0.013	9.19+/-0.339

The mean male dry weights were the lowest of any sample area in which sexuals were collected.

Dates at which stages were first observed in 1986. The first small pupae were seen on 27/5, the first adult males on 17/7. The first gyne pupae were seen on 4/6 and the first adult gynes on 8/7.

10.8.2. Management. This was as described in Figure 10.1. The sample area was grazed in May-June 1981 and 1882, July-September 1983, October-December 1984 and March-April 1989. Thus, at the time the quadrats were examined this area had received approximately 7,500 sheep days per hectare in total in the previous 3 years.

10.8.3. The physical environment.

Altitude - 167 metres.
Slope - 16^{o}, facing 190^{o} (SSW).
Mean soil depth - 8.9 +/- 0.31 cm.
Mean soil pH - 7.33
Mean soil core density - 0.605+/-0.014 g/cm^{3}

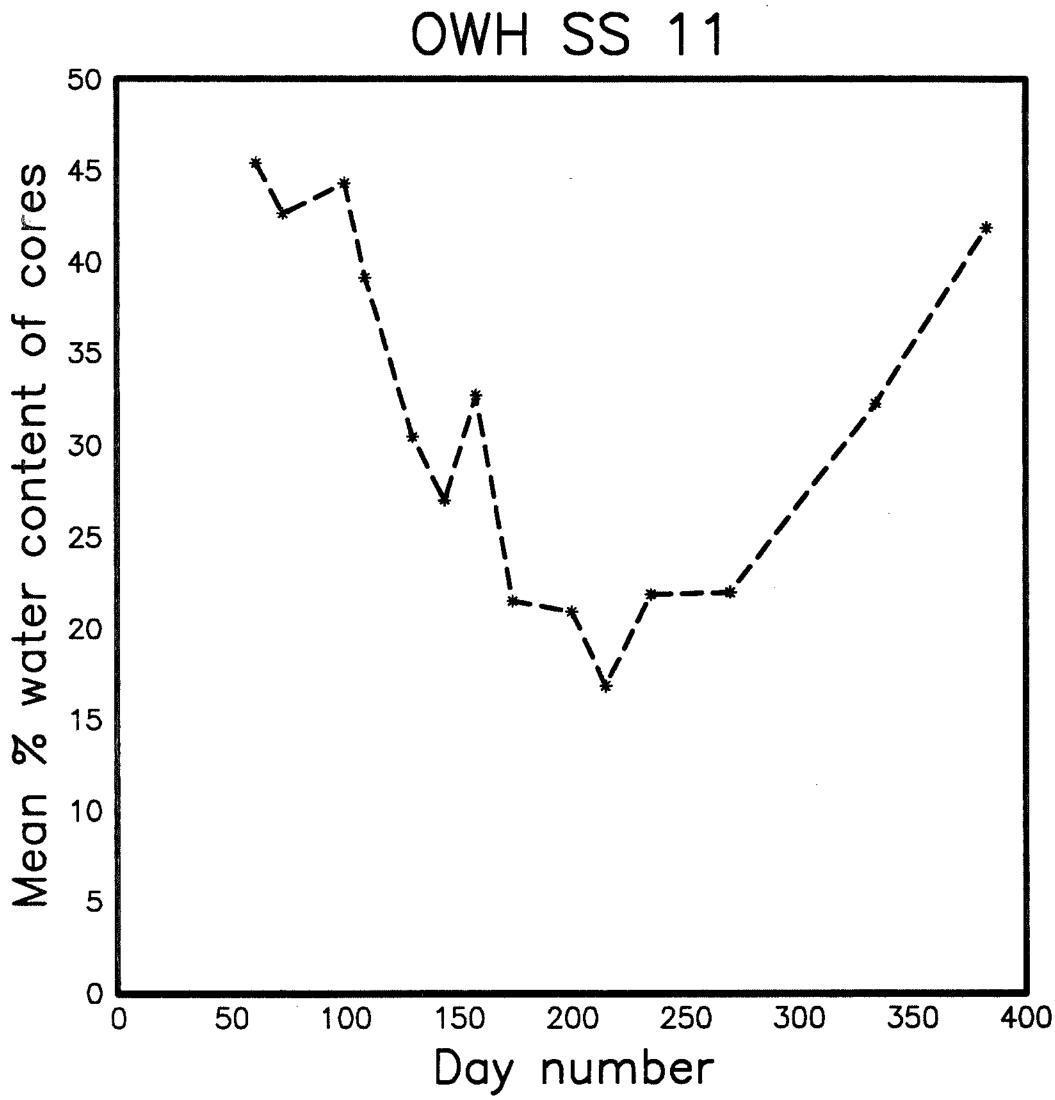
The maximum recorded mean water content of the soil cores was 45.43% on 2/3/89 and the minimum 16.84% on 3/8/89. The change in water content of the soil throughout the year is presented graphically in Figure 10.16. The mimimum figure of 16.85% was the lowest in any of the sample quadrats. As in OWH SS 4 the annual mean ground temperatures were high. This was another relatively hot, dry area. The annual mean temperatures are presented in Figure 10.17.

10.8.4. The biological environment.

The flora. Throughout the period of observation of the quadrats (1984 to 1989) this area appeared to maintain a short herb rich turf. When the quadrats were examined in 1984 it had been grazed in the previous 3 years. This type of turf would thus be expected. The short turf was maintained until 1989 when the next grazing took place, possibly due to rabbit activity. This type of turf is reflected in the abundance of plants such as *Thymus serpyllum*, *Gymnadena conopsea*, *Anthyllis vulneraria* and *Hieracium pilosella* compared to the other areas on the south slope and also possibly by the relative lack of

Figure 10.16.

Water contents of soil cores collected in OWH SS 11.



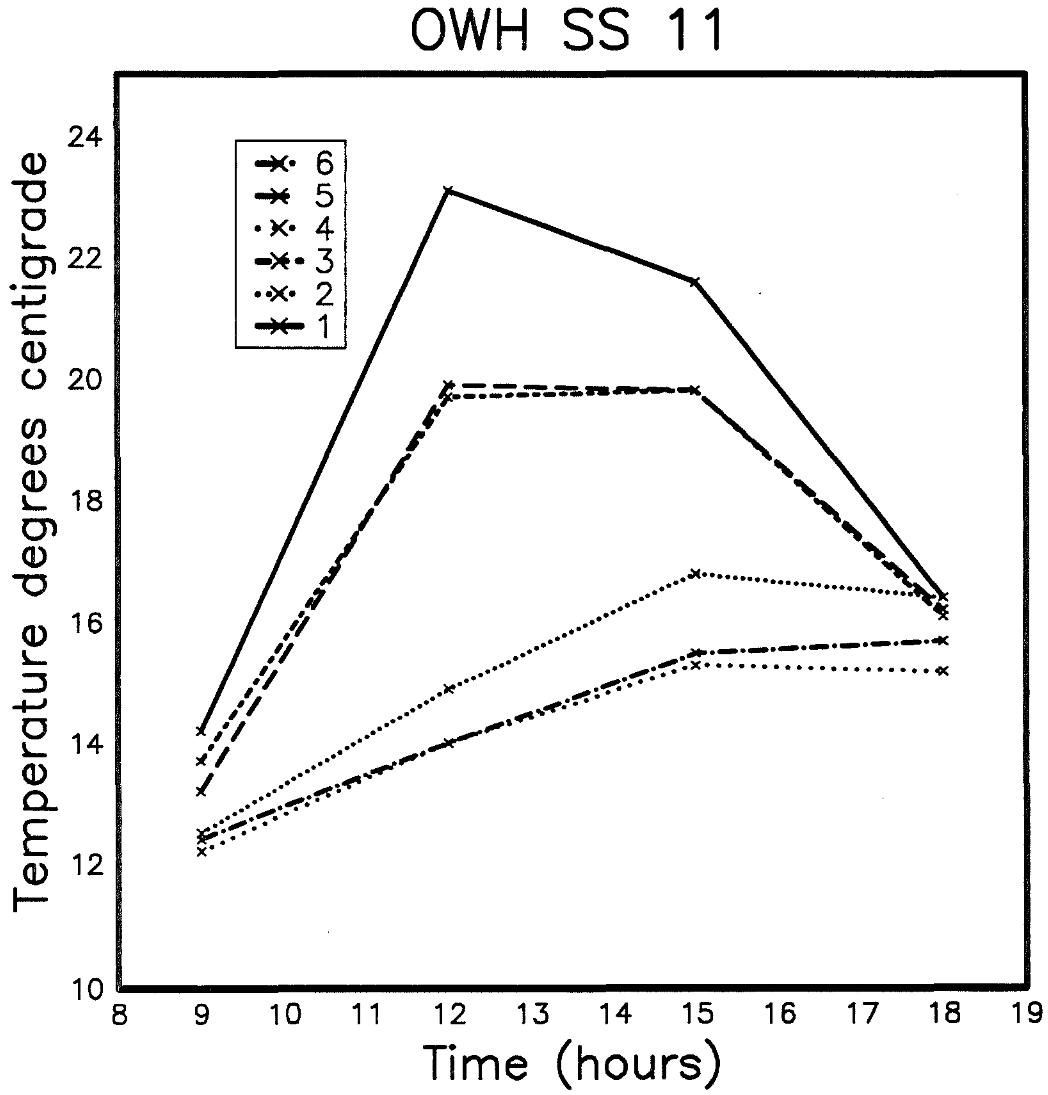
Day number 1 = 1/1/89.

Each point represents the mean water content of a sample of cores collected on that day. The dates of sampling, sample size, mean water contents and standard errors are given in Appendix 4.

Figure 10.17.

Summary of the annual mean temperatures in OWH SS 11.

The mean annual temperatures at four times of day are shown. Times are British Summer Time. In the table below the graph, the mean figures are shown, together with the mean annual air temperatures. 1 - 6 refer the locations as follows.
1, south side of mound, top 1 cm. of soil. 2, same location 10 cm. deep. 3, north side of mound top 1 cm. of soil. 4, same location 10 cm. deep. 5, ground, top 1 cm. of soil. 6, same location 10 cm. deep.



	1	2	3	4	5	6	AIR
9.00	14.2	12.5	13.7	12.2	13.2	12.4	12.6
12.00	23.1	14.9	19.7	14.0	19.9	14.0	16.1
15.00	21.6	16.8	19.8	15.3	29.8	15.5	15.9
18.00	16.4	16.4	16.1	15.2	16.2	15.7	14.1

The temperature raw data is given in Appendix Eight. The methods are further explained in section 7.3.2. Each point represents the mean of all the temperatures recorded in that location at that time throughout the year.

moss species. Spiranthes spiralis, the Autumn Ladies Tresses Orchid, which also likes short turf was also most common in this quadrat.

There was a small amount of Juniperus communis in the lower half of the sample area. There were no plants in this area that were not recorded elsewhere on the south slope but it supported a wide range of typical chalk grassland species.

In all 47 species of plant were recorded from this quadrat. One plant which may have been missed was the Bee Orchid (Ophrys apifera) which was seen in several years previous to the examination of the flora but not recorded in 1989.

Rabbit droppings. The maximum mean number of rabbit droppings found on the mounds was 52.3 on 27/9 and the minimum 4.5 on 10/4. Off of the mounds the maximum was 1.9 on 3/8 and the minimum 0 on several occasions. The full data is presented in graphical form in Figure 10.18.

Root aphids and other invertebrates.

The root aphids. The overall mean number of root aphids extracted per core was 2.78+/-0.72, higher than OWH SS 4 from the same slope.

This included confirmed records of the following species.

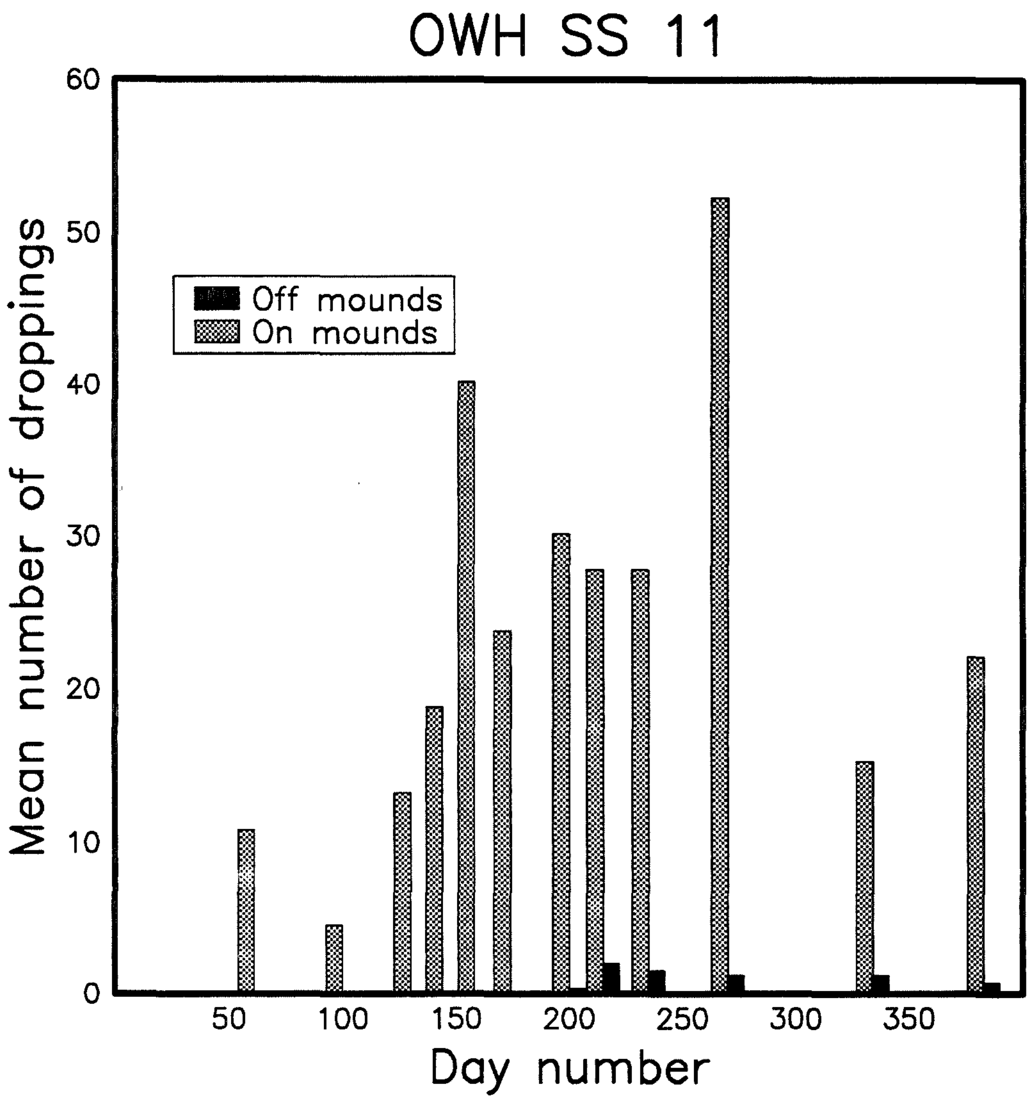
Forda marginata	52	(45.6%)
Neanoecia zirnitsi	8	(7.0%)
Neotrama caudata	35	(30.7%)
Protrama radicis	1	(0.9%)
Teraneura ulmi	4	(3.5%)
Unidentified	14	(12.3%)

The dominance of Forda marginata was not found in any of the other sample areas.

Others invertebrates. For the major groups of invertebrates the mean number extracted per core was:

Figure 10.18.

Rabbit dropping densities in OWH SS 11.



Day number 1 = 1/1/89.

Each bar represents the mean number of droppings recorded in 10, 25 x 25 cm. quadrats. The dates of sampling and numbers of droppings recorded in each quadrat are given in Appendix 10.

This sample area was grazed in March 1989.

Mites	166.94+/-14.01
Colembollans	35.59+/- 0.81
Platyarthrus hoffmanseggi	0.59+/- 0.23
Geophilomorph centipedes	0.80+/- 0.20
Beetle larvae	0.22+/- 0.08
Ants (excluding L. flavus)	0.20+/- 0.12

The other ant species found in this area were Lasius alienus and Myrmica scabrinodis. This was the only record of Lasius alienus in any of the sample areas. This ant prefers drier conditions than L. flavus. Only four worker ants were found, extracted from a core collected on 19/4/89.

The centipedes Schendyla nemorensis and Lithobius duboscqui were found in this area.

Orange coloured pseudococcids of the same species as found in OWH SS 4 were also extraced from cores in this sample area on several occasions. These too were probably Chnaurococcus subterraneous. The Tingids Campylosteira verna and Agramma laeta were also extracted from the cores collected in this area.

Mites of the genus Antennophorus were found in ant samples from colonies number 2 and 5 on 23/9/85.

10.9. Quadrat 7, OWH SS 12.

Site - Old Winchester Hill.

Location - on the south slope of the reserve, on its south east corner. South of OWH SS 8 and south-east of OWH SS 11 and the small enclosure.

10.9.1. The characteristics of the ant population.

The ant mounds.

No.of mounds - 71
Mean diameter of mounds (D) - 42.1 +/- 1.7 cm.
Mean height of mounds (H) - 11.4 +/- 0.8 cm.
Ratio D/H - 3.7
Area of quadrat occupied by the mounds - 2.8%
Mean above ground volume of soil in the mounds - 15.4 litres.
Mean distance to nearest neighbour - 1.27 +/- 0.06 metres.

In Figure 10.19 the percentage of mounds in each 10cm. size band is shown.

A slightly higher than average population of mounds for the south slope. In the middle of the size range for the slope quadrats. Only OWH SS 9 had a higher density of mounds present.

10.9.2. Management. This is as outlined in Figure 10.1. This plot was grazed in March-April 1983, May-June 1984 and 1985, July-September 1986 and October-December 1987. Thus at the time that the quadrats were examined it had had an estimated 5,000 sheep days per hectare in the previous 3 years.

10.9.3. The physical environment.

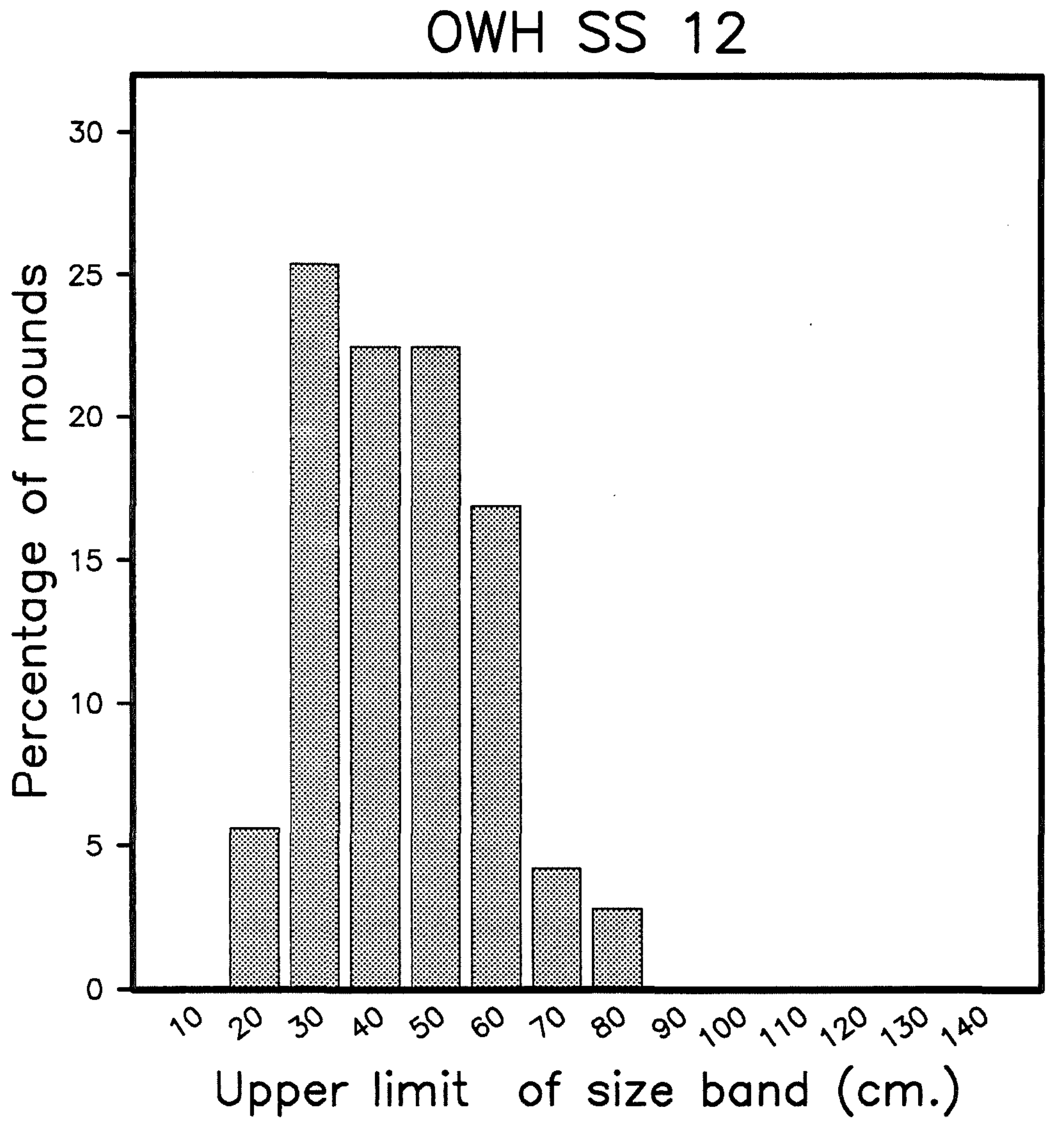
Altitude - 165 metres.
Slope - 16^{o}, facing 195^{o} (SSW).
Mean soil depth - 9.7 +/- 0.87 cm.
Mean soil pH - 7.49

10.9.4. The biological environment.

The flora. This area had quite a rich flora possessing elements of both OWH SS 8 and 11, ie. it had areas of short herb rich turf, mixed

Figure 10.19.

The distribution of mound sizes in OWH SS 12.



A total of 71 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

in with other patches of ranker vegetation.

Thus, there were patches of vegetation with Spiranthes spiralis, Blackstonia perfoliata, Asperula cynanchica etc, and other areas dominated by coarser grasses, such as Brachypodium pinnatum and Arrhenatherum elatius with patches of short scrubby vegetation.

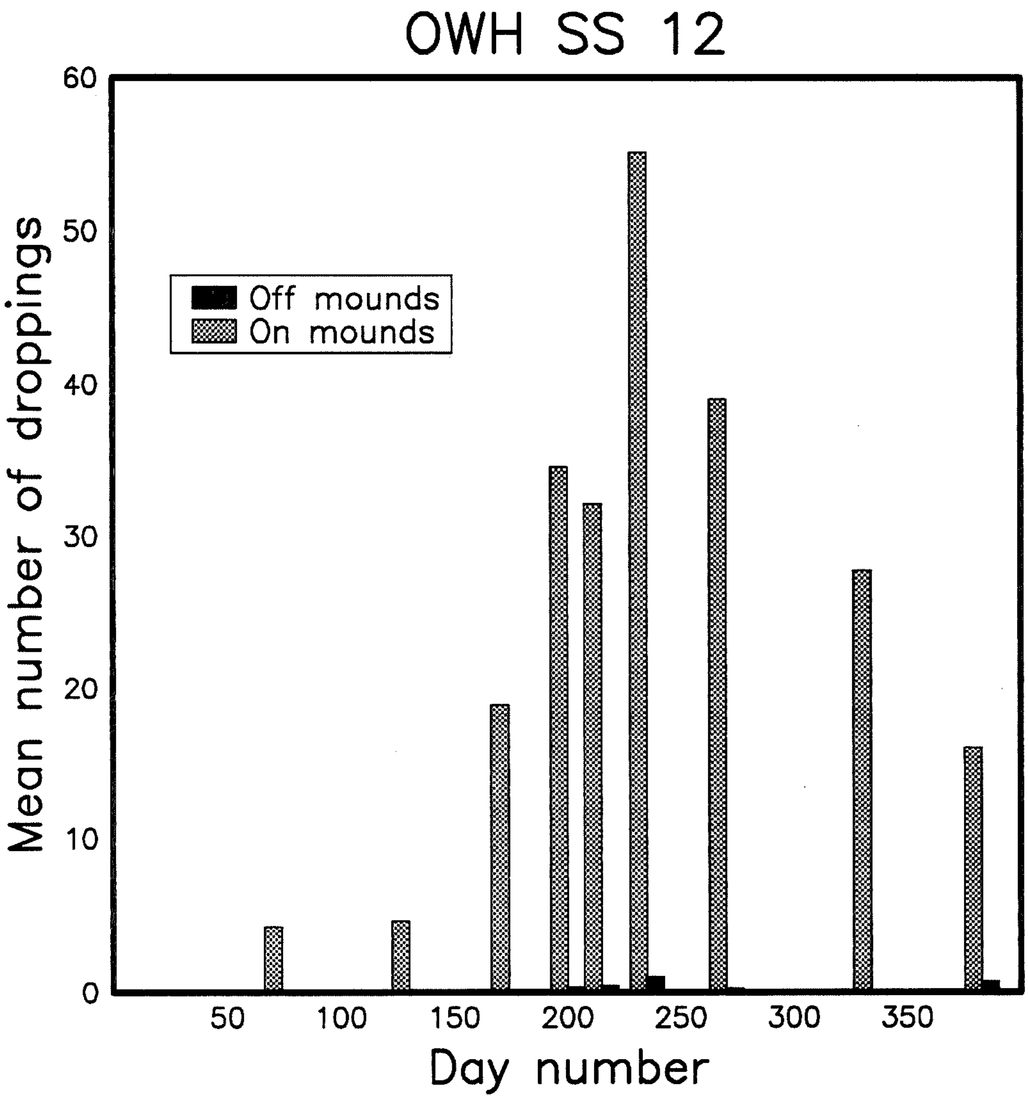
Gallium mollugo was more abundant here than in any of the other south slope quadrats, as was Blackstonia perfoliata and Rosa canina. These species illusatrate the mixed nature of the area.

In all 57 species of plant were recorded from this quadrat.

Rabbit droppings. The maximum mean number of droppings found on the mounds was 55.1 on 23/8 and the minimum 4.2 on 15/3. The maximum off the mounds was 1.0 on 23/8 and the minimum 0 on several occasions from March to June. The full data is presented in graphical form in Figure 10.20.

Figure 10.20.

Rabbit dropping densities in OWH SS 12.



Day number 1 = 1/1/89.

Each bar represents the mean number of droppings recorded in 10, 25 x 25 cm. quadrats. The dates of sampling and numbers of droppings recorded in each quadrat are given in Appendix 10.

10.10. Quadrat 8, OWH NFS.

Site - Old Winchester Hill.

Location - North facing slope, opposite side of hill to the south slope. The sample area was positioned at the bottom of the slope to the east of the footpath running down from the Wardens Hut and Public Display (see Figure 5.2.). Part of the area is shown in Figure 13.2.

10.10.1. The characteristics of the ant population.

The ant mounds.

No.of mounds - 70
Mean diameter of mounds (D) - 54.6 +/- 3.1 cm.
Mean height of mounds (H) - 14.6 +/- 0.9 cm.
Ratio D/H - 3.7
Area of quadrat occupied by the mounds - 5.0%
Mean above ground volume of soil in the mounds - 39.9 litres.
Mean distance to nearest neighbour - 1.52 +/- 0.07 metres.

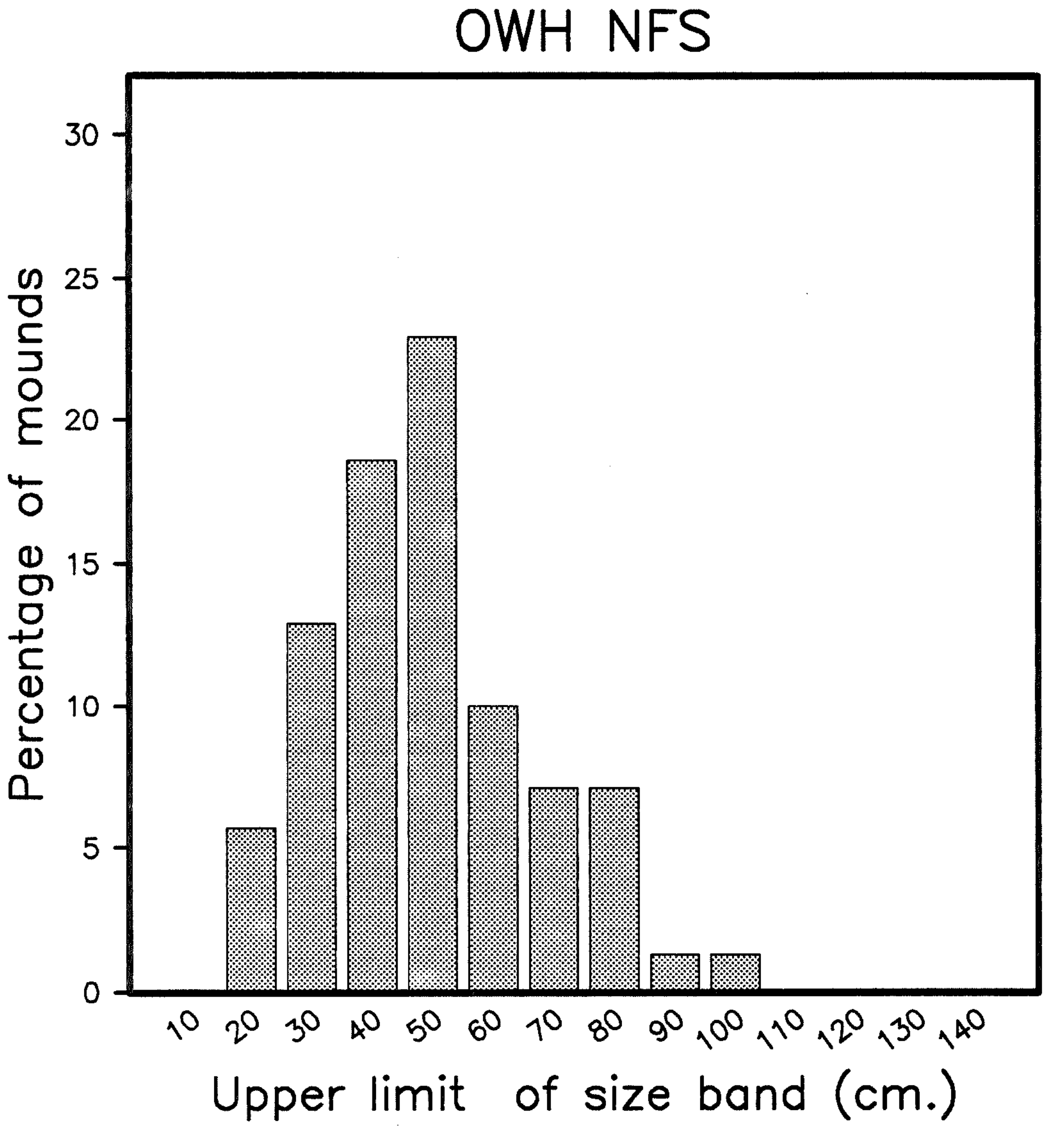
Figure 10.21 shows the percentage of the mounds in each 10cm. diameter band.

The mounds in this area were much larger than the typical south slope populations of mounds. Mean diameter, height and volume were larger in all the south slope quadrats, except OWH SS 7. The percentage area of the quadrat covered by the mounds was also larger. Overall this quadrat had the third highest mean mound volume, mound diameter and percentage area covered in the 20 sample quadrats.

10.10.2. Management. This area has had a similar history to the south slope of the reserve but has been maintained as one large area and not subdivided into small plots. Up to 1979 the history of the slope was as on the south slope. Since then it has been biennially winter grazed, typically at an estimated 1,105 sheep days per hectare per grazing period. Grass growth is generally poor and so less grazing is needed to keep the turf in condition. The estimated total grazing

Figure 10.21.

The distribution of mound sizes in OWH NFS.



A total of 70 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

for the last 3 years prior to the examination of the quadrat in 1984 was 1,653 sheep days per hectare.

10.10.3. The physical environment.

Altitude - 150 metres.
Slope - 11°, facing 015° (NNE).
Mean soil depth - 9.15 +/- 0.83 cm.
Mean soil pH - 7.68

The soil survey by New (1969) places the soil type of this area in a slightly different category to that of the south slope soils. While belonging to the same Icknield series of soils it belongs to the Steepland phase (Avery 1964). A soil sample from the top of the slope is described as a rendzina overlying middle chalk. The upper 7.5 cm. layer is described as:

> Dark greyish brown slightly sandy silty loam, frequent small and few large chalk and flint fragments, also few small marcastite nodules; hard small crumb; good porosity; abundant fine roots; dry; few earthworms; pH 7.7.

Underlying this is a layer of chalk rubble (5cm.). It should be emphasized that this sample was collected further up and facing further west than the quadrat in the sample area. Soil cores collected in this area contained a large amount of chalk rubble.

The annual mean temperatures in the area are summarised in Figure 10.22. The ground temperatures were much lower than those in OWH SS 4 and 11 on the south slope.

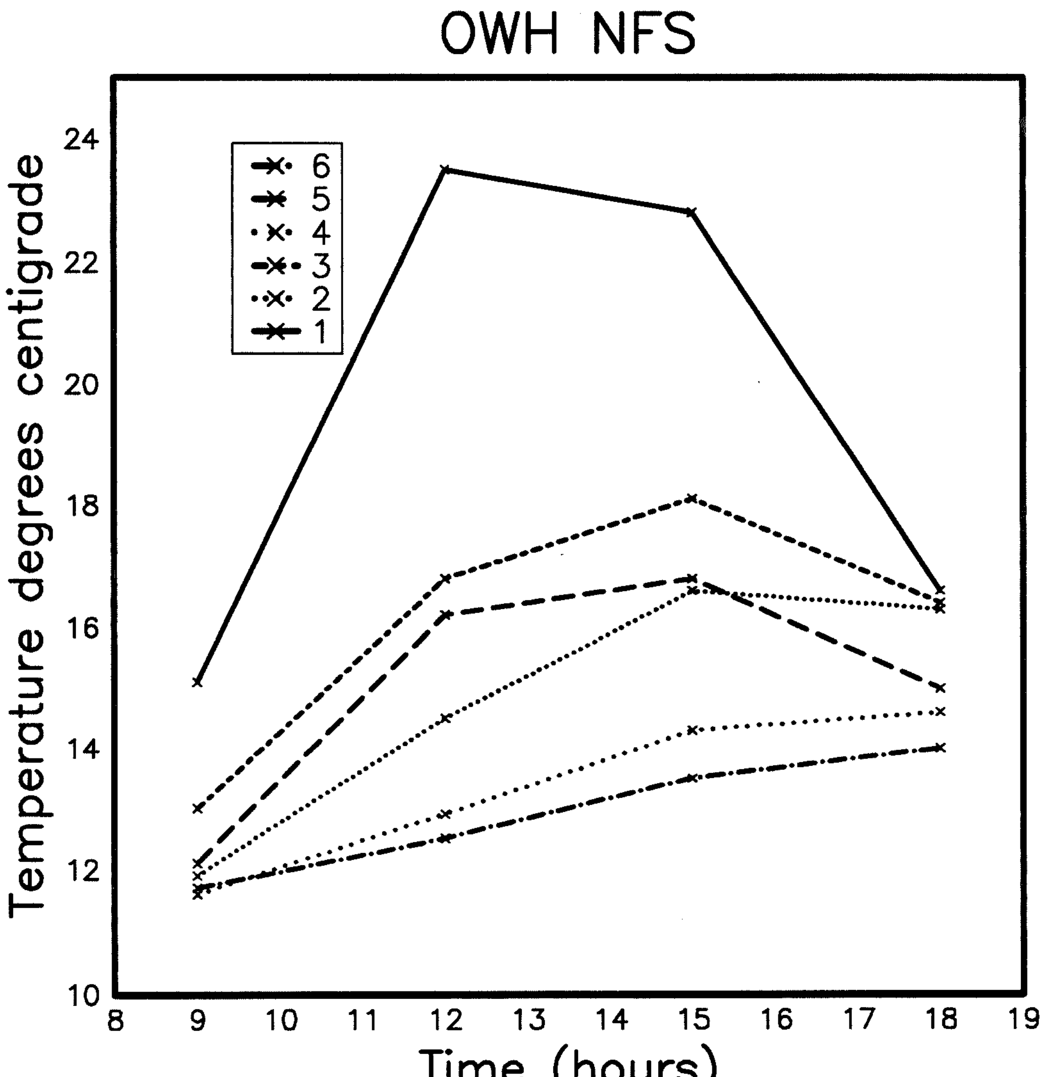
10.10.4. The biological environment.

The flora. This area supports a rich flora but lacks the plants which favour the very dry hot conditions found on the south slope of the reserve, such as *Blackstonia perfoliata*, *Spiranthes spiralis*,

Figure 10.22.

Summary of the annual mean temperatures in OWH NFS.

The mean annual temperatures at four times of day are shown. Times are British Summer Time. In the table below the graph, the mean figures are shown, together with the mean annual air temperatures. 1 - 6 refer the locations as follows.
1, south side of mound, top 1 cm. of soil. 2, same location 10 cm. deep. 3, north side of mound top 1 cm. of soil. 4, same location 10 cm. deep. 5, ground, top 1 cm. of soil. 6, same location 10 cm. deep.



	1	2	3	4	5	6	AIR
9.00	15.1	11.9	13.0	11.6	12.1	11.7	12.1
12.00	23.5	14.5	16.8	12.9	16.2	12.5	15.3
3.00	22.8	16.6	18.1	14.3	16.8	13.5	16.4
6.00	16.6	16.3	16.4	14.6	15.0	14.0	13.7

The temperature raw data is given in Appendix Eight. The methods are further explained in section 7.3.2. Each point represents the mean of all the temperatures recorded in that location at that time throughout the year.

Gymnodenia conopsea and Leucanthemum vulgare.

It is particularly noticeable that the common orchid on this slope is the Common Spotted (Dactylorhiza fuchsii) which completely replaces the Fragrant (G. conopsea) found on the south slope and prefers moist calcareous soils (Clapham et al 1987). The moss Rhytidiadelphus squarrosus was only found here and in OWH C10 on this reserve both north facing areas. It is a tall acrocarpous species which again will only grow in reasonably moist conditions. The moss Pseudoscleropodium purum was particularly common on the north facing sides of the ant mounds in this area.

To add to the diversity on this slope, there is also an element of woodland plants with seedlings of Quercus petraea and Acer pseudoplatanus and occasional plants of Mercuralis perennis.

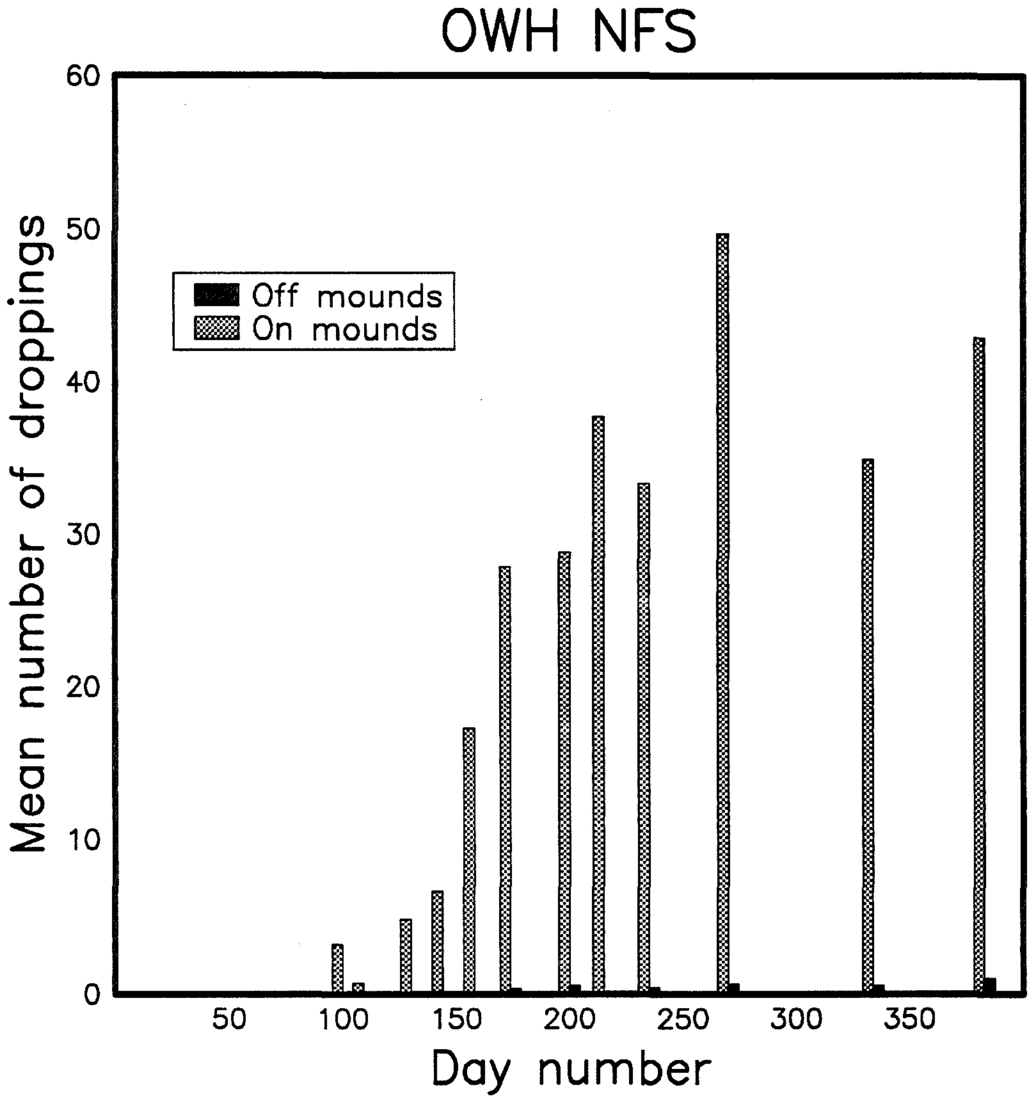
In all 61 species of plant were recorded from this quadrat.

Rabbit droppings. The maximum mean number of droppings found on the mounds was 49.7 on 27/9 and the minimum 0.7 on 19/4. Off the mounds the maximum was 1.0 on 18/1/90 and the minimum 0 on 3 separate times between 19/4 and 24/5. The full data is presented in graphical form in Figure 10.23.

Other invertebrates. The ant Myrmica scabrinodis was found in this sample area.

Figure 10.23.

Rabbit dropping densities in OWH NFS.



Day number 1 = 1/1/89.

Each bar represents the mean number of droppings recorded in 10, 25 x 25 cm. quadrats. The dates of sampling and numbers of droppings recorded in each quadrat are given in Appendix 10.

This area was grazed in March 1989.

10.11. Quadrat 9, OWH C10.

Site - Old Winchester Hill.

Location - In a north facing Coombe, adjacent to OWH NFS. On the opposite side of the reserve to the south slope (see Figure 5.2.). A photograph of the area is shown in Figure 10.24.

10.12.2. The characteristics of the ant population.

The ant mounds.

No.of mounds - 119
Mean diameter of mounds (D) - 59.9 +/- 2.5 cm.
Mean height of mounds (H) - 18.2 +/- 0.7 cm.
Ratio D/H - 3.3
Area of quadrat occupied by the mounds - 10.1%
Mean above ground volume of soil in the mounds - 52.0 litres.
Mean distance to nearest neighbour - 1.15 +/- 0.04 metres.

Figure 10.25. shows the percentage of the mounds in each 10 cm. diameter band.

The quadrat had the highest density of mounds found at OWH. They were also the largest mounds of any sample area, both in diameter and height, and were only exceeded in mean volume by the mounds in OWH SS 7. The percentage area of the quadrat covered by the mounds was by far the highest of any quadrat, 3.2% ahead of the next highest (AR 15).

Estimates of colony sizes and worker ant densities.

Mark-release-recapture estimates.

Set 1. July/August 1985.		Set 2. September/October 1985.	
Colony 1.	8,646 +/- 1,843	Colony 1.	4,280 +/- 879
Colony 2.	9,605 +/- 1,846	Colony 2.	-
Colony 3.	34,534 +/- 10,832	Colony 3.	-
Colony 4.	15,101 +/- 5,279	Colony 4.	14,369 +/- 3,413
Colony 5.	6,116 +/- 1,262	Colony 5.	10,270 +/- 2,518
Mean	14,800 +/- 5,147	Mean	9,640 +/- 2,929

No recaptures of marked ants were made in colonies 2 and 3 for the second set of estimates. The means of both the first and second sets of estimates were in the middle of the range of the sample areas in

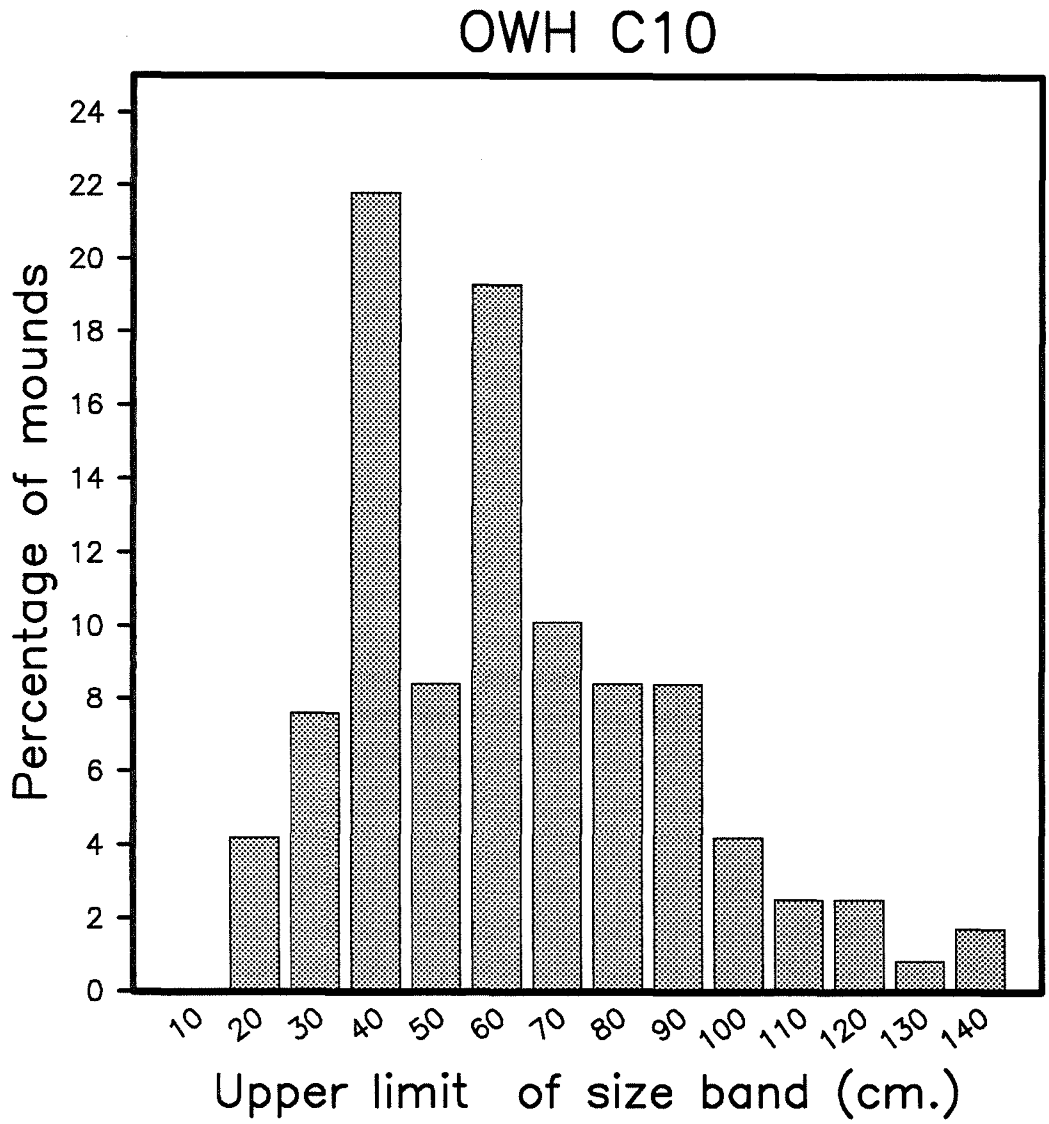
Figure 10.24.

A view of quadrat 9, OWH C10.

This photograph was taken in Winter. The dense population of large mounds is obscured due to the vegetation. The sample quadrat was positioned towards the rear of the open area. The photograph was taken looking due south. The evergreen trees in the background are Yews, (*Taxus baccata*).

Figure 10.25.

The distribution of mound sizes in OWH C10.



A total of 119 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

which estimates were made. The first estimate mean was higher than in the south slope sample areas.

Numbers of worker ants found in core samples. The mean number of worker ants extracted per core over the whole year was 12.44+/-4.88 in a total of 41 cores were collected. The was the highest of any area in which cores were collected.

The sexual production of colonies.

	1985		1986		1987	
	Gynes	Males	Gynes	Males	Gynes	Males
Colony 1.	77	247	252	2,473	21	1,110
Colony 2.	115	737	0	0	0	2,316
Colony 3.	362	499	73	592	317	604
Colony 4.	86	1,584	50	997	95	1,009
Colony 5.	215	399	440	726	457	580
Mean	171.0	693.2	163.0	957.6	178.0	1,123.8
SE	53.7	236.5	81.3	412.4	89.5	316.3

The highest gyne production of any sample area in 1985. Production of sexuals was higher than the south slope quadrats in 1985 but lower than OWH SS 4 in 1986 and 1987.

Head widths of male and gyne samples. All measurements are in millimetres.

	Males	Gynes
Colony 1.	0.81 +/- 0.006 (10)	1.44 +/- 0.015 (10)
Colony 2.	0.73 +/- 0.012 (10)	1.37 +/- 0.012 (9)
Colony 3.	0.73 +/- 0.006 (9)	1.43 +/- 0.008 (9)
Colony 4.	0.74 +/- 0.009 (10)	1.41 +/- 0.010 (10)
Colony 5.	0.74 +/- 0.006 (10)	1.42 +/- 0.013 (10)
Mean	0.75 +/- 0.015	1.41 +/- 0.012

The males were the largest measured in any sample area but the gynes were of average size.

Dry weights of male and gyne samples. All measurements are in milligrams The mean dry weight of an individual ant is given and the sample size shown.

	Males		Gynes	
Colony 1.	0.445	(20)	9.52	(10)
Colony 2.	0.384	(19)	9.01	(8)
Colony 3.	0.422	(9)	9.63	(7)
Colony 4.	0.415	(20)	11.11	(10)
Colony 5.	0.390	(20)	10.73	(10)
Mean	0.411+/-0.011		10.00+/-0.394	

The males were the heaviest measured in any sample area, but again the gynes were only of average weights.

Dates at which stages were first observed in 1986. The first small pupae were seen on 26/6, the first adult males on 8/7. The first gyne pupae were seen on 4/6 and the first adult gynes on 8/7.

10.11.2. Management. Unlike any of the other quadrats in this survey this area recieved no formal management whatsoever aside from a very occasional scrub cutting (not seen to be done from 1984 to 1989). There was no organised sheep grazing at all. Examination of the quadrat showed that the only grazing came from either rabbits (see section 10.11.4.) and deer (probably fallow deer, Dama dama or less frequently roe deer, Capreolus capreolus) which were heard in the area on several occasions. Deer droppings were seen on many occasions. The area is not visited by the public.

10.11.3. The physical environment.

Altitude - 130 metres.
Slope - 11^{o}, facing 360^{o} (N).
Mean soil depth - 10.75 +/- 0.87 cm.
Mean soil pH - 6.97
Mean soil core density - 0.521+/-0.019 g/cm^3.

This quadrat had the lowest pH and soil density of any of the quadrats.

New (1969) describes the soil of this area as a brown calcareous soil usually less than 15 inches thick and belonging to the Soil Surveys Coombe series (Hodgson 1967). However, his sampling area lies slightly to the south of the quadrat in which the ant mounds were measured and was described as woodland. Therefore, it is not possible to be sure of the level of correspondance between his sample and the Coombe quadrat soils.

The changes in water content in this quadrat are shown in Figure 10.26. The maximum water content of the cores was 54.1% on 10/4/89 and the minimum 23.76% on 19/7/89. These figures were the highest for any sample area tested. This sample area had consistently higher water contents than any of the sample areas in which cores were collected.

A summary of the mean annual temperatures is shown in Figure 10.27. The mean ground temperatures were coldest of the sample areas in which temperatures were measured.

10.11.4. The biological environment.

The flora. The vegetation in this area was dominated by tall grasses with no patches of shorter herb rich turf. Thus the vegetation of this area was not diverse with only 40 species of plants recorded.

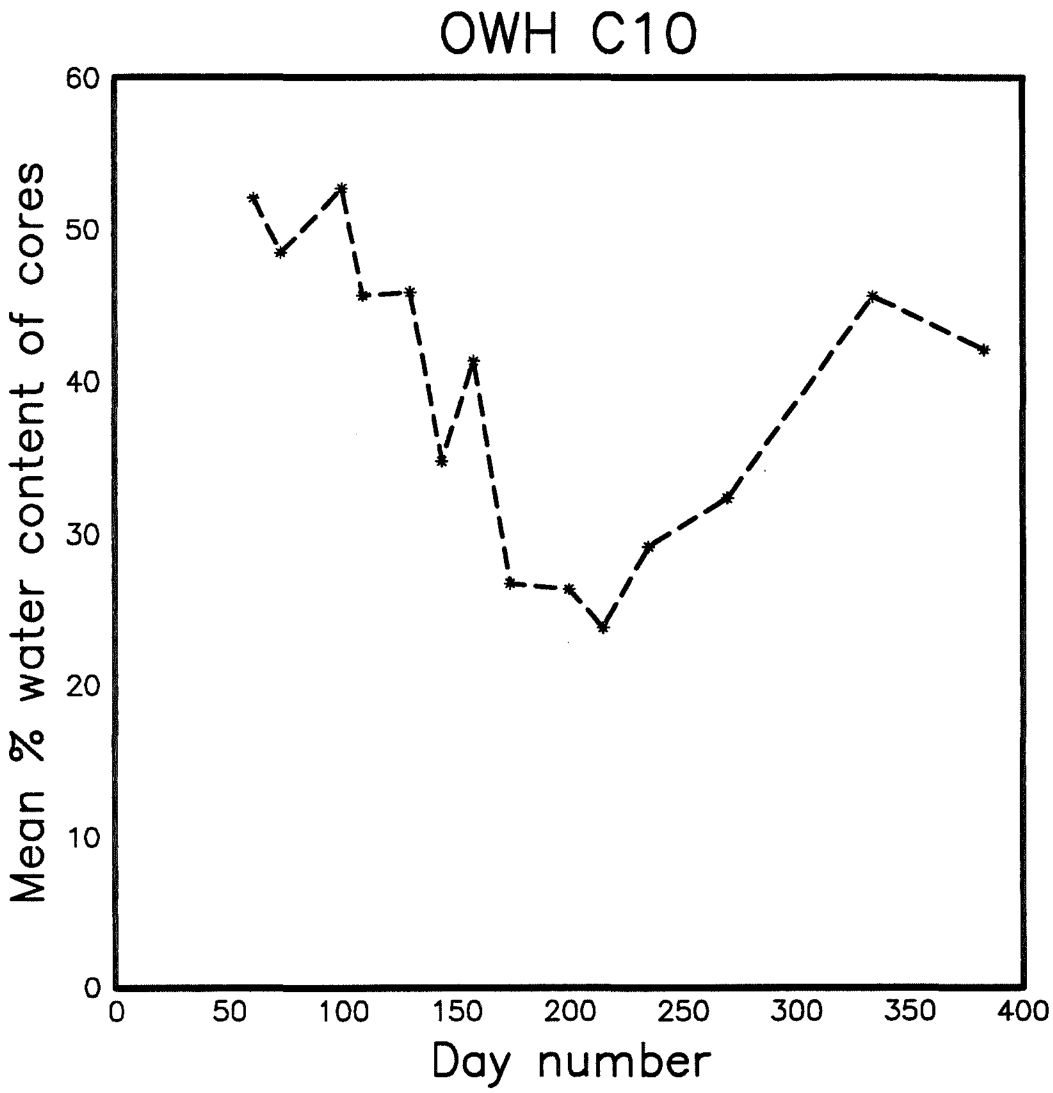
The dominant species were *Festuca rubra/ovina*, *Poa trivialis*, *Holcus lanatus* and the moss *Rhytidiadelphus squarrosus*. The examination of the 1 m^2 quadrats in this area particularly revealed the poverty of the flora compared to other areas on the reserve.

Early in the year *Veronica chamaedrys* and *Cruciata laevipes* were the dominant herb species. In contrast to the rest of the sample areas there was also very little sedge (*Carex* spp.). There was as a result of the lack of grazing, a thick litter layer of dead grass and other material in this area.

Late in summer 1989 a large amount of the flowering heads of the grass *Arrhenatherum elatius* were found to be infected with the spore

Figure 10.26.

Water contents of soil cores collected in OWH C10.



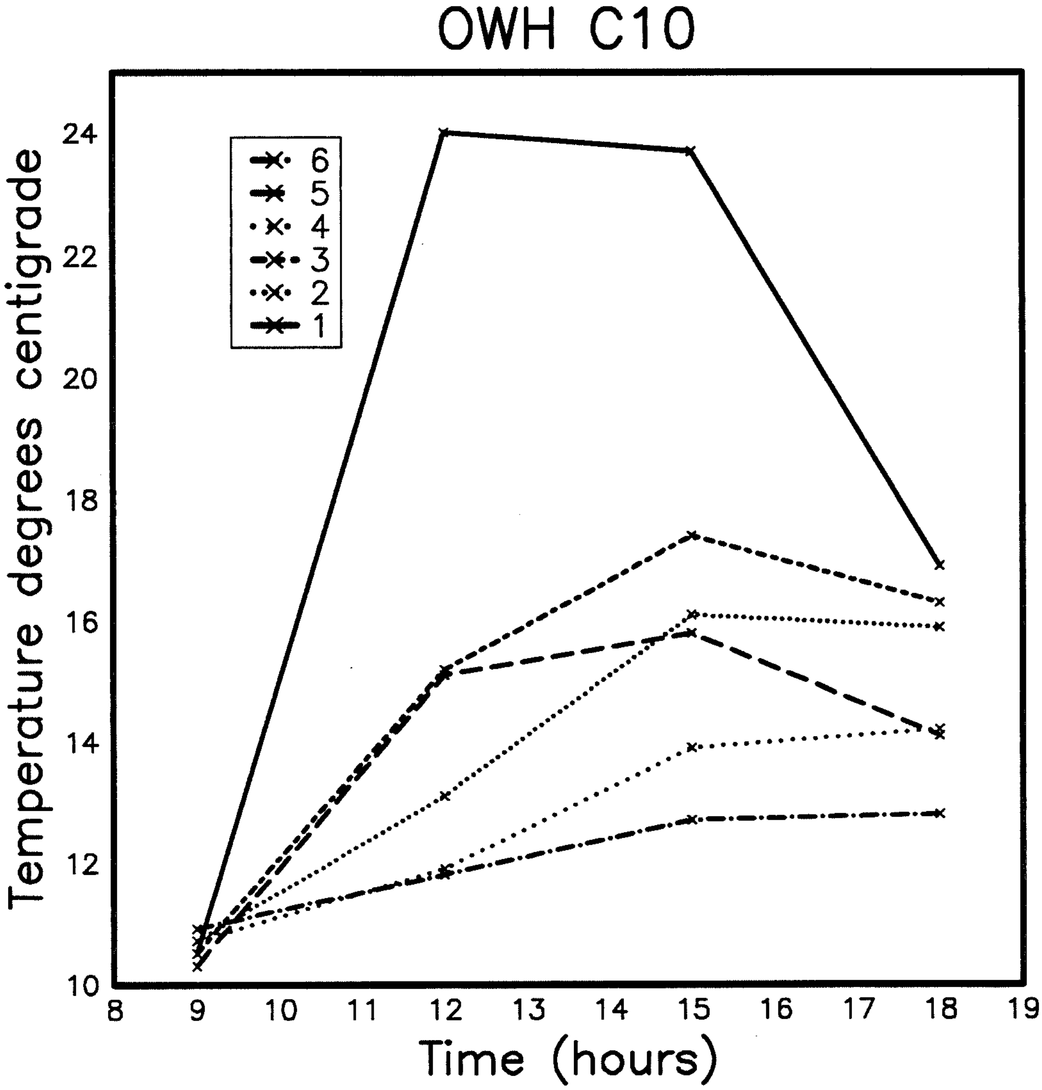
Day number 1 = 1/1/89.

Each point represents the mean water content of a sample of cores collected on that day. The dates of sampling, sample size, mean water contents and standard errors are given in Appendix 4.

Figure 10.27.

Summary of the annual mean temperatures in OWH C10.

The mean annual temperatures at four times of day are shown. Times are British Summer Time. In the table below the graph, the mean figures are shown, together with the mean annual air temperatures. 1 - 6 refer the locations as follows.
1, south side of mound, top 1 cm. of soil. 2, same location 10 cm. deep. 3, north side of mound top 1 cm. of soil. 4, same location 10 cm. deep. 5, ground, top 1 cm. of soil. 6, same location 10 cm. deep.



	1	2	3	4	5	6	AIR
9.00	10.5	10.7	10.5	10.7	10.3	10.9	10.8
12.00	24.0	13.1	15.2	11.9	15.1	11.8	15.1
15.00	23.7	16.1	17.4	13.9	15.8	12.7	16.1
18.00	16.9	15.9	16.3	14.2	14.1	12.8	13.9

The temperature raw data is given in Appendix Eight. The methods are further explained in section 7.3.2. Each point represents the mean of all the temperatures recorded in that location at that time throughout the year.

producing bodies of two parasitic fungi, *Claviceps purpurea* (Ergot) and *Ustilago avaenae* (a smut fungus). The fungus *Paxillus involutus* was also found in this area.

Rabbit droppings. The maximum mean number of droppings found on the mounds was 27.2 on 27/9 and the minimum 1.2 on 7/6. The maximum off the mounds was only 0.7 on 18/1/90 and very few droppings were found off the mounds, none being found on many occasions. The full data are presented in graphical form in Figure 10.28.

Root aphids and other invertebrates.

Root aphids. The overall mean number of root aphids extracted per core was 3.76+/-1.00, the highest of any of the areas in which cores were collected.

This included confirmed records of the following species.

Brachycaudus spp.	2	(1.3%)
Jacksonia papillata	22	(14.4%)
Geoica eragrostidis	11	(7.2%)
Geoica setulosa	10	(6.5%)
Neanoecia corni	1	(0.7%)
Neanoecia zirnitsi	52	(34.0%)
Tetraneura ulmi	36	(23.5%)
Unidentified	19	(12.4%)

The diversity of species was higher than in OWH SS 11 or 4.

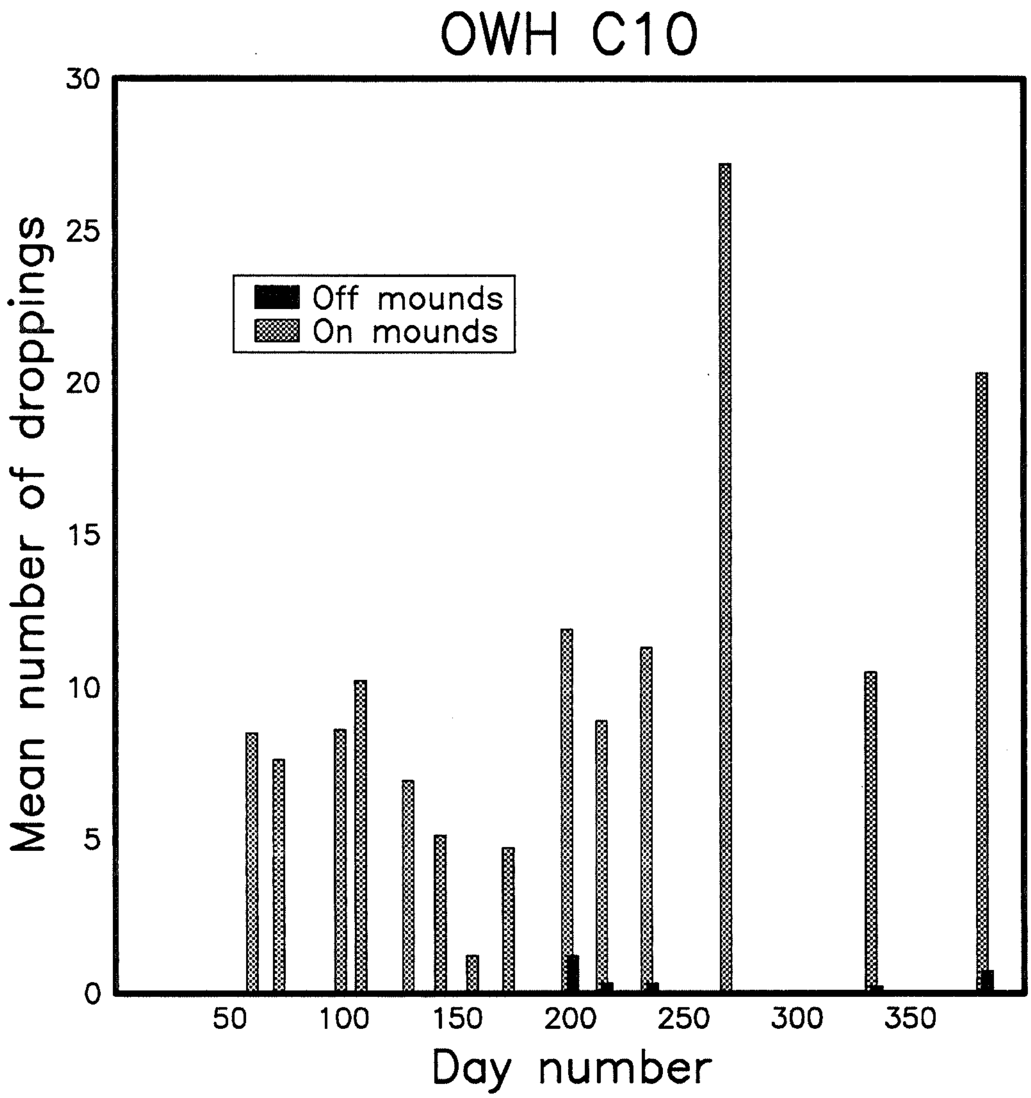
Other invertebrates. The mean numbers of the major groups of invertebrates extracted from the cores was as follows:

Mites	258.85+/- 3.35
Collembolans	83.32+/- 1.49
Platyarthrus hoffmanseggi	0.15+/- 0.17
Geophilomorph centipedes	1.34+/- 0.25
Beetle larvae	0.20+/- 0.07
Ants (excluding *L. flavus*)	0.51+/- 0.34

This area had the greatest density of invertebrates extracted from the cores. The numbers of mites and geophilomorph centipedes were the highest, and the number of collembolans the second highest in any of the sample areas in which cores were collected. In contrast, the

Figure 10.28.

Rabbit dropping densities in OWH C10.



Day number 1 = 1/1/89.

Each bar represents the mean number of droppings recorded in 10, 25 x 25 cm. quadrats. The dates of sampling and numbers of droppings recorded in each quadrat are given in Appendix 10.

numbers of *P. hoffmanseggi* and the beetle larvae were among the lowest in any sample area.

The other ant species found in this sample area were *Myrmica scabrinodis* and *M. rubra*.

The uncommon Harvestman *Anelasmocephalus cambridgei* was found amongst the animals extracted from one core on 10/5/89.

The only Pseudoscorpion found at Old Winchester Hill, a solitary individual of *Chthonius* spp. was found here, extracted from a core collected on 19/7/89.

The centipede *Haplophilus subterraneous* was also extracted from a core in this area. This was the only area in which this species was found. This area also had the centipedes which were found in all the areas in which cores were collected, *Schendyla nemorensis* and *Lithobius duboscqui*.

10.12. The Aston Rowant Barn Plots.

As four of the Aston Rowant sample areas lay in these plots a brief consideration of them as a whole, will be first given. In these plots an experimental grazing regime was maintained from 1965 right up to the beginning of 1983. The original plan was to graze the plots at either 1 or 3 sheep per 0.405 hectares (= 1 acre), and to compare the differences on the flora and the growth of the sheep. Throughout the period the grazing records show that sheep were put on the plots twice a year, firstly in spring, and secondly in late Autumn/early Winter. The quadrats were in areas 11, 12, 15 and 16 on the reserve (AR 11 to 16). Quadrats 12 and 16 were 3 sheep per acre plots. An analysis of the records for 1974 to 83 shows an average of 733 and 716 sheep days/hectare/year for AR 11 and 15 respectively, and 2,535 and 2,007 sheep days/hectare/year for AR 12 and 16. Thus AR 12 was the most heavily grazed plot and AR 15 the least. These plots clearly provide a fine opportunity for comparing the effects of so many years grazing on the ant populations. Since the second half of 1983 the experimental regime has been neglected, and the plots are now generally grazed whenever it is convenient and with more regard to the flora of the individual areas.

However, at the time the quadrats were examined in these plots, the ant populations represented the end point of this long term grazing regime.

10.13. Quadrat 10, AR 11.

Site - Aston Rowant (AR).

Location - Barn plots at the base of the escarpment slope. Enclosure 11, the first in a row of 6 enclosures (see Figure 5.3.).

10.13.1. The characteristics of the ant population.

The ant mounds.

Number of mounds - 113
Mean diameter (D) - 45.2 +/- 1.3 cm.
Mean height (H) - 12.0 +/- 0.6 cm.
Ratio D/H - 3.8
Area of quadrat occupied by the mounds - 5.0%
Mean above ground volume of soil in the mounds - 17.1 litres.
Mean distance to nearest neighbour - 1.16 +/- 0.04 metres.

In Figure 10.29. the percentage of mounds in each 10 cm. diameter band is show.

A high density of mounds, in comparison to the OWH south slope quadrats, and similar to that found in AR 15 and OWH C10.

10.13.2. Management. The management plan for this area is as described in Section 10.13. As a result of this, in the three years prior to the examination of the quadrats, this area had received approximately 2,200 sheep days/hectare. Since that period grazing has been erratic and posibly slightly higher than this level.

10.13.3. The physical environment.

Altitude - 165 metres.
Slope - 11^{o}, facing 300^{o} (NW).
Mean soil depth - 13.6 +/- 1.58 cm.
Mean soil pH - 7.71

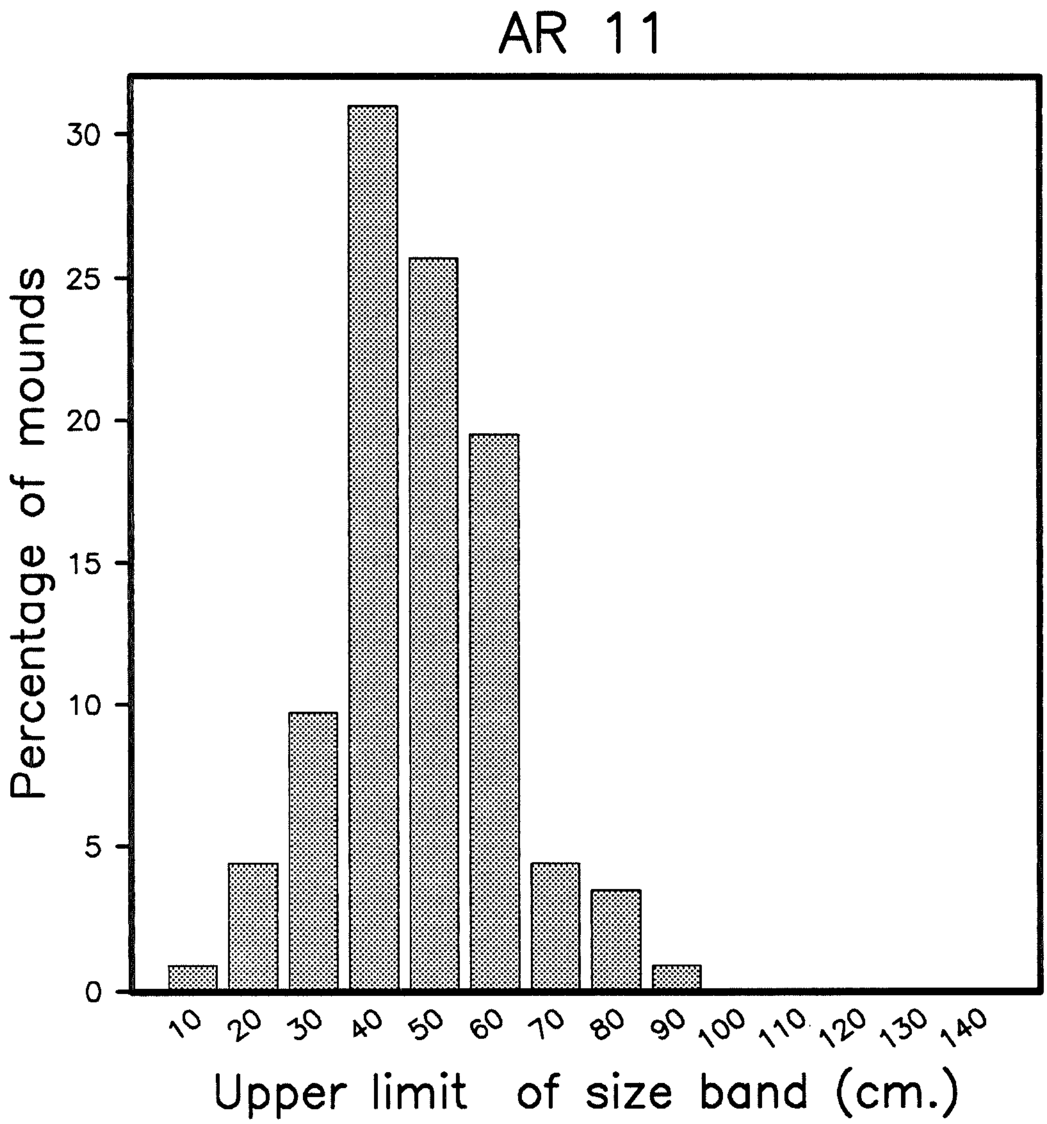
The thinnest soil of the barn quadrats and the highest pH.

10.13.4. The biological environment.

The flora. In all 47 species of plants were recorded in this quadrat, the least of any of the barn plots. In general this area supported species found in the other barn plots but without quite

Figure 10.29.

The distribution of mound sizes in AR 11.



A total of 113 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

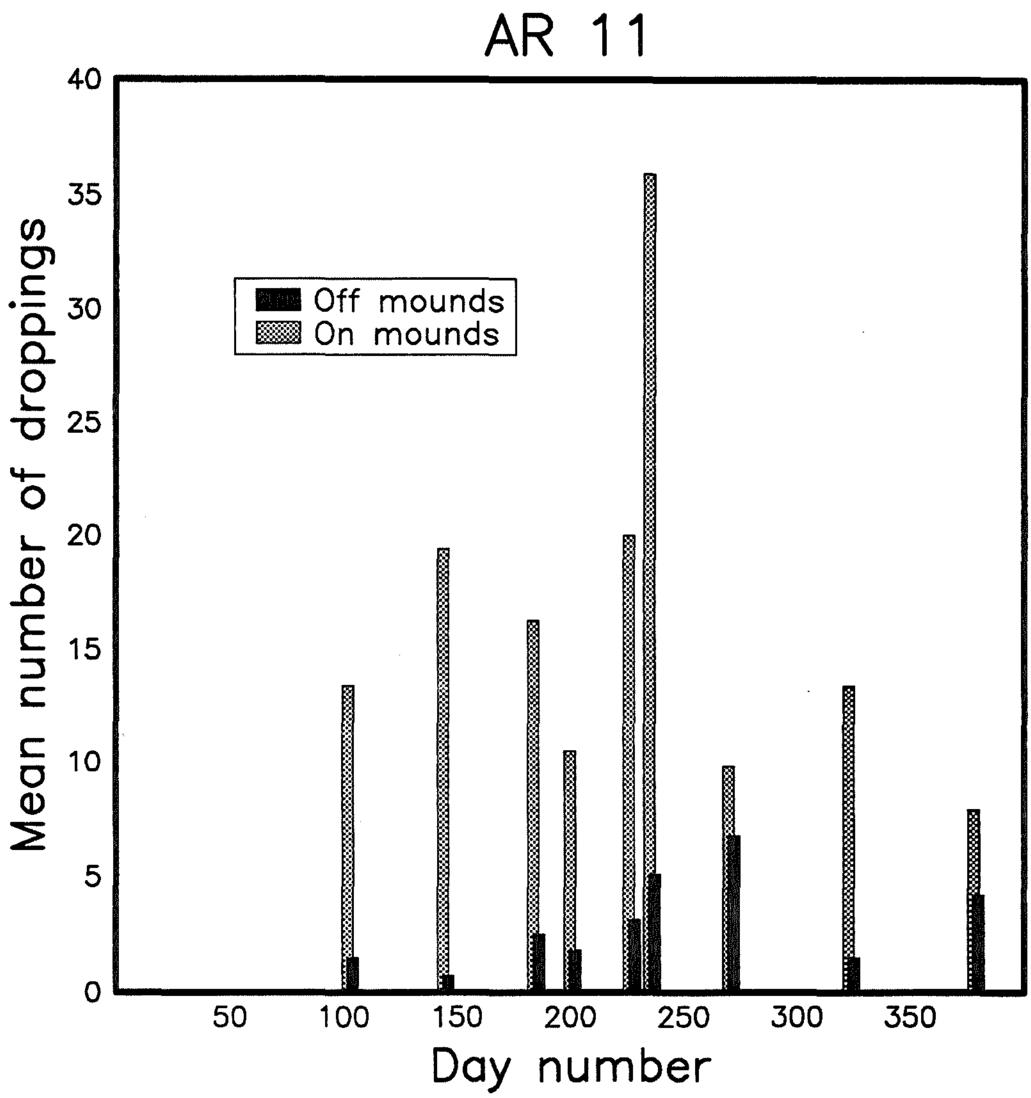
the diversity. One exception to this was finding Iberis amara in this area. This uncommon plant is scattered about several areas on the reserve, but was only found within one of the quadrats here. It is a plant which is often associated with rabbit activity.

There were large populations of many plants typical of short chalk turf, Thymus serpyllum, Asperula cynanchica and Linum catharticum for example. Surprisingly Avenula pubescens was not recorded in this area and the dominant grasses were Festuca sp. and Agrostis stolonifera.

Rabbit droppings. The maximum mean number of droppings found on the mounds was 35.9 on 24/8 and the minimum 7.9 on 12/1/90. The maximum off the mounds was 6.8 on 28/9 and the minimum 0.7 on 25/4. This area appeared to be fairly heavily rabbit grazed and the dropping counts certainly indicated a consistent high presence of rabbits in the area. The changes in the density of rabbit droppings recorded throughout the year are shown in Figure 10.30.

Figure 10.30.

Rabbit dropping densities in AR 11.



Day number 1 = 1/1/89.

Each bar represents the mean number of droppings recorded in 10, 25 x 25 cm. quadrats. The dates of sampling and numbers of droppings recorded in each quadrat are given in Appendix 10.

10.14. Quadrat 11, AR 12.

Site - Aston Rowant.

Location - One of the barn plots, lying next to AR 11 on the east side of it (see Figure 5.3.).

10.14.1. The characteristics of the ant population.

The ant mounds.

Number of mounds - 273
Mean diameter of mounds (D) - 25.9 +/- 0.8 cm.
Mean height of mounds (H) - 9.3 +/- 0.2 cm.
Ratio D/H - 7.1
Area of quadrat occupied by the mounds - 4.6%
Mean above ground volume of soil in the mounds - 2.7 litres.
Mean distance to nearest neighbour - 0.75 +/- 0.02 metres.

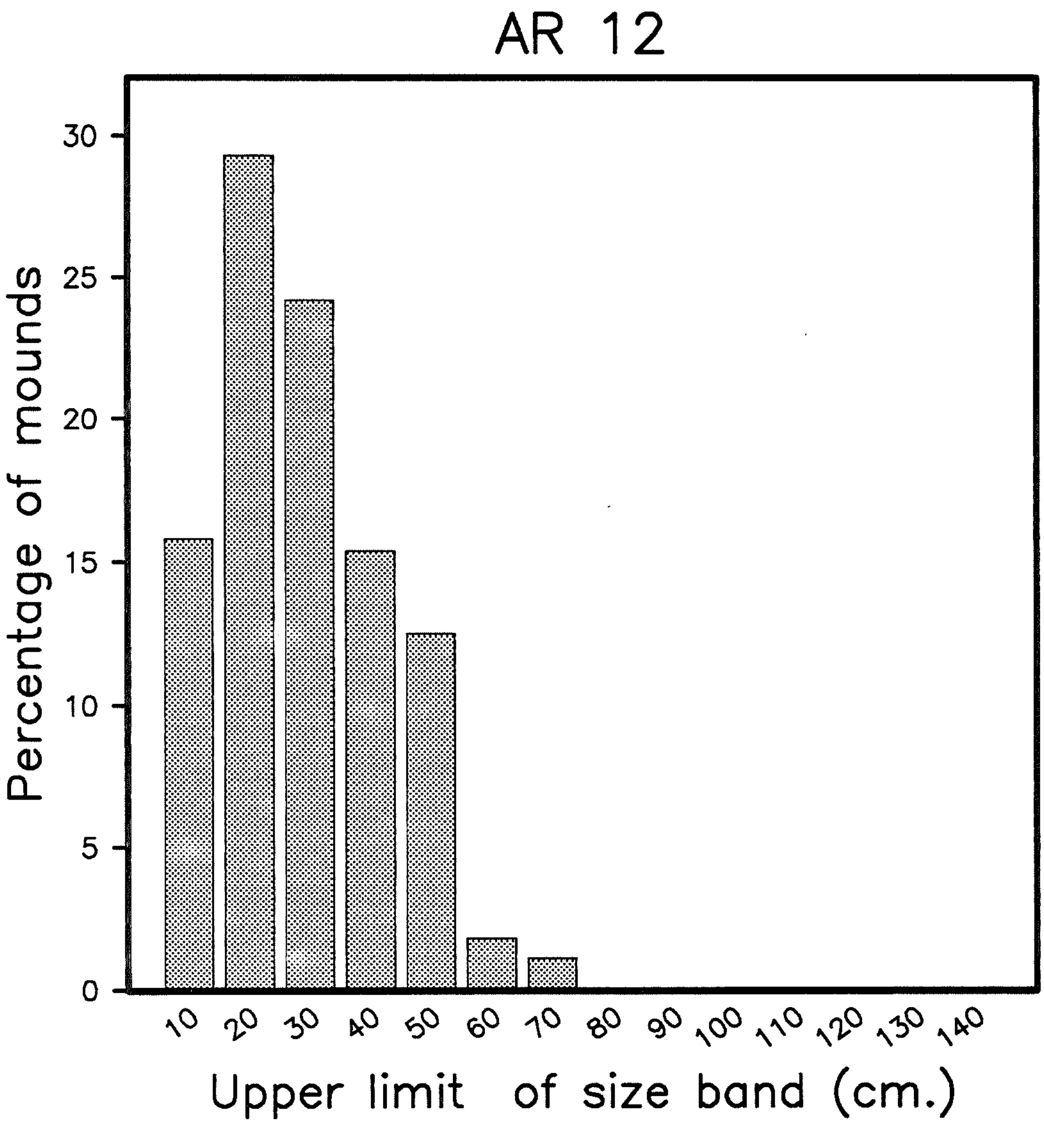
The distribution of the sizes of the mounds is shown in Figure 10.31.

The ant mounds in this quadrat were unlike any of the other quadrats, barring AR NWS. There were a large number of extremely small mounds (see Figure 10.31.). The mean diameter of the mounds was the second smallest of all of the sample quadrats and the mean height the smallest. The mean volume was the least of any of the sample quadrats. Because of the high density of mounds, the mean distance to nearest neighbour was also the smallest of any of the quadrats.

10.14.2. Management. The basic management is as described in Section 10.13. above. Thus over the three year period prior to the examination of the quadrat in this sample area it received approximately 7,600 sheep days/hectare in total grazing. Since that time the grazing plan has been dropped but the character of the area appears not to have changed significantly. Rabbits are regularly shot to keep their numbers down.

Figure 10.31.

The distribution of mound sizes in AR 12.



A total of 273 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

10.14.3. The physical environment.

Altitude - 165 metres.
Slope - 14°, facing 300° (NW).
Mean soil depth - 17.45 +/- 1.39 cm.
Mean soil pH - 7.66

This area had the highest soil depth of the barn quadrats, with only AR NWS and MD 7B having higher figures recorded of all the sample areas.

10.14.4. The biological environment.

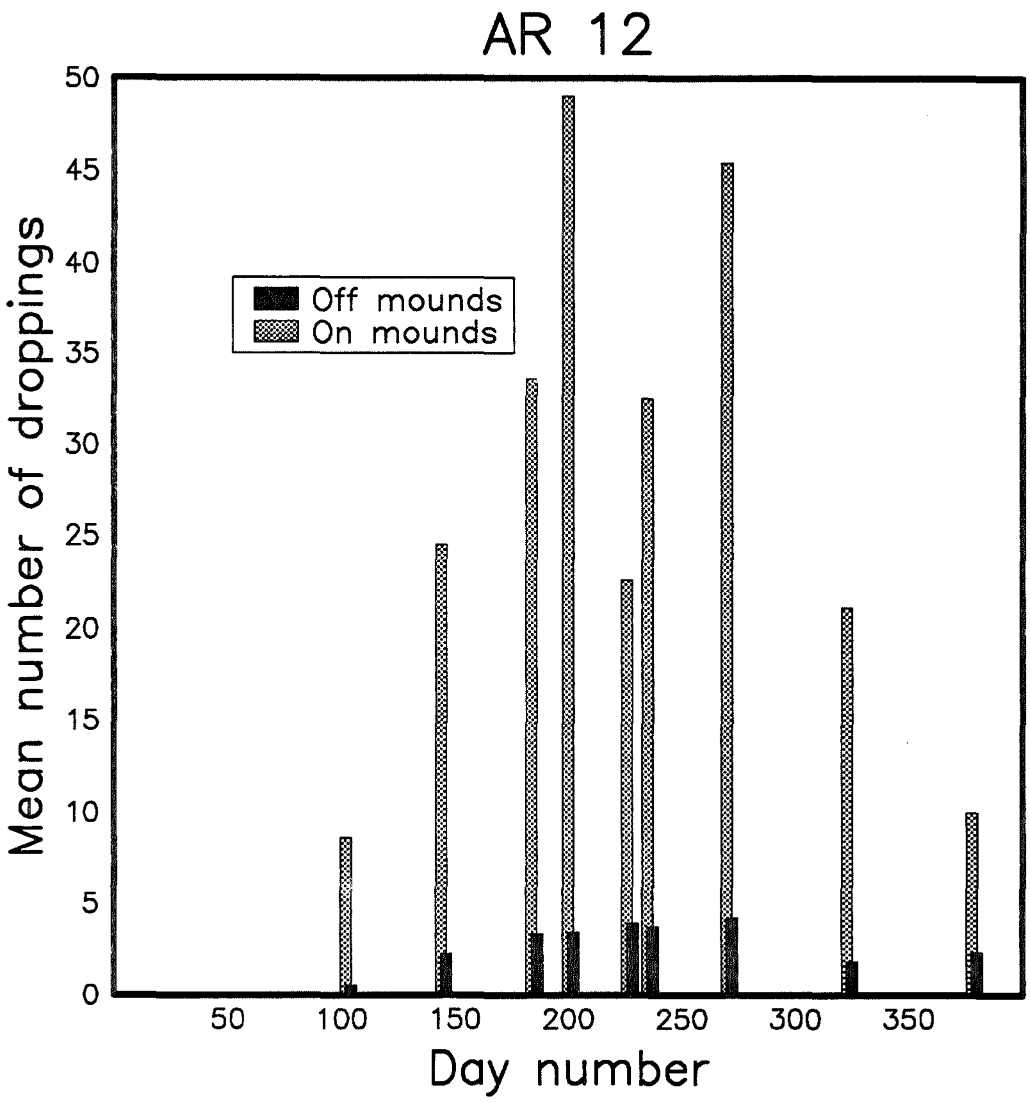
The flora. In spite of, or perhaps because of, the intense grazing in this quadrat, the number of species found was high, in all 60 species of plant were recorded in this quadrat, second only to AR 15 at this reserve and to OWH NFS elsewhere.

Only one species found in this area was not found elsewhere at Aston Rowant, *Veronica serpyllifolia*. The grass was generally very short and herb rich, with large amounts of *Thymus serpyllum*. As in most of the barn plots there was some short scrub developed.

Rabbit droppings. The maximum mean number of droppings found on the mounds was 49.0 on 20/7 and the minimum was 8.6 on 13/4. Off the mounds the maximum was 4.2 on 28/9 and the minimum 0.5 on 13/4. The full data are presented in graphical form in Figure 10.32. As in AR 11 rabbit activity appeared to be extremely high in this sample area.

Figure 10.32.

Rabbit dropping densities in AR 12.



Day number 1 = 1/1/89.

Each bar represents the mean number of droppings recorded in 10, 25 x 25 cm. quadrats. The dates of sampling and numbers of droppings recorded in each quadrat are given in Appendix 10.

10.15. Quadrat 12, AR 15.

Site - Aston Rowant.

Location - Barn plots, eastern side, opposite end to AR 11 and 12 (see Figure 5.3.). A photograph of this area is shown in Figure 10.33.

10.15.1. The characteristics of the ant population.

The ant mounds.

Number of mounds - 126
Mean diameter of mounds (D) - 49.8 +/- 1.6 cm.
Mean height of mounds (H) - 16.3 +/- 0.7 cm.
Ratio D/H - 3.1
Area of quadrat occupied by the mounds - 6.9%
Mean above ground volume of soil in the mounds - 29.7 litres.
Mean distance to nearest neighbour - 1.07 +/- 0.03 metres.

In Figure 10.34 the percentage of mounds in each 10 cm. diameter band is shown.

This quadrat had a dense population of large mounds. The number of mounds in the quadrat was only bettered by AR 12, and the mounds were the largest recorded at Aston Rowant. The percentage area of the sample quadrat covered by the mounds was second only to OWH C10 of all of the sample quadrats.

Estimates of colony sizes and worker ant density.

Mark-release-recapture estimates.

Set 1. July/August 1985.		Set 2. September/October 1985	
Colony 1.	2,215 +/- 453	Colony 1.	3,892 +/- 909
Colony 2.	16,564 +/- 5,174	Colony 2.	5,765 +/- 2,492
Colony 3.	51,450 +/- 25,216	Colony 3.	7,920 +/- 2,661
Colony 4.	10,272 +/- 5,903	Colony 4.	1,962 +/- 702
Colony 5.	29,299 +/- 9,220	Colony 5.	3,674 +/- 1,405
Mean	21,960 +/- 8,600	Mean	4,642 +/- 1,017

Colony 3 with an estimated size of 51,450, was the largest estimate in the first set of mark-release-recaptures. The first set of estimates gave the highest mean population for any sample area, but in contrast, the second set gave the lowest.

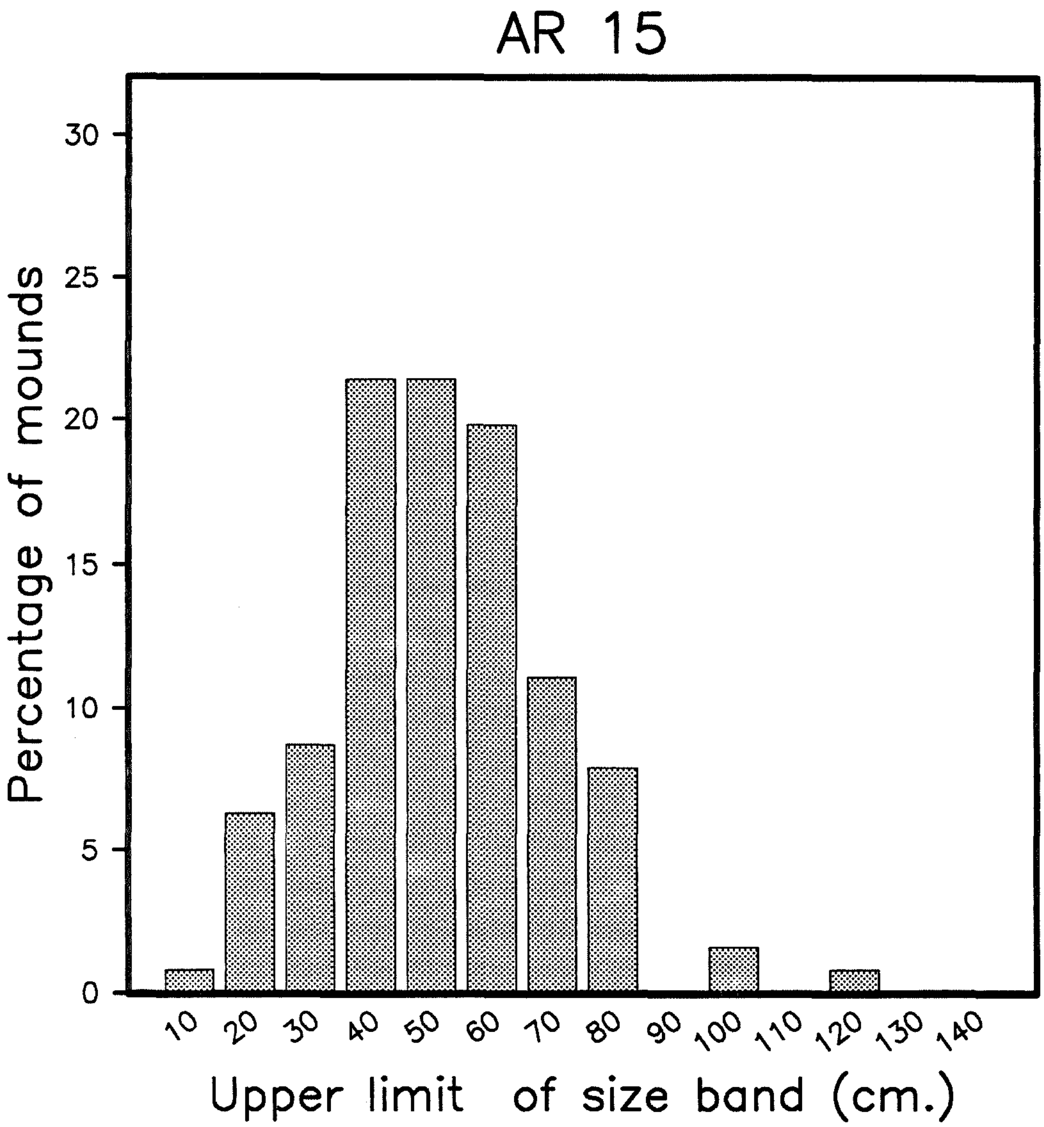
Figure 10.33.

A view of quadrat 12, AR 15.

A dense population of large mounds. The photograph was taken just after Spring grazing. Grazing is just intense enough to prevent excessive development of scrub.

Figure 10.34.

The distribution of mound sizes in AR 15.



A total of 126 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

Digging up colonies. Five colonies were dug up and the worker ants sorted out and counted in this sample area. The number of worker ants found was as follows.

Colony 1.	27,566
Colony 2.	18,072
Colony 3.	4,025
Colony 4.	16,705
Colony 5.	14,496
Mean	16,173 +/- 3,769

The mean number of workers was higher than in AR 16 in which 5 mounds were also dug up.

Numbers of worker ants found in core samples. A total of 49 cores were collected. The mean number of worker ants extracted per core year was 9.51+/-2.18, one of the highest of the sample quadrats.

The sexual production of colonies.

The numbers of sexuals produced.

	1985		1986		1987	
	Gynes	Males	Gynes	Males	Gynes	Males
Colony 1.	34	57	0	515	440	3,123
Colony 2.	65	130	263	582	584	2,264
Colony 3.	73	741	255	1,443	526	3,994
Colony 4.	0	52	21	92	80	348
Colony 5.	75	700	47	1,421	90	1,199
Mean	49.4	336.0	117.2	810.6	344.0	2,185.6
SE	14.4	157.7	58.4	267.3	108.2	652.1

Sexual productivity was similar to that in AR 16, but quite low in the context of all of the sample areas in which sexuals were collected.

Head widths of male and gyne samples. All measurements are in millimetres.

	Males	Gynes
Colony 1.	0.68 +/- 0.010 (10)	1.42 +/- 0.013 (9)
Colony 2.	0.70 +/- 0.006 (10)	1.43 +/- 0.013 (10)
Colony 3.	0.73 +/- 0.009 (10)	1.45 --- (1)
Colony 4.	0.68 +/- 0.009 (10)	---
Colony 5.	0.69 +/- 0.010 (10)	1.47 +/- 0.012 (6)
Mean	0.70 +/- 0.009	1.44 +/- 0.011

The gynes were the largest of any of the sample areas in which sexuals were collected in 1985. The males were quite small in contrast. Both males and gynes were, on average, larger than in AR 16.

Dry weights of male and gyne samples. All measurements are in milligrams. The mean dry weight of an individual ant is given.

	Males	Gynes
Colony 1.	0.295 (20)	7.37 (7)
Colony 2.	0.325 (20)	9.00 (10)
Colony 3.	0.360 (20)	9.00 (1)
Colony 4.	0.265 (20)	----
Colony 5.	0.295 (20)	11.32 (6)
Mean	0.308+/-0.016	9.17+/-0.812

Both males and gynes were heavier than in AR 16 but of a moderate weight for the sample areas as a whole.

Dates at which stages were first observed in 1986. The first small pupae were seen on 27/5, the first adult males on 16/7. The first gyne pupae were seen on 12/6 and the first adult gynes on 16/7.

10.15.2. Management. This was basically as described in section 10.12. above. Prior to the examination of the quadrats in 1984, this area had thus received approximately 2,148 sheep days/hectare in total. Again, the character of this plot does appear to have altered since 1983 when the grazing regime was abandoned.

10.15.3. The physical environment.

Altitude - 165 metres.
Slope - 11^{o}, facing 360^{o} (N).
Mean soil depth - 15.6 +/- 1.19 cm.
Mean soil pH - 7.58
Mean soil core density - 0.779+/-0.011 g/cm^{3}

The soil core density in this area was the second highest (AR 16 was the highest) of the sample areas in which cores were collected.

The maximum mean water contents recorded were 41.3% on 15/3/89 and 41.4% on 13/4/89. The minimum mean water content recorded was 18.0% on 24/8/89. The changes in water contents throughout the year are graphically presented in Figure 10.35. Water regimes were damper than in the south facing slope quadrats at OWH, and the minima higher than at Martin Down.

The temperature regime of the sample area is summarised in Figure 10.36. where the mean annual temperatures recorded are graphed. The mean air and ground temperatures in this quadrat were similar to those in AR 16, and were lower than in all of the other sample quadrats, except OWH C10.

10.15.4. The biological environment.

The flora. This was the richest quadrat of all those examined, with in all 68 species of plant recorded, more than any other. The vegetation was quite lush with good grass growth throughout the year. The sward was herb rich with abundant flowering of plants such as *Picris hieracioides* and *Dactylorhiza fuschii*, perhaps more typical of damper chalk grassland, but also *Asperula cynanchica*, *Lotus corniculatus* and *Thymus serpyllum* all typical chalk grassland herbs.

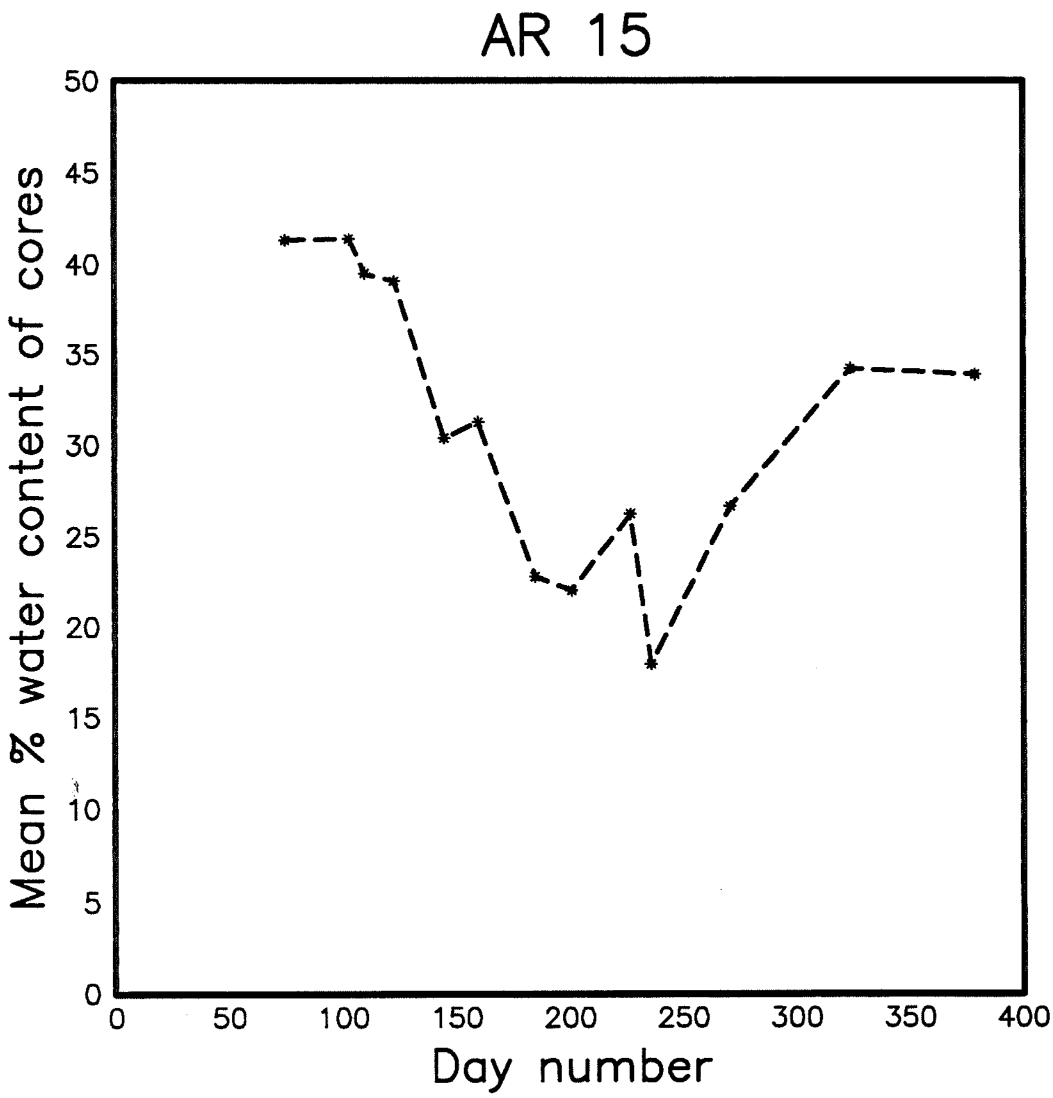
The plot had more orchid species than the others at Aston Rowant, with *D. fuschii* abundant, and *Anacamptis pyramidalis* and *Coeloglossum viride* occasional. As well as these in a small patch of woodland at the edge of the plot *Cephalanthera damasonium* was found, together with other more typical woodland plants such as *Campanula trachelium*.

Because of the light grazing pressure in this area scrub species were well developed, although scrub cutting is practised, with *Crataegus monogyna*, *Cornus sanguinea* and *Viburnum lantanum* having quite large populations of small plants present. There were also a few free standing trees, mainly at the edges of the plot, with small *Betula pendula* trees the most noticeable of these.

Three species of moss were abundant in this area,

Figure 10.35.

Water contents of soil cores collected in AR 15.



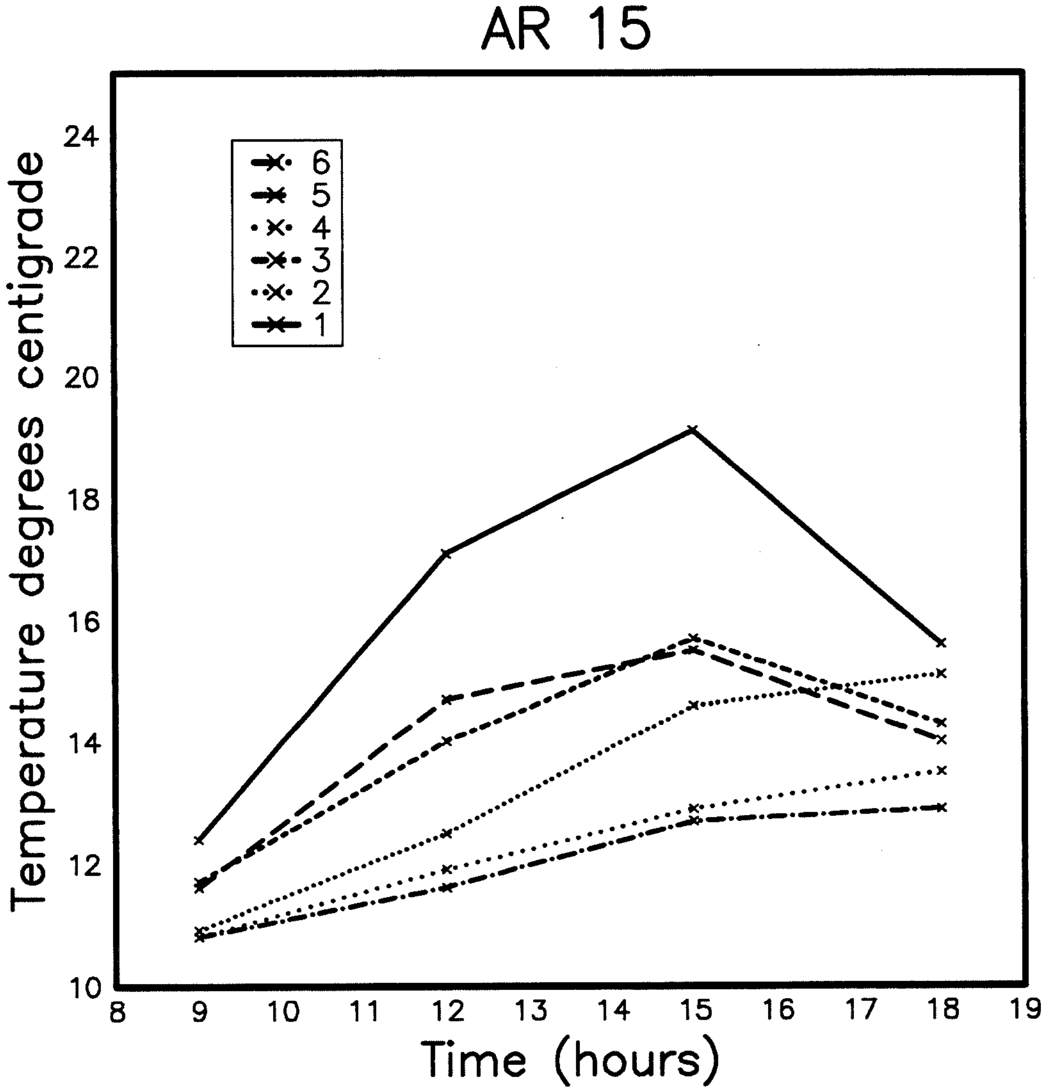
Day number 1 = 1/1/89.

Each point represents the mean water content of a sample of cores collected on that day. The dates of sampling, sample size, mean water contents and standard errors are given in Appendix 4.

Figure 10.36.

Summary of the annual mean temperatures in AR 15.

The mean annual temperatures at four times of day are shown. Times are British Summer Time. In the table below the graph, the mean figures are shown, together with the mean annual air temperatures. 1 - 6 refer the locations as follows.
1, south side of mound, top 1 cm. of soil. 2, same location 10 cm. deep. 3, north side of mound top 1 cm. of soil. 4, same location 10 cm. deep. 5, ground, top 1 cm. of soil. 6, same location 10 cm. deep.



	1	2	3	4	5	6	AIR
9.00	12.4	10.9	11.7	10.8	11.6	10.8	11.3
12.00	17.1	12.5	14.0	11.9	14.7	11.6	13.2
15.00	19.1	14.6	15.7	12.9	15.5	12.7	14.7
18.00	15.6	15.1	14.3	13.5	14.0	12.9	13.6

The temperature raw data is given in Appendix Eight. The methods are further explained in section 7.3.2. Each point represents the mean of all the temperatures recorded in that location at that time throughout the year.

Pseudoscleropodium purum, Hypnum cupressiforme and Rhytideadelphus squarrosus. The first and last of these mosses demonstrate the affinity of this quadrat with OWH C10, in which these mosses were also abundant. The moss Rhytidiadelphus triquetus was only found in this area and OWH NFS. As AR 15, OWH NFS and C10 are all north facing slopes this demonstrates how the aspect is influencing the flora of these areas in similar ways. On the other hand H. cupressiforme was only abundant at Aston Rowant in the barn plots.

Rabbit droppings. The maximum mean number of droppings found on the mounds was 26.9 on 16/3 and the minimum was 2.7 on 25/5. Off the mounds the maximum was 1.6 on 16/3 and the minimum 0.2 on 3/5/89 and 12/1/90. The number of droppings on the mounds may have been underestimated in this area. Because of the domed nature of the mounds in this plot it was clear that droppings would roll off the mounds much easier than in the other areas examined. The full data is presented in graphical form in Figure 10.37.

Root aphids and other invertebrates.

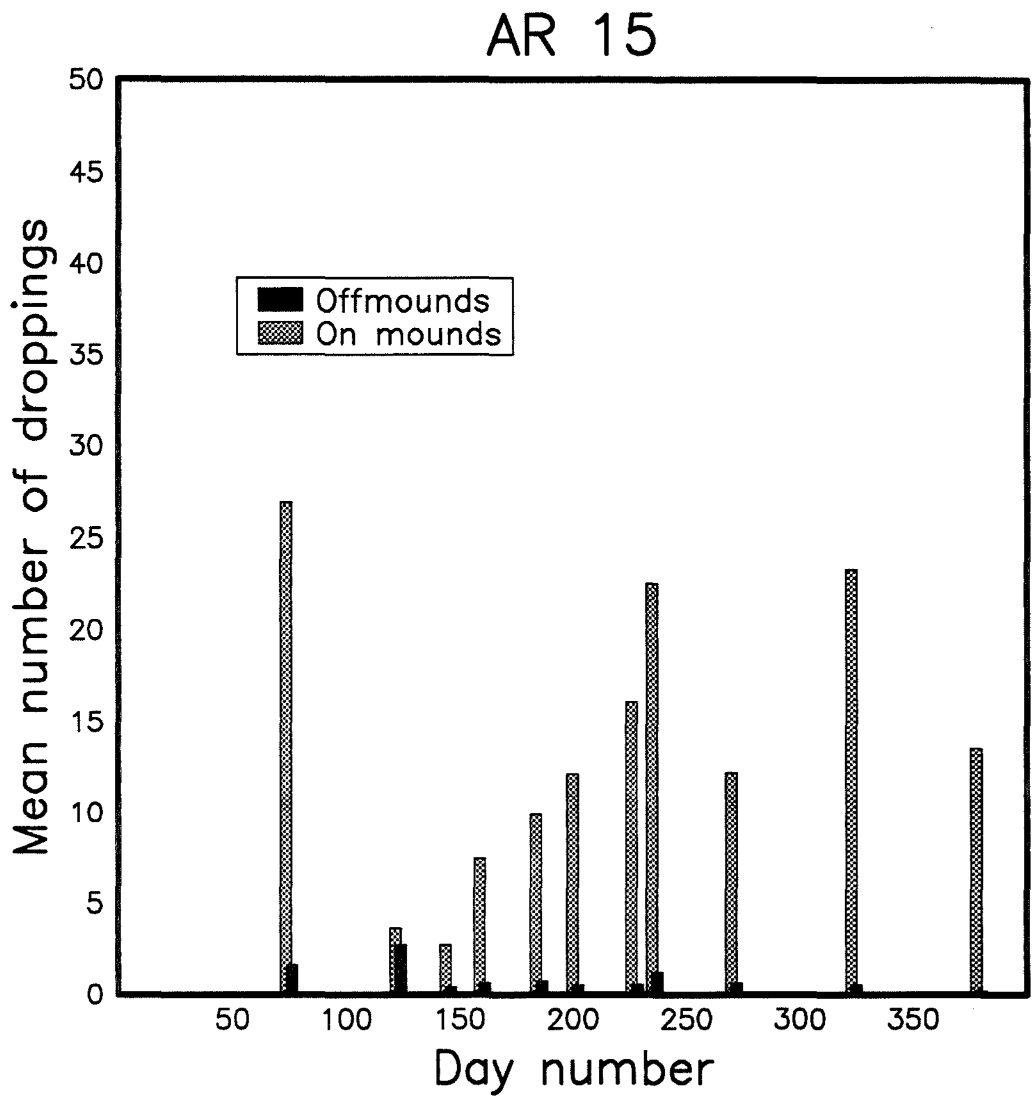
Root aphids. The mean number of root aphids extracted per core was 2.31+/-0.65. The following species of root aphids were found, in the following numbers.

Aphis vandergooti	2	(1.7%)
Aploneura lentisci	26	(22.4%)
Brachycaudus spp.	8	(6.9%)
Forda marginata	26	(22.4%)
Geoica eragrostidis	5	(4.3%)
Neanoecia zirnitsi	7	(6.0%)
Neotrama caudata	7	(6.0%)
Trama troglodytes	2	(1.7%)
Tetraneura ulmi	19	(16.4%)
Unidentified	14	(12.1%)

A high diversity of aphid species without any one species dominating. This was the only quadrat in which Aploneura lentisci was

Figure 10.37.

Rabbit dropping densities in AR 15.



Day number 1 = 1/1/89.

Each bar represents the mean number of droppings recorded in 10, 25 x 25 cm. quadrats, except on 3/5/89 when the sample size was only 5 quadrats. The dates of sampling and numbers of droppings recorded in each quadrat are given in Appendix 10.

The sample area was grazed in April 1989.

common.

Other invertebrates. The mean numbers per core of the major invertebrate groups were as follows:

Mites	122.80+/- 9.92
Collembolans	77.71+/- 6.92
Platyarthrus hoffmanseggi	0.61+/- 0.22
Geophilomorph centipedes	0.53+/- 0.12
Beetle larvae	0.55+/- 0.12
Ants (excluding *L. flavus*)	0.22+/- 0.10

The number of ants found in this area was the lowest of any of the sample areas in which cores were collected. Despite this it had one the richest ant faunas. *Myrmica* species were well represented in this area with workers of *Myrmica ruginodis*, *M. scabrinodis* and more surprisingly *M. schenki* being extracted from the cores. As well as this a female sexual of *M. rubra* was found in the area.

Several queens of the ant *Lasius mixtus* were found associated with the slates laid on some of the mounds in the area. Wright (1989) suggests that it is possible that *L. mixtus* queens could initiate their colonies as parasites of *L. flavus* colonies.

A single individual of the pseudoscorpion *Dinocheirus panzeri* was extracted from the cores collected in this area. Otherwise, all pseudoscorpions were identified as *Pselaphochernes dubius*, a known chalk grassland specialist pseudoscorpion (Legg and Jones 1988).

From cores collected on 24/8 some pink coloured pseudococcids were collected. These were unlike the coccids collected at Old Winchester Hill. On examination they appeared to belong to the species *Euripersia europaea* or *E. tomlinii* (Williams 1962). Only 6 individuals were found.

The beetle *Malthinus flaveolus* was extracted from a core in this sample area.

10.16. Quadrat 13, AR 16.

Site - Aston Rowant.

Location - Barn plots, eastern side, opposite end of plots to AR 11. Next to AR 15 on its eastern side (see Figure 5.3.). A photograph of the area is shown in Figure 10.38.

10.16.1. The characteristics of the ant population.

The ant mounds.

Number of mounds - 63
Mean diameter of mounds (D) - 43.4 +/- 2.2 cm.
Mean height of mounds (H) - 11.3 +/- 0.9 cm.
Ratio D/H - 3.9
Area of quadrat occupied by the mounds - 2.7%
Mean above ground volume of soil in the mounds - 16.5 litres.
Mean distance to nearest neighbour - 1.53 +/- 0.07 metres.

In Figure 10.39. the percentage of mounds in each 10 cm. diameter band is shown.

Despite being very close by to AR 15 the ant mound population in this sample quadrat was very different. The density of mounds was lower and they were smaller on average. The differences between the two areas can clearly be seen in the photographs shown in Figure 10.33 and 10.38.

Estimates of colony sizes and worker ant density.

Mark-release-recapture estimates.

Set 1. July/August 1985.		Set 2. September/October 1985	
Colony 1.	14,109 +/- 5,279	Colony 1.	19,019 +/- 8,410
Colony 2.	23,557 +/- 8,281	Colony 2.	4,709 +/- 1,854
Colony 3.	21,606 +/- 6,451	Colony 3.	10,725 +/- 4,608
Colony 4.	4,407 +/- 918	Colony 4.	2,432 +/- 1,167
Colony 5.	9,424 +/- 2,370	Colony 5.	2,024 +/- 965
Mean	14,621 +/- 3,607	Mean	7,782 +/- 3,211

The mean of the first set of estimates was lower than in AR 15, but for the second set of estimates was slightly higher.

Digging up colonies. Five colonies were dug up and the worker ants extracted and counted in this sample area. The number of worker

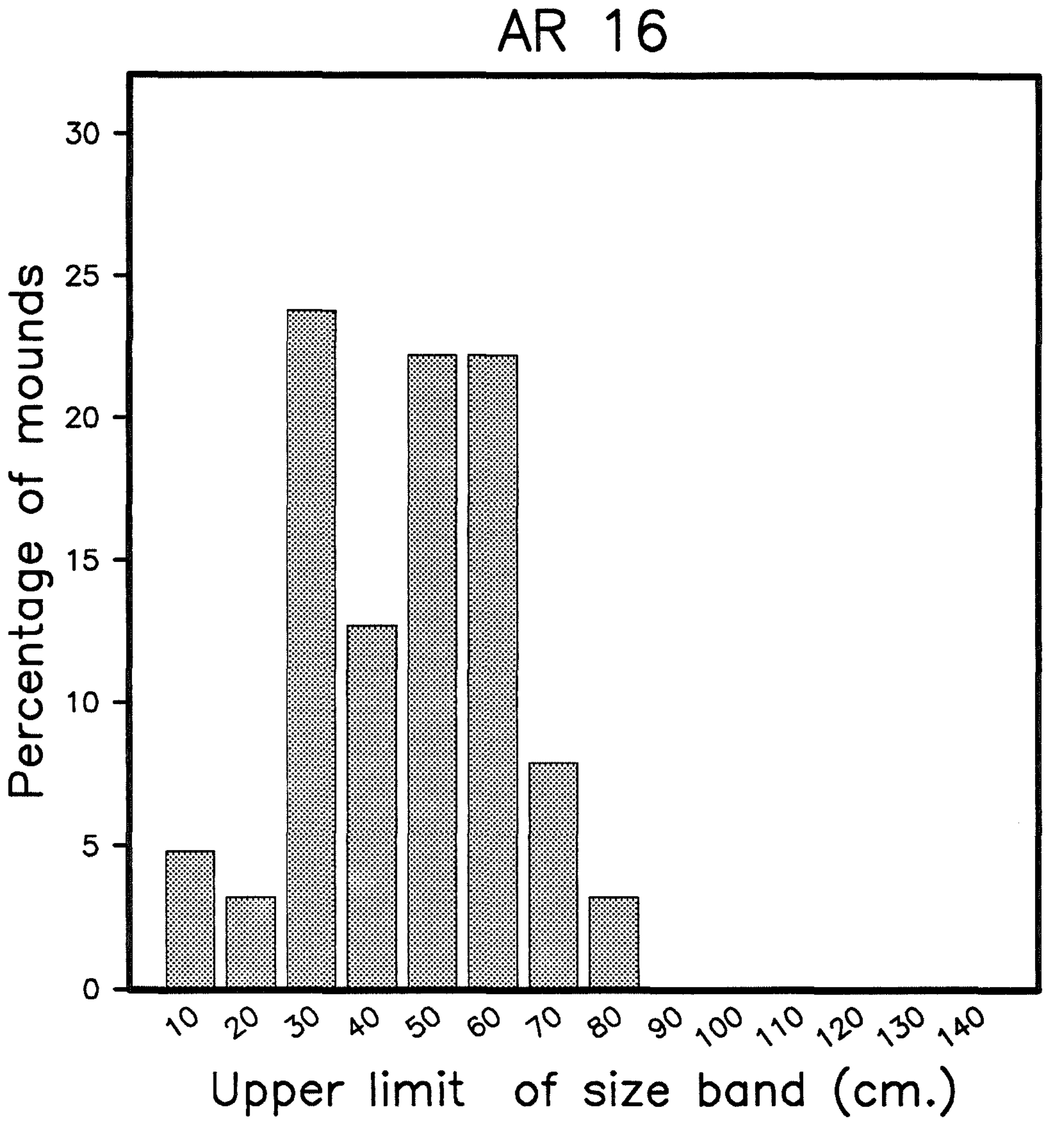
Figure 10.38.

<u>A view of quadrat 13, AR 16.</u>

As in the photograph of the last quadrat, AR 15, this photograph was taken just after Spring grazing. AR 16 lies next to AR 15 and the difference in their ant mound populations is considerable, as can be seen by comparing the photographs of the two areas.

Figure 10.39.

The distribution of mound sizes in AR 16.



A total of 63 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

ants found was as follows.

Colony 1.	11,809
Colony 2.	16,257
Colony 3.	5,712
Colony 4.	3,997
Colony 5.	15,991
Mean	10,753 +/- 2,549

The mean was 9,500 lower than in AR 15. It was also lower than in MD 7B, the only area in which mounds were dug up.

Numbers of worker ants found in core samples. A total of 50 cores were collected. The mean number of worker ants extracted per core was 6.12+/-2.86, lower than in AR 15. Only two of the Martin Down quadrats, MD 4A and 4B had lower numbers of ants extracted.

The sexual production of colonies.

The numbers of sexuals produced.

	1985		1986		1987	
	Gynes	Males	Gynes	Males	Gynes	Males
Colony 1.	101	30	204	1,227	92	2,978
Colony 2.	3	1,014	13	1,276	2	2,682
Colony 3.	33	1,456	429	1,834	48	5,190
Colony 4.	10	1	13	335	412	1,582
Colony 5.	0	0	135	376	38	1,461
Mean	29.4	500.2	158.8	1,009.6	118.4	2,778.6
SE	18.8	308.1	76.9	287.6	74.8	672.0

Similar in sexual productivity to AR 15 but generally low for the sample areas as a whole.

Head widths of male and gyne samples. All measurements are in millimetres.

	Males	Gynes
Colony 1.	0.71 +/- 0.006 (10)	1.46 +/- 0.019 (6)
Colony 2.	0.67 +/- 0.008 (10)	1.38 --- (1)
Colony 3.	0.70 +/- 0.012 (10)	1.42 +/- 0.014 (8)
Colony 4.	---	1.45 +/- 0.007 (10)
Colony 5.	---	---
Mean	0.69 +/- 0.012	1.43 +/- 0.018

Males and gynes were smaller than in AR 15. The males were some of the smallest found.

Dry weights of male and gyne samples. All measurements are in milligrams. The average dry weight of an individual ant is given.

	Males	Gynes
Colony 1.	0.305 (20)	10.42 (6)
Colony 2.	0.240 (20)	4.70 (1)
Colony 3.	0.350 (20)	9.80 (8)
Colony 4.	--	8.83 (10)
Colony 5.	--	--
Mean	0.298+/-0.032	8.44+/-1.29

Males and gynes were less heavy than in AR 15 and the gynes had the smallest mean dry weight of any sample area in which sexuals were collected in 1985.

Dates at which stages were first observed in 1986. The first small pupae were seen on 27/5, the first adult males on 16/7. The first gyne pupae were seen on 12/6 and the first adult gynes on 16/7.

10.16.2. Management. This is basically as described in Section 10.13. above. Thus at the time of the examination of the quadrats this area had received approximately 6,020 sheep days/hectare in total in the last three years. As this area lies next to AR 15 it provides an immediate contrast to it.

10.17.4. The physical environment.

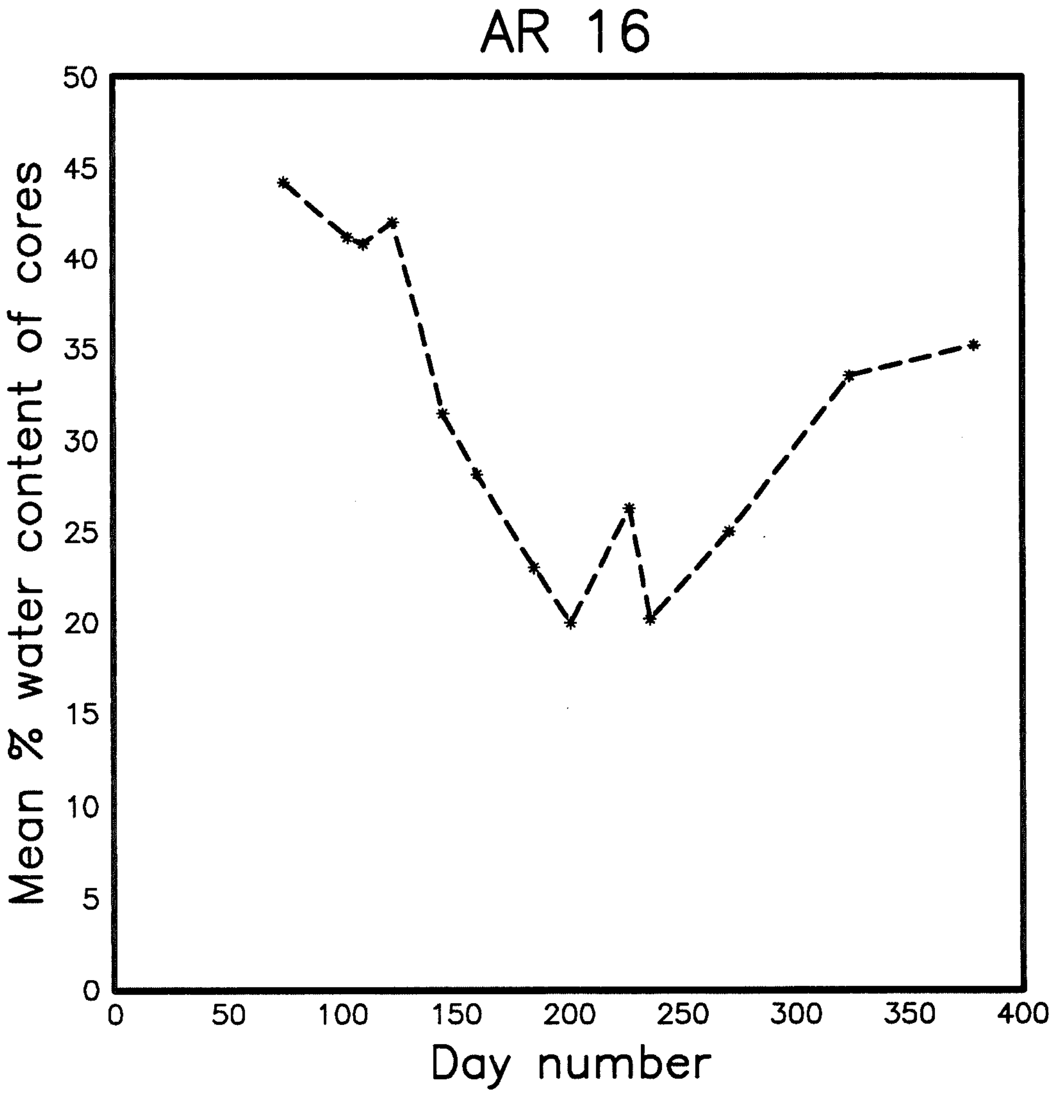
Altitude - 175 metres.
Slope - 11^{o}, facing 15^{o} (N).
Mean soil depth - 15.6 +/- 1.27 cm.
Mean soil pH - 7.64
Mean soil core density - 0.800+/-0.015 g/cm^{3}.

The soil core density was the highest recorded for any sample area in which cores were collected.

Water contents of soil - The maximum water content recorded was 44.23% on 15/3/89 and the minmum was 19.98% on 20/7/89. The changes in water contents of the cores are presented as a graph in Figure 10.40. Minimum and maximum water levels were slightly higher than in AR 15, but over the year there was no consistent difference between the two

Figure 10.40.

Water contents of soil cores collected in AR 16.



Day number 1 = 1/1/89.

Each point represents the mean water content of a sample of cores collected on that day. The dates of sampling, sample size, mean water contents and standard errors are given in Appendix 4.

areas.

The mean annual temperatures are summarised and presented in Figure 10.41. The physical characteristics of the environment in this area were very similar to those of AR 15, a relatively cool north facing slope.

10.16.4. The biological environment.

The flora. The flora of this area was similar to that of AR 15 but slightly less rich, with, in all, 54 species of plant recorded in this quadrat, compared to 68 in AR 15. A wide variety of plants such as *Medicago lupulina*, *Asperula cynanchica*, *Onionis repens* and *Plantago media* were absent from this area, in contrast to AR 15.

A single large bush of *Juniperus communis* was present in the area, at the southern border of the sample quadrat. Similar scrub species were present to AR 15 but these were less abundant.

Arrhenatherum elatius and *Brachypodium pinnatum* were quite common, but in clumps rather than spread out and more common at the edges of and outside of the chosen sample quadrat than in it. The ascomycete fungus *Xylaria hypoxylon* was also found in this sample area.

Rabbit droppings. The maximum mean number of droppings found on the mounds was 54.9 on 20/11, the minimum 5.9 on 16/3. Off the mounds the maximum was 1.3 on 25/5 and the minimum 0 on 3/5. The data is presented as a graph in Figure 10.42. The maximum number of droppings found on the mounds was the highest of the barn plots, although the overall level of rabbit activity appeared lower than in AR 11 and 12.

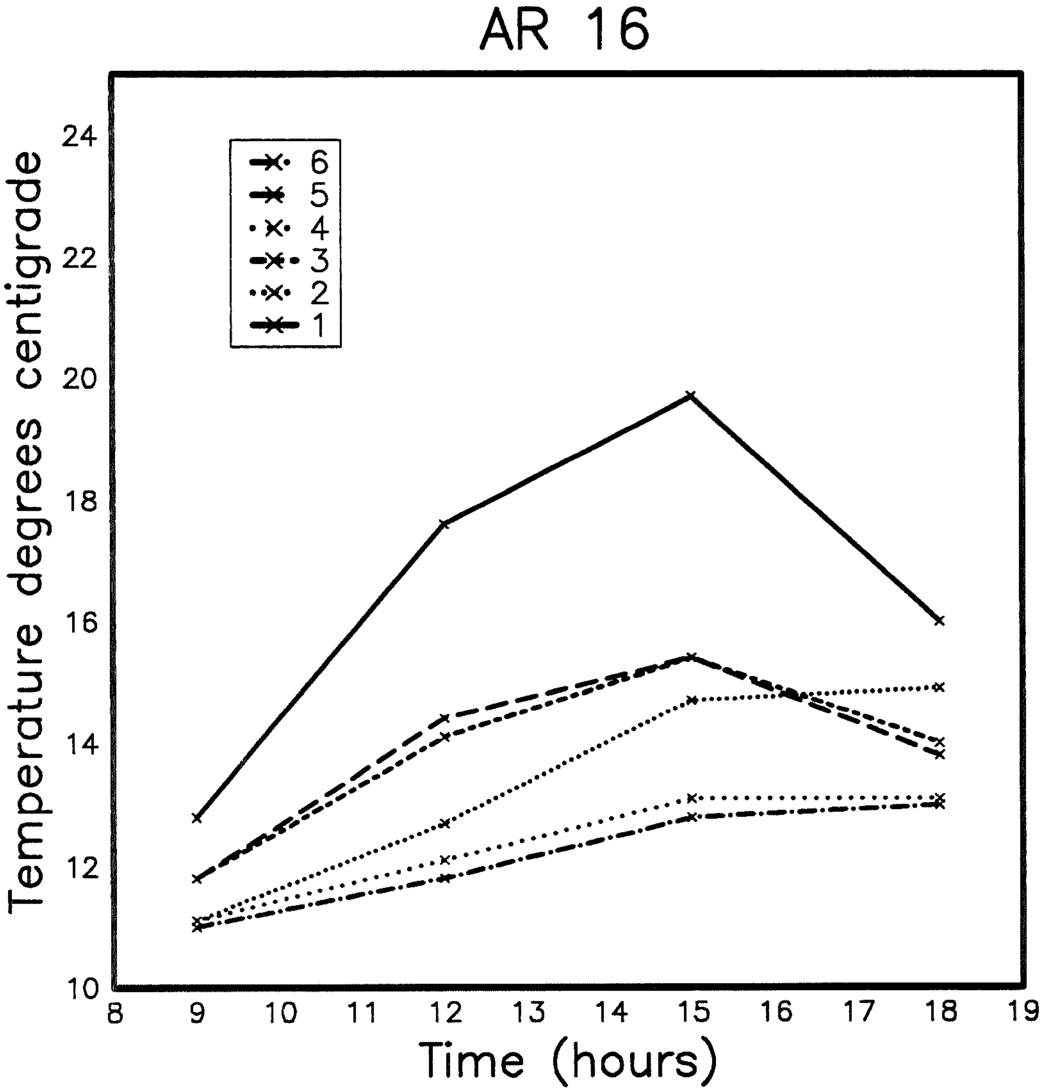
Root aphids and other invertebrates.

Root aphids. The mean number of root aphids extracted per core was 1.94+/-0.90. These comprised the following species.

Figure 10.41.

Summary of the annual mean temperatures in AR 16.

The mean annual temperatures at four times of day are shown. Times are British Summer Time. In the table below the graph, the mean figures are shown, together with the mean annual air temperatures. 1 - 6 refer the locations as follows.
1, south side of mound, top 1 cm. of soil. 2, same location 10 cm. deep. 3, north side of mound top 1 cm. of soil. 4, same location 10 cm. deep. 5, ground, top 1 cm. of soil. 6, same location 10 cm. deep.

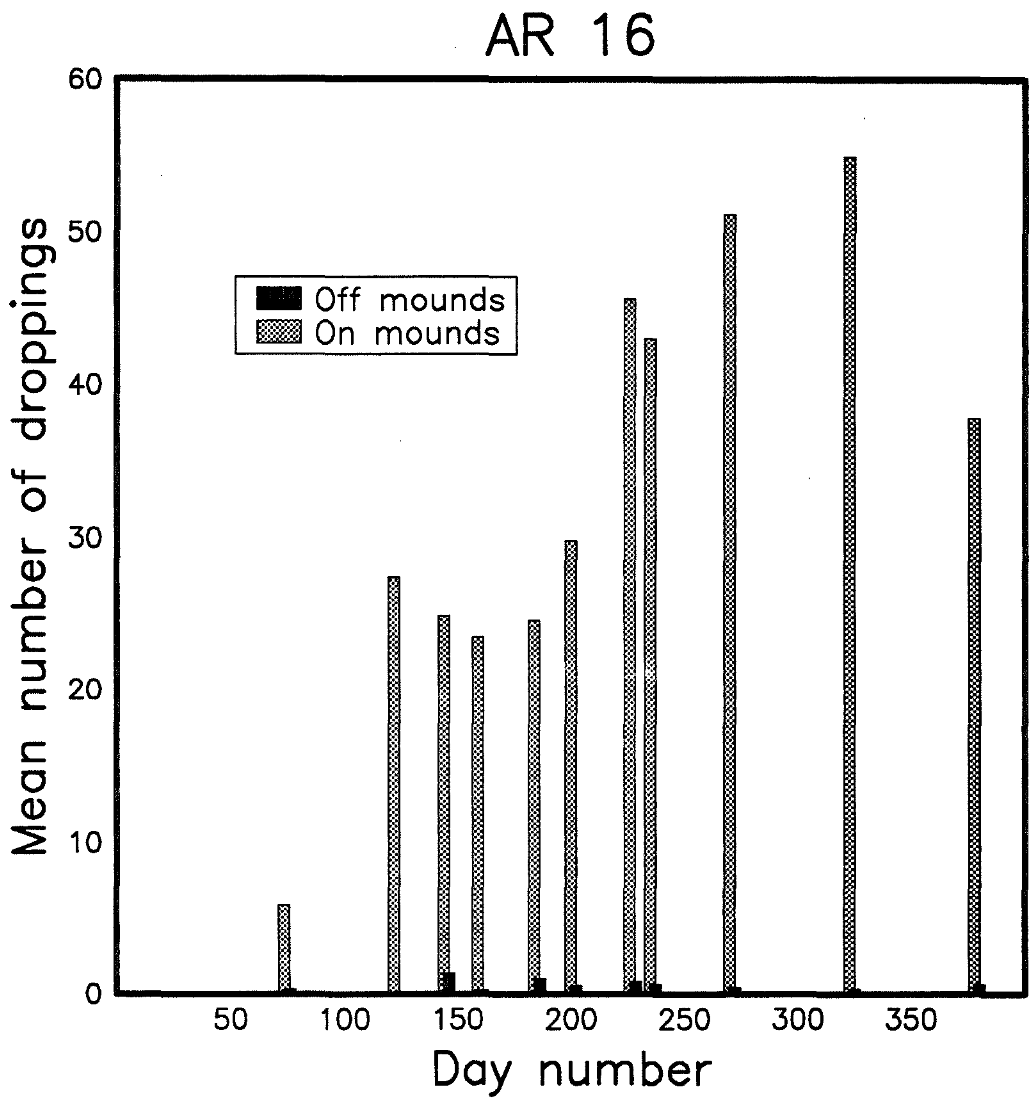


	1	2	3	4	5	6	AIR
9.00	12.8	11.1	11.8	11.1	11.8	11.0	10.8
12.00	17.6	12.7	14.1	12.1	14.4	11.8	13.5
15.00	19.7	14.7	15.4	13.1	15.4	12.8	14.6
18.00	16.0	14.9	14.0	13.1	13.8	13.0	13.6

The temperature raw data is given in Appendix Eight. The methods are further explained in section 7.3.2. Each point represents the mean of all the temperatures recorded in that location at that time throughout the year.

Figure 10.42.

Rabbit dropping densities in AR 16.



Day number 1 = 1/1/89.

Each bar represents the mean number of droppings recorded in 10, 25 x 25 cm. quadrats, except on 3/5/89 when the sample size was only 5 quadrats. The dates of sampling and numbers of droppings recorded in each quadrat are given in Appendix 10.

The sample area was grazed in April 1989.

Aphis vandergooti	2	(2.1%)
Brachycaudus spp.	8	(8.3%)
Forda formicaria	4	(4.2%)
Geoica setulosa	4	(4.2%)
Neanoecia zirnitsi	9	(9.4%)
Neotrama caudata	14	(14.6%)
Paracletus cimiciformis	3	(3.1%)
Paranoecia pskovica	2	(2.1%)
Unidentified	50	(52.1%)

This was the highest number of unidentified aphids in any sample area. Diversity was similar to AR 15 and high compared to the OWH south slope quadrats.

Other invertebrates. The mean numbers per core of the major groups of invertebrates extracted from the cores was as follows.

Mites	121.10+/-10.99
Collembolans	90.40+/- 7.65
Platyarthrus hoffmanseggi	0.38+/- 0.90
Geophilomorph centipedes	0.52+/- 0.12
Beetle larvae	0.88+/- 0.15
Ants (excluding *L. flavus*)	1.04+/- 0.73

This area supported the lowest number of geophilomorph centipedes and the second lowest number of mites on average. In contrast, it had the highest numbers of collembolans recorded per core.

Workers of *Myrmica ruginodis* and *Myrmica scabrinodis* were extracted from soil cores. *Lasius mixtus* queens were also noted in this area.

The pseudoscorpion *Pselaphochernes dubius* was extracted from cores as was the Tingid *Campylosteira verna*. The centipedes *Lithobius duboscqui* and *Shendyla nemorensis* were frequent. The dipluran *Campodea sylvestri* was also found.

10.17. Quadrat 14, AR 5.

Site - Aston Rowant.

Location - Western side of the reserve, on the opposite side of the M40 to all of the other sample areas on this reserve. The sample area was on top of Bald Hill (see Figure 5.3.).

10.18.2. The characteristics of the ant population.

The ant mounds.

No.of mounds - 75
Mean diameter of mounds (D) - 43.5 +/- 1.5 cm.
Mean height of mounds (H) - 4.8 +/- 0.3 cm.
Ratio D/H - 9.1
Area of quadrat occupied by the mounds - 3.0%
Mean above ground volume of soil in the mounds - 6.5 litres.
Mean distance to nearest neighbour - 1.33 +/- 0.06 metres.

In Figure 10.43. the percentage of the mounds in each 10cm. diameter bands is shown.

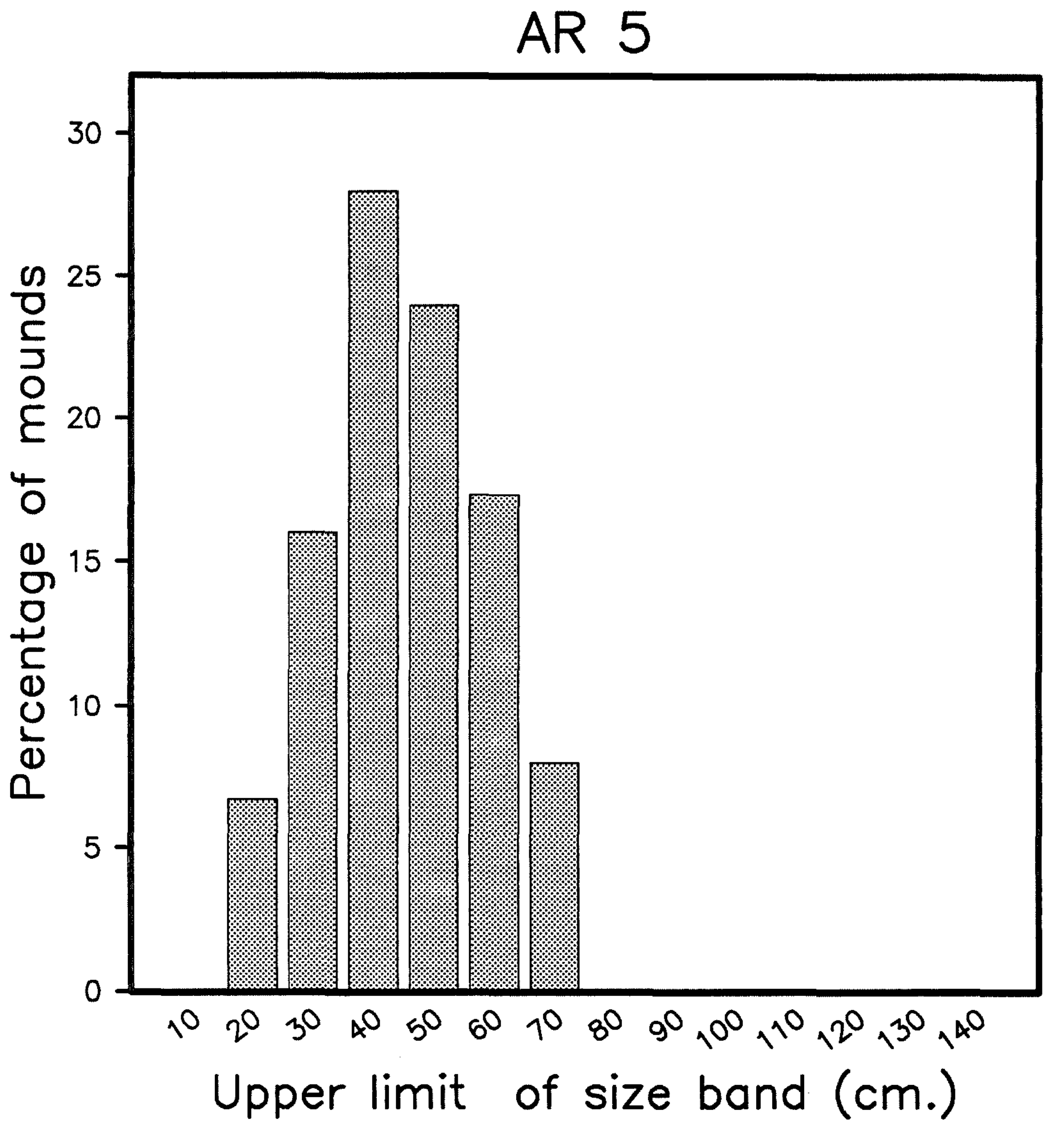
These mounds were average in diameter for the quadrats as a whole, but their mean height was very low. As the a result the D/H ratio was the highest of any of the sample quadrats and the mean volume low.

10.17.2. Management It is difficult to be precise in the management of this area as it has often been grazed as part of a much larger unit of pasture, some of which is better grassed and thus probably receives more attention from the sheep. Examination of the records for this area suggest that it received between 300 and 600 sheep days/hectare/year prior to the examination of the quadrats, with no particular time of year specified. Such a low level of grazing would be compatible with the poor grass growth. However, because of the low level of grazing scrub develops quite quickly and has to be regularly cut. It had been given such a cut just prior to the examination of the mounds in the sample quadrat in 1984.

Records also show that during the Second World War, 1939 to 1945,

Figure 10.43.

The distribution of mound sizes in AR 5.



A total of 75 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

this area was ploughed by the army.

10.17.3. The physical environment.

Altitude - 243 metres.
Slope - 11°, facing 250° (W).
Mean soil depth - 6.85 +/- 1.47 cm.
Mean soil pH - 7.80.

This area had the lowest recorded soil depth and the highest pH of any of the sample areas. The altitude of the area was also the highest of any of the sample areas.

10.17.4. The biological environment.

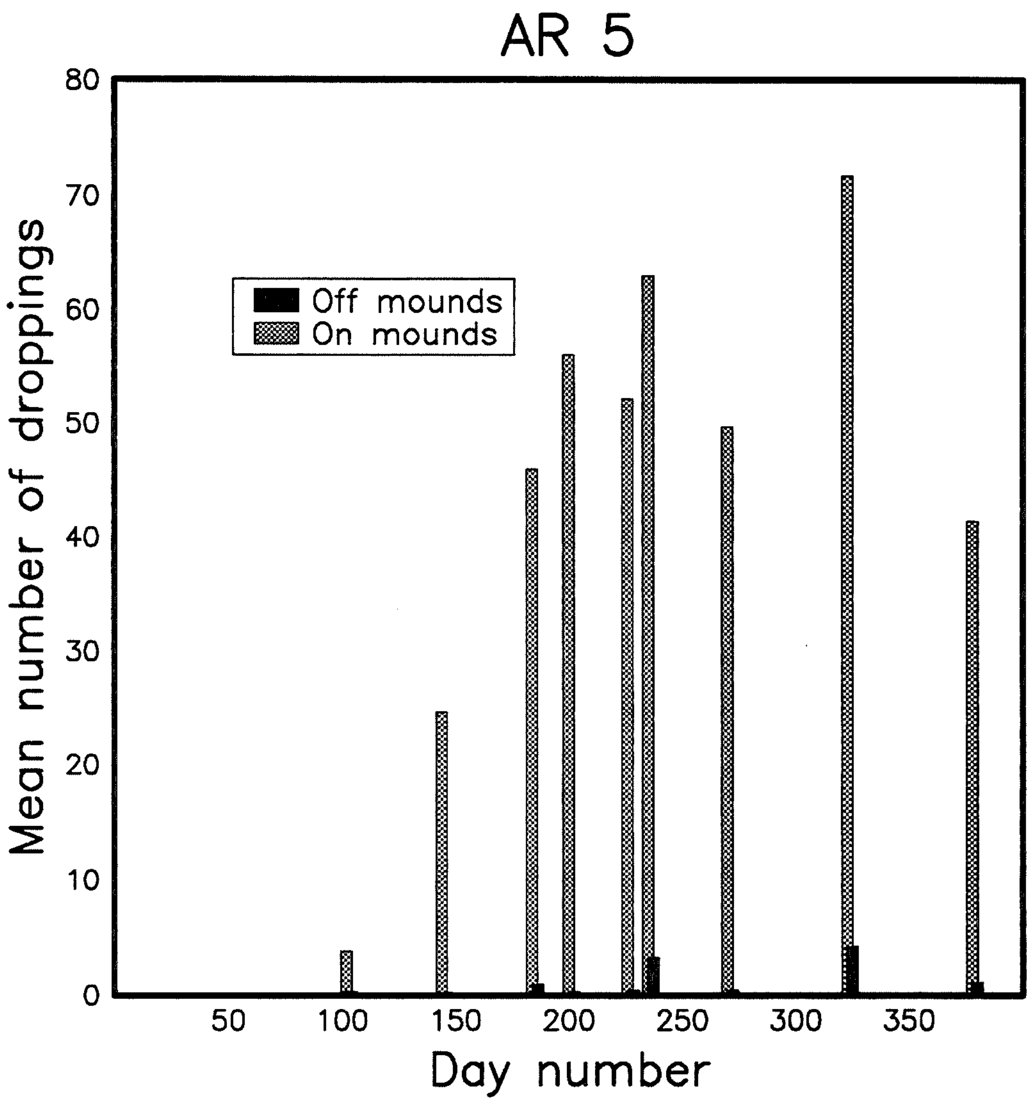
The flora. In this area there were considerable differences from any other of the quadrats. Plants found only in this sample area included *Centaurium erythraea*, *Echium vulgare*, *Trifolium dubium* and *Knautia arvensis*. The only liverwort found in any of the sample areas came from here, *Lophocolea bidentata*, a common liverwort of grasslands, often found in garden lawns for example. The grass cover appears sparse in places in this area and it may well be that it has not fully recovered from previous ploughing (see management above). The thin soil appeared dry and plants such as *Blackstonia perfoliata* and *Gentianella amarella*, which favour dry conditions, were abundant.

In all 48 species of plant were recorded in this quadrat, the flora being much less diverse than AR 15 and 16 for example.

Rabbit droppings. The maximum mean number of droppings recorded on the mounds was 71.7 on 20/11 and the minimum 3.8 on 13/4. Off the mounds the maximum was 4.2 on 20/11 and the minimum 0.2 on 25/5. The full data are presented in graphical form in Figure 10.44. The maximum number of droppings found on the mounds (71.7) was the highest figure recorded in any of the quadrats and rabbit activity was high in this sample area throughout the year.

Figure 10.44.

Rabbit dropping densities in AR 5.



Day number 1 = 1/1/89.

Each bar represents the mean number of droppings recorded in 10, 25 x 25 cm. quadrats. The dates of sampling and numbers of droppings recorded in each quadrat are given in Appendix 10.

10.18. Quadrat 15, AR NWS.

Site - Aston Rowant.

Location - Section 60 of the reserve at the crest of a hillside which sweeps around Beacon Hill from the Barn plots to face the motorway (M40) (see Figure 5.3.). A photograph of the area is shown in Figure 10.45.

10.18.1. The characteristics of the ant population.

The ant mounds.

No.of mounds - 119
Mean diameter of mounds (D) - 21.9 +/- 1.3 cm.
Mean height of mounds (H) - 4.7 +/- 0.4 cm.
Ratio D/H - 4.7
Area of quadrat occupied by the mounds - 1.6%
Mean above ground volume of soil in the mounds - 3.3 litres.
Mean distance to nearest neighbour - 0.87 +/- 0.04 metres.

Figure 10.46. shows the distribution of the sizes of the mounds in the quadrat.

This area had similarities with AR 12. It contained a large number of very small mounds. The mounds found in this quadrat were the smallest in diameter and the second smallest in height of all the quadrats. The percentage area of the quadrat covered by the mounds was the second smallest, with only OWH SS 7 lower, that area having a small number of large mounds present, in complete contrast to this area.

10.18.2. Management. Precise details of the management of this area were not clear. The grazing records examined suggested that it received a high level of grazing, probably comparable with Sample areas AR 12 and 16, at over 1,000 sheep days/ hectare/year. There is no set time of year at which the area was grazed. It forms part of a large area of pasture around the north to the south west of Beacon Hill. Sheep are placed on this area when grass is unavailable on

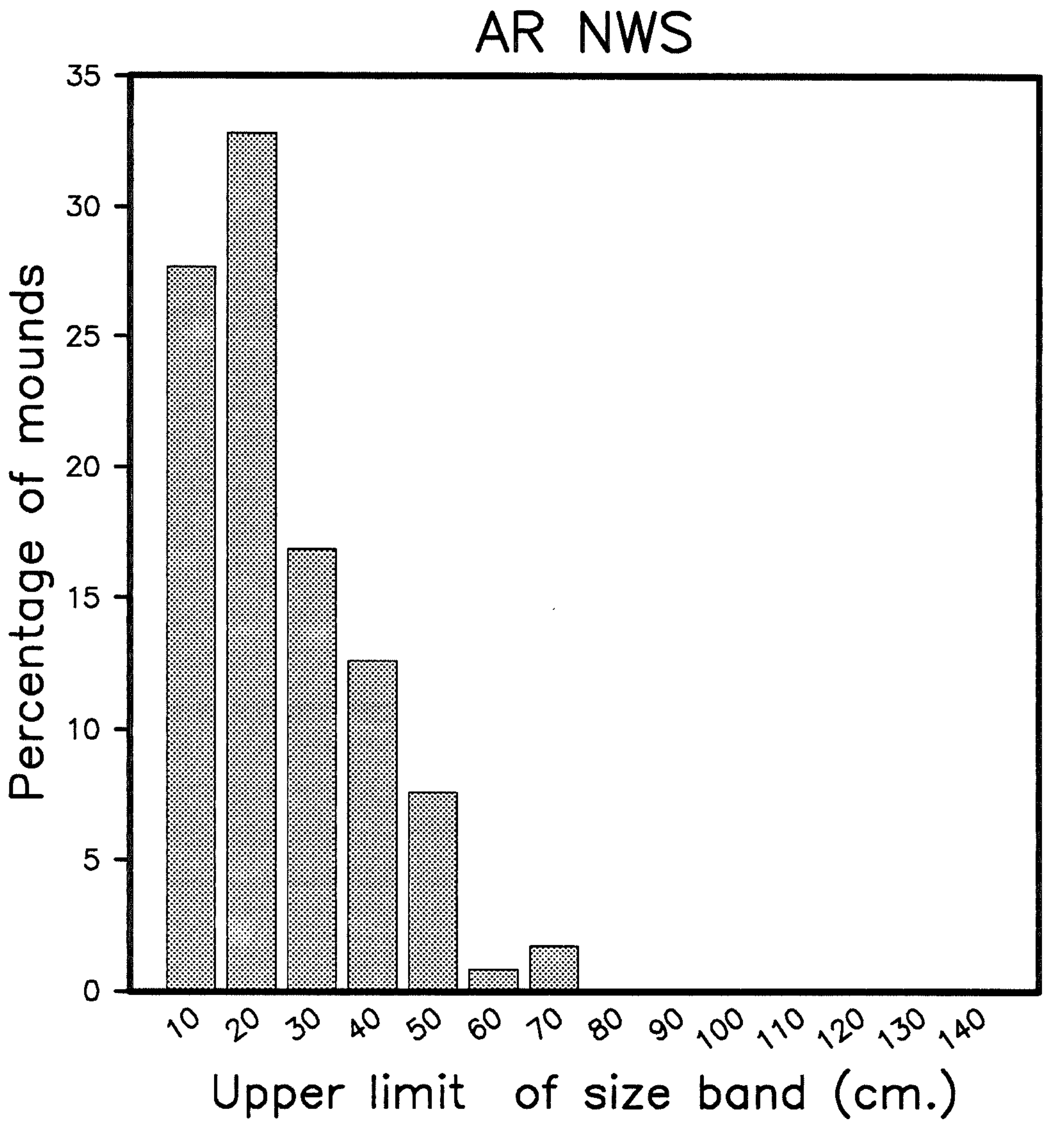
Figure 10.45.

A view of quadrat 15, AR NWS.

The sample quadrat was positioned towards the top of the hillside. As can be seen this is an exposed area and gives the appearance of being well grazed.

Figure 10.46.

The distribution of mound sizes in AR NWS.



A total of 119 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

other parts of the reserve.

10.18.3. The physical environment.

Altitude - 195 metres.
Slope - 38°, facing 295° (WNW).
Mean soil depth - 16.15 +/- 1.60 cm.
Mean soil pH - 7.59

This quadrat was on the steepest slope of any of the sample quadrats and had the second highest altitude.

10.18.4. The biological environment.

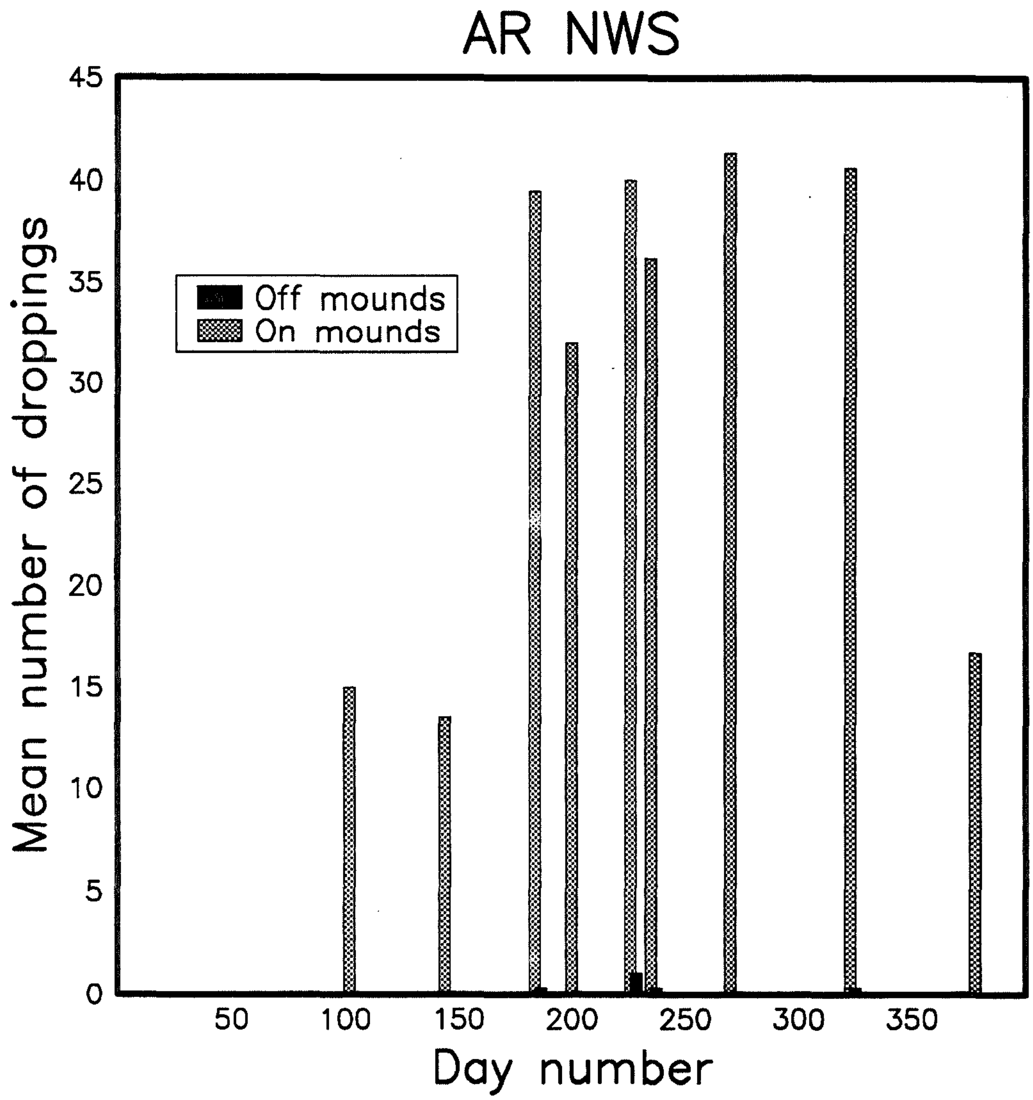
The flora. This area supported several plants not found in the other sample areas on this reserve, notably *Arenaria serpyllifolia*, *Bromus erectus*, *Poa annua*, *Dicranum bonjeani* and *Fissidens taraxifolius*. *Myosotis arvensis* was found growing on an ant mound in the sample area, although not within the quadrat area. This is a mixed selection of plants and indeed it seems hard to pin down the essential character of this area. The grassland is probably dominated by *Festuca* and *Avenula pubescens* which is typical enough but the *Bromus erectus* would suggest a lesser degree of grazing, the opposite suggested by the very small amount of *Brachypodium pinatum* present.

In all 46 species were recorded in this quadrat, the least of the Aston Rowant sample areas.

Rabbit droppings. The maximum mean number of dropping found on the mounds was 41.3 on 28/9/89 and the minimum 13.5 on 25/5/89. Off the mounds the maximum was 1.0 on 15/8/89 and the minimum 0 on 12/1/90. Droppings on the mounds remained high through the year. A substantial population of rabbits was known to be located at the top of the slope on which the sample area lay. The changes in the number of droppings recorded throughout the year are shown in Figure 10.47.

Figure 10.47.

Rabbit dropping densities in AR NWS.



Day number 1 = 1/1/89.

Each bar represents the mean number of droppings recorded in 10, 25 x 25 cm. quadrats. The dates of sampling and numbers of droppings recorded in each quadrat are given in Appendix 10.

10.19. Quadrat 16, MD 7B.

Site - Martin Down (MD).

Location - At the west of the reserve, a short distance south of the visitor car park (see Figure 5.5.). A photograph of the area is shown in Figure 10.48.

10.19.1. The characteristics of the ant population.

The ant mounds.

Number of mounds - 86
Mean diameter (D) - 38.2 +/- 1.77 cm.
Mean height (H) - 6.0 +/- 0.50 cm.
Ratio D/H - 6.4
Area of quadrat occupied by the mounds - 2.9%
Mean above ground volume of soil in the mounds - 7.7 litres.
Mean distance to nearest neighbour - 1.21 +/- 0.05 metres.

In Figure 10.49. the percentage of mounds in each 10 cm. diameter band is shown.

This quadrat had the most dense population of mounds at Martin Down. They were, though, the smallest in mean diameter and height. The D/H ratio was the highest at Martin Down and only two quadrats at Aston Rowant had higher values of this ratio (AR 12 and AR NWS). The mean volume of mounds was also low.

Estimates of colony sizes and worker ant density.

Mark-release-recapture estimates.

Set 1. July/August 1985.

Permission was not granted in time to carry out the procedure in this area. Being close to a public car park on the reserve some worry was expressed as to the use of radio-isotopes, with the required warning notices, in this area. After the Set 1 estimates had been made in other areas of the reserve, without problems, it was concluded that it would be safe to go ahead and permission was granted.

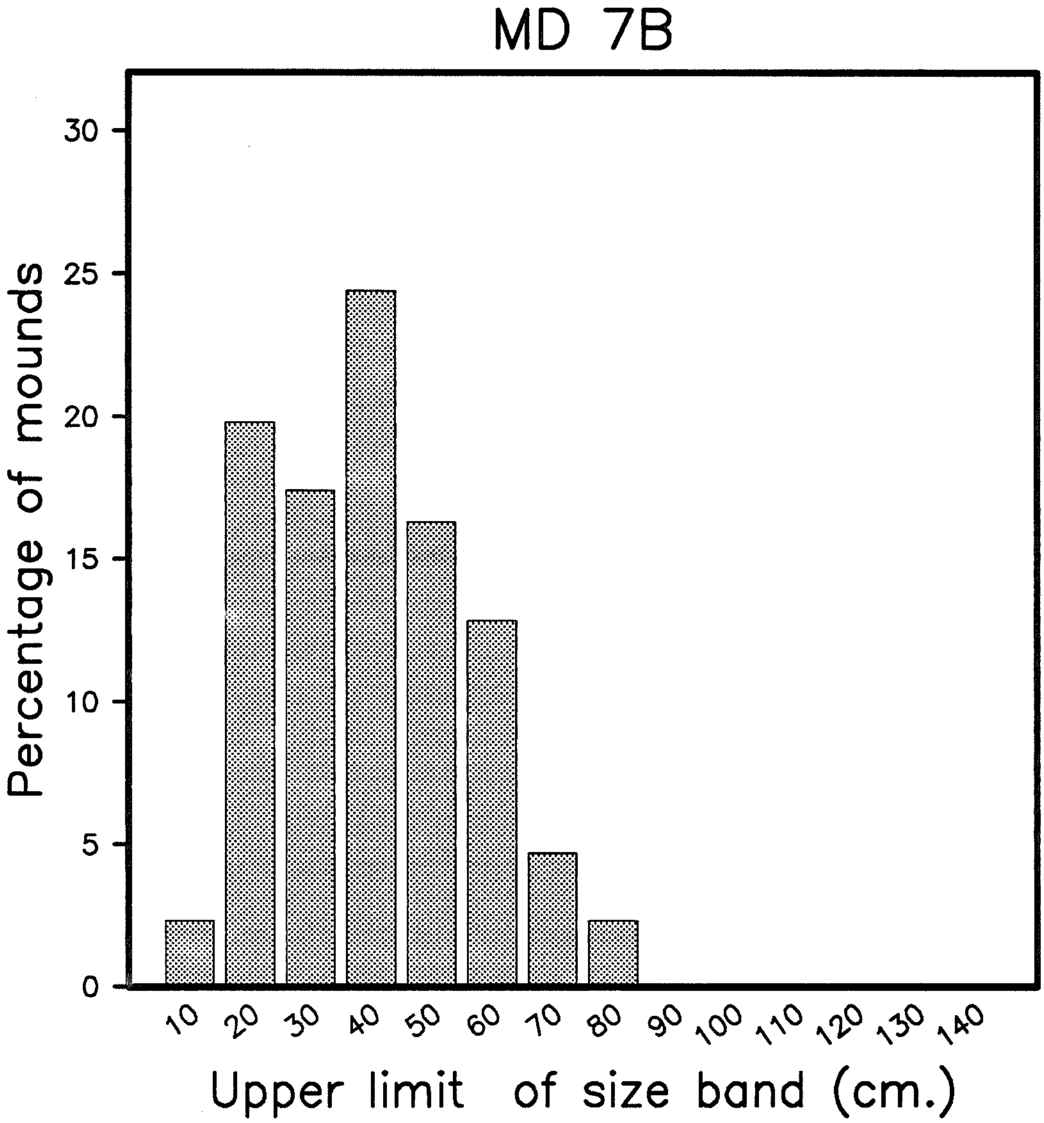
Figure 10.48.

A view of quadrat 16, MD 7B.

The sample quadrat was positioned in the centre of the view shown. The wooden poles, which are just visible, were placed around the quadrat. The tall grass is primarily *Bromus erectus*. The photograph was taken facing north-west.

Figure 10.49.

The distribution of mound sizes in MD 7B.



A total of 86 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

Set 2. September/October 1985.

Colony 1.	8,075	+/-	3,729
Colony 2.	7,374	+/-	3,577
Colony 3.	476	+/-	168
Colony 4.		-	
Colony 5.	30,762	+/-	7,876
Mean	11,665	+/-	6,592

In the mid-range of the means for the second set of estimates, although the estimate of 476 for colony 3 was not accurate, see Chapter Thirteen. No recaptures of marked ants were made in colony 4.

Digging up of colonies. Five colonies were dug up in this sample area. The number of worker ants found in each was as follows.

Colony 1.	34,936
Colony 2.	16,450
Colony 3.	9,545
Colony 4.	35,817
Colony 5.	6,372
Mean	20,624 +/- 6,241

Similar in mean numbers to AR 15, but much more variable individual colony sizes.

Numbers of worker ants found in core samples. The mean number of worker ants extracted per core over the whole year was 11.55+/-3.67. A total of 38 cores were collected. This was the second highest mean of ants extracted per core in any sample area, the highest being OWH C10 at 12.44 per core.

The sexual production of colonies.

The numbers of sexuals produced.

	1985		1986		1987	
	Gynes	Males	Gynes	Males	Gynes	Males
Colony 1.	134	594	0	3	10	908
Colony 2.	163	885	176	8	9	0
Colony 3.	156	695	798	1,599	**48	1,622
Colony 4.	250	1,641	259	1,345	412	838
Colony 5.	148	2,509	158	1,464	38	209
Mean	170.2	1,264.8	278.2	883.8	103.4	715.4
SE	20.5	361.1	136.5	360.8	77.5	286.6

** Thought not to be an accurate figure. Gynes and males were seen in an area away from the main centre of activity under the slate on this mound and it is possible that not all were collected.

Sexual production was high in 1985 in this sample area but subsequently declined.

Headwidths of male and gyne samples. All measurements are in millimetres.

	Males	Gynes
Colony 1.	0.69 +/- 0.013 (10)	1.46 +/- 0.011 (10)
Colony 2.	0.70 +/- 0.006 (10)	1.43 +/- 0.008 (10)
Colony 3.	0.74 +/- 0.009 (10)	1.40 +/- 0.018 (10)
Colony 4.	0.74 +/- 0.009 (10)	1.49 +/- 0.008 (10)
Colony 5.	0.72 +/- 0.010 (10)	1.39 +/- 0.007 (10)
Mean	0.72 +/- 0.010	1.43 +/- 0.02

The second largest mean male size, with only OWH C10 higher. The gynes were the same mean size as in several other sample areas.

Dry weights of male and gyne samples. All measurements are in milligrams.

	Males	Gynes
Colony 1.	0.280 (20)	9.690 (10)
Colony 2.	0.310 (20)	10.210 (10)
Colony 3.	0.375 (20)	9.210 (10)
Colony 4.	0.365 (20)	10.430 (10)
Colony 5.	0.365 (20)	9.810 (10)
Mean	0.339 +/- 0.019	9.870 +/- 0.212

The second heaviest males, again, only OWH C10 had a higher mean weight. The gyne dry weight was in the mid-range of the sample areas in which sexuals were collectedin 1985.

Dates at which stages were first recorded in 1986. In this quadrat the first small pupae were seen on 4/6 and the first males on 17/7. The first gyne pupae were seen on 26/6 and the first adult gynes on 8/7.

10.19.2. Management. As with the rest of the reserve organised grazing was restarted in 1979. Grazing was initially quite intense to reduce the accumulated grass growth but has since dropped. The aim of management in this area was to produce an area of taller vegetation with tussocks of grass, in which particular plants, invertebrates and small mammals could flourish. Of the plants this included *Primula veris* and *Filipendula vulgaris* and the invertebrates included *Argynnis aglaja* (Dark Green Fritillary Butterfly) and *Melanargia galathea* (Marbled White Butterfly). Adders (*Vipera berus*) were also noted in this area.

To accomplish this aim, this quadrat was grazed each year only in Winter, up to mid-March. It was usually grazed before Christmas, with a light follow up graze in late Winter. As a result this sample area had a total of 3840 sheep days/hectare in the three years prior to the examination of the quadrats. This level of grazing successfully reduced the grass growth to a more acceptable level and since then grazing has been reduced to around 700 sheep days/hectare/year.

The area has an interesting past history and it is essential to understand this to make sense of the current situation of the ants in the area. After the advent of myxomatosis this area was chained and harrowed by a local farmer. After this the grazing was much reduced and the grass became very tall, dominated by *Arrhenatherum elatius* and *Bromus erectus*.

10.19.3. The physical environment.

Altitude - 79 metres.
Slope - Flat (3.2^{o}).
Mean soil depth - 25.4 +/- 5.90 cm.
Mean soil pH - 7.53
Mean soil core density - 0.695+/-0.012 g/cm^3

This area was at the lowest altitude of any of the sample areas. The mean soil depth was by far the highest of the sample areas. The soil core density was the lowest at Martin Down.

The maximum mean water content recorded was 40.35% on 1/3/89 and the minimum 17.46% on 22/6/89. The changes in water contents of the cores throughout the year are shown in Figure 10.50. Compared to the other sample areas, in which cores were collected at Martin Down, this area had the highest maximum and minimum water contents.

The annual mean temperatures are presented in Figure 10.51. The mean air temperatures in this sample area were the warmest at Martin Down, but two areas, MD 4A and 4B were warmer in terms of ground temperatures.

10.19.4. The biological environment.

The flora. The vegetation in this area was generally quite tall with tall grasses and herbs such as *Bromus erectus* and *Filipendula vulgaris* dominating. Taller herb species such as *Agrimonia eupatoria*, *Rhinanthus minor*, *Senecio jacobaea* and *Centaurea scabiosa* were more abundant than short species such as *Asperula cynachica* and *Thymus serpyllum* but these latter were found in small patches of shorter vegetation within the sample area.

There was a poor moss flora in the area with only *Pseudoscleropodium purum* being at all abundant. In all 48 species of plant were recorded in this quadrat, with one odd species being found, *Triticum aestivum*, the Bread Wheat.

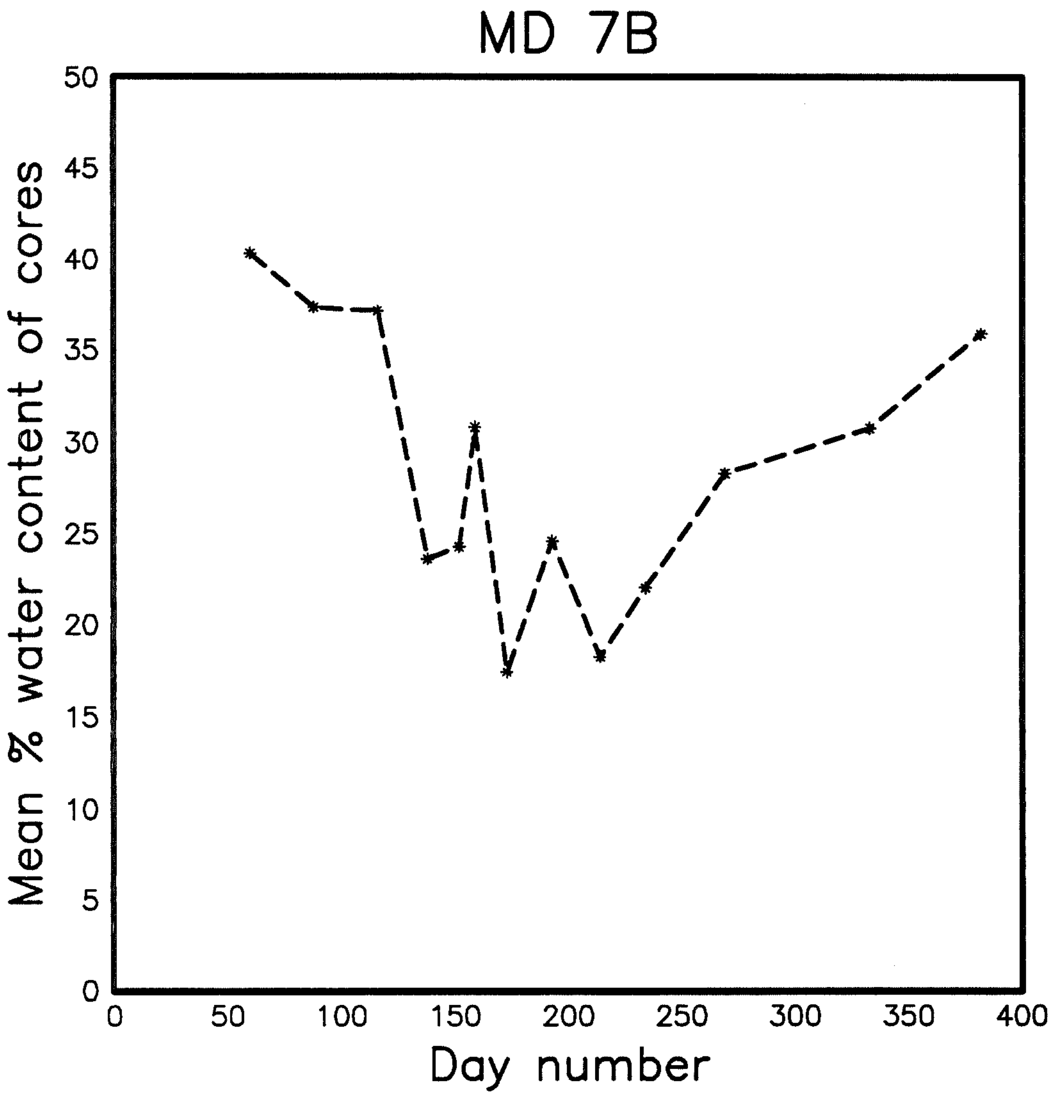
Rabbit droppings. Very few droppings were found in this area. The maximum on the mounds was a mean of only 0.4 per mound on 26/4 and frequently no droppings at all were found. Off the mounds only 3 droppings were found in 120 quadrats throughout the year. The full data are presented graphically in Figure 10.52. This area had the lowest number of rabbit droppings recorded of any of the sample areas.

Root aphids and other invertebrates.

Root aphids. The overall mean number of root aphids per core was

Figure 10.50.

Water contents of soil cores collected in MD 7B.



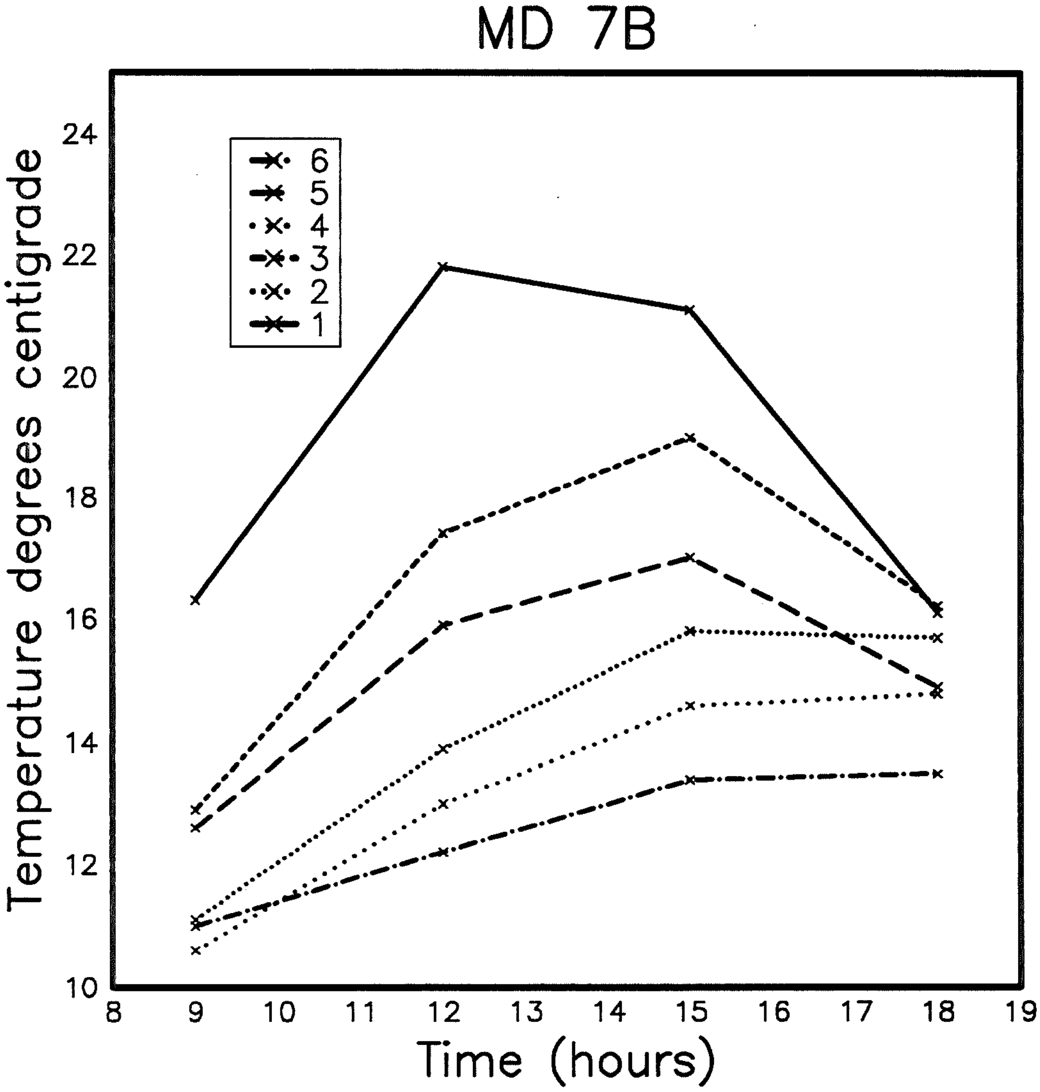
Day number 1 = 1/1/89.

Each point represents the mean water content of a sample of cores collected on that day. The dates of sampling, sample size, mean water contents and standard errors are given in Appendix 4.

Figure 10.51.

Summary of the annual mean temperatures in MD 7B.

The mean annual temperatures at four times of day are shown. Times are British Summer Time. In the table below the graph, the mean figures are shown, together with the mean annual air temperatures. 1 - 6 refer the locations as follows.
1, south side of mound, top 1 cm. of soil. 2, same location 10 cm. deep. 3, north side of mound top 1 cm. of soil. 4, same location 10 cm. deep. 5, ground, top 1 cm. of soil. 6, same location 10 cm. deep.

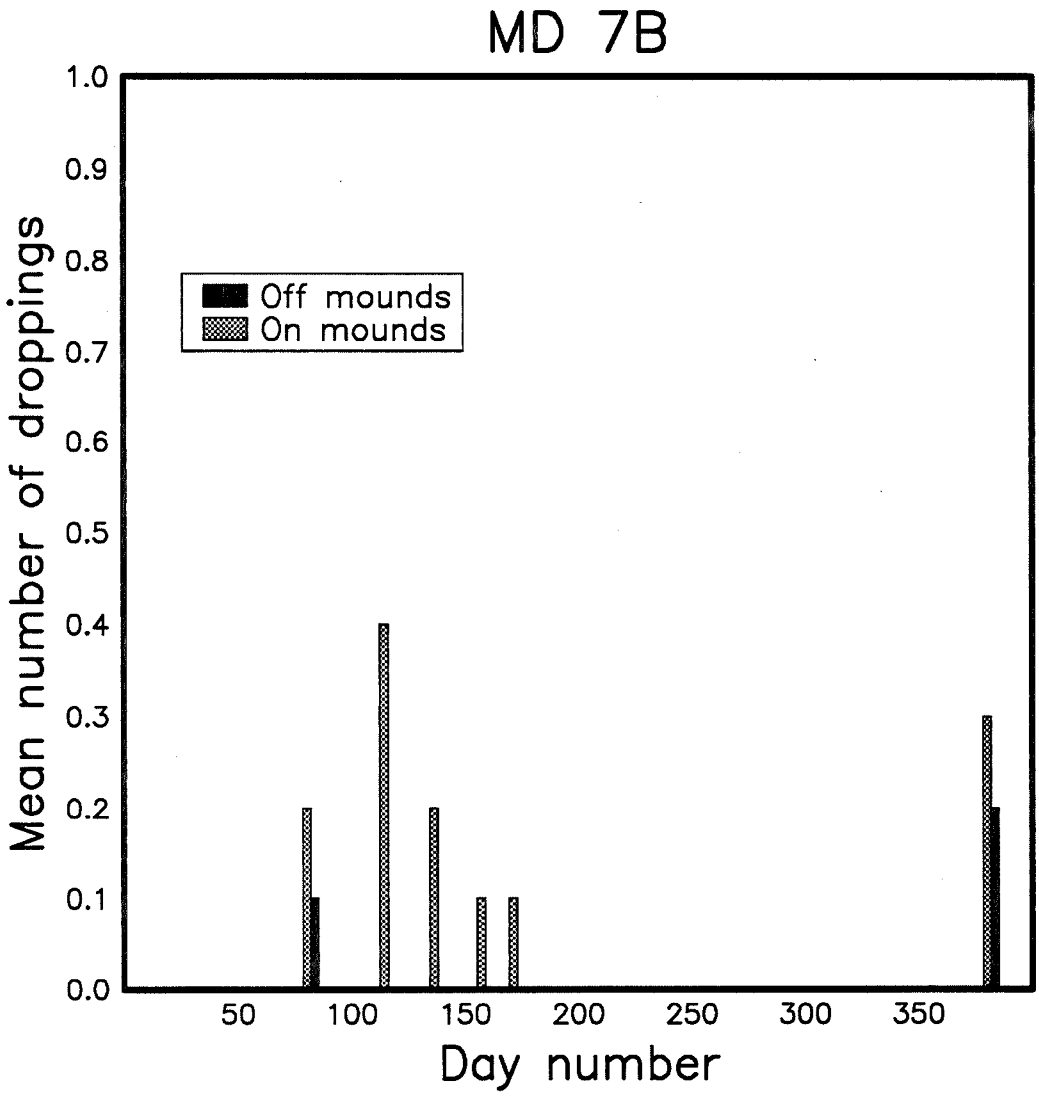


	1	2	3	4	5	6	AIR
9.00	16.3	11.1	12.9	10.6	12.6	11.0	12.2
12.00	21.8	13.9	17.4	13.0	15.9	12.2	15.4
15.00	21.1	15.8	19.0	14.6	17.0	13.4	16.5
18.00	16.1	15.7	16.2	14.8	14.9	13.5	14.1

The temperature raw data is given in Appendix Eight. The methods are further explained in section 7.3.2. Each point represents the mean of all the temperatures recorded in that location at that time throughout the year.

Figure 10.52.

Rabbit dropping densities in MD 7B.



Day number 1 = 1/1/89.

Each bar represents the mean number of droppings recorded in 5 or 10, 25 x 25 cm. quadrats. The dates of sampling and numbers of droppings recorded in each quadrat are given in Appendix 10.

This area was grazed in April 1989. Note the scale of the Y axis. Dropping numbers were very low in this sample quadrat. No droppings at all were recorded on several occasions between days 200-350.

3.37+/-1.31, the highest of the Martin Down sample areas, and only bettered by OWH C10 of the other sample areas in which cores were collected. This included confirmed records of the following species.

Aphis vandergooti	1	(0.8%)
Dysaphis spp.	2	(1.6%)
Forda formicaria	2	(1.6%)
Forda marginata	3	(2.4%)
Geoica eragrostidis	3	(2.4%)
Neanoecia corni	7	(5.5%)
Neanoecia zirnitsi	69	(54.3%)
Neotrama caudata	9	(7.1%)
Paranoecia pskovika	1	(0.8%)
Tetraneura ulmi	17	(13.4%)
Trama troglodytes	1	(0.8%)
Unidentified	12	(9.4%).

A high diversity of species but clearly dominated by Neanoecia zirnitsi.

Other invertebrates. The mean numbers per core of the major invertebrate groups was as follows:

Mites	129.16+/-10.93
Collembollans	28.66+/- 3.16
Platyarthrus hoffmanseggi	0.74+/- 0.33
Geophilomorph centipedes	1.29+/- 0.22
Beetle larvae	1.05+/- 0.17
Ants (excluding L. flavus)	2.42+/- 2.34

The ant species collected was Myrmica scabrinodis. The mean number of collembollans per core was the lowest of any of the sample areas from which cores were collected. The pseudoscorpion Roncus lubricus was extracted from cores collected in this area. The centipedes Schendyla nemorensis and Lithobius duboscqui were abundant. The myrmecophilus beetle Claviger testacea was found to be present in reasonable numbers in the ant mounds of this quadrat. It was found in at least 2 of the 5 marked mounds. This beetle is thought to be of a restricted distribution and uncommon in this Country. It was a new record for the reserve. Beetles appeared under the slates in spring when large numbers of workers and brood were also present.

10.20. Quadrat 17, MD 4A.

Site - Martin Down.

Location - At the foot of the north facing escarpment slope, 50 metres from MD 4B which is on its eastern side (see Figure 5.5.). A photograph of the area is shown in Figure 10.53.

10.20.1. The characteristics of the ant population.

The ant mounds

Number of mounds - 61
Mean diameter of mounds (D) - 40.6 +/- 1.8 cm.
Mean height of mounds (H) - 9.2 +/- 0.8 cm.
Ratio D/H - 4.4
Area of quadrat occupied by the mounds - 2.2%
Mean above ground volume of soil in the mounds - 11.7 litres.
Mean distance to nearest neighbour - 1.44 +/- 0.07 metres.

The distribution of the mound sizes is shown in Figure 10.54.

The number of mounds in the sample quadrat was the lowest of any of the Martin Down quadrats. Only two quadrats on the south slope at OWH had less mounds in them. The mounds also had the lowest mean height and covered the least area of the quadrat at Martin Down.

Worker ant densities. The mean number of worker ants extracted per core was 3.86+/-0.78. This was the second lowest figure for any of the sample quadrats in which cores were collected. Only MD 4B was lower.

The sexual production of colonies.

The numbers of sexuals produced. Sexuals were only collected in 1987 in this quadrat.

	1987	
	Gynes	Males
Colony 1.	341	4,329
Colony 2.	954	4,083
Colony 3.	163	7,602
Colony 4.	**71	92
Colony 5.	1,325	3,861
Mean	570.8	3,993.4
SE	243.4	1,191.2

** Thought not to be an accurate figure. As in colony 3 in MD 7B there

Figure 10.53.

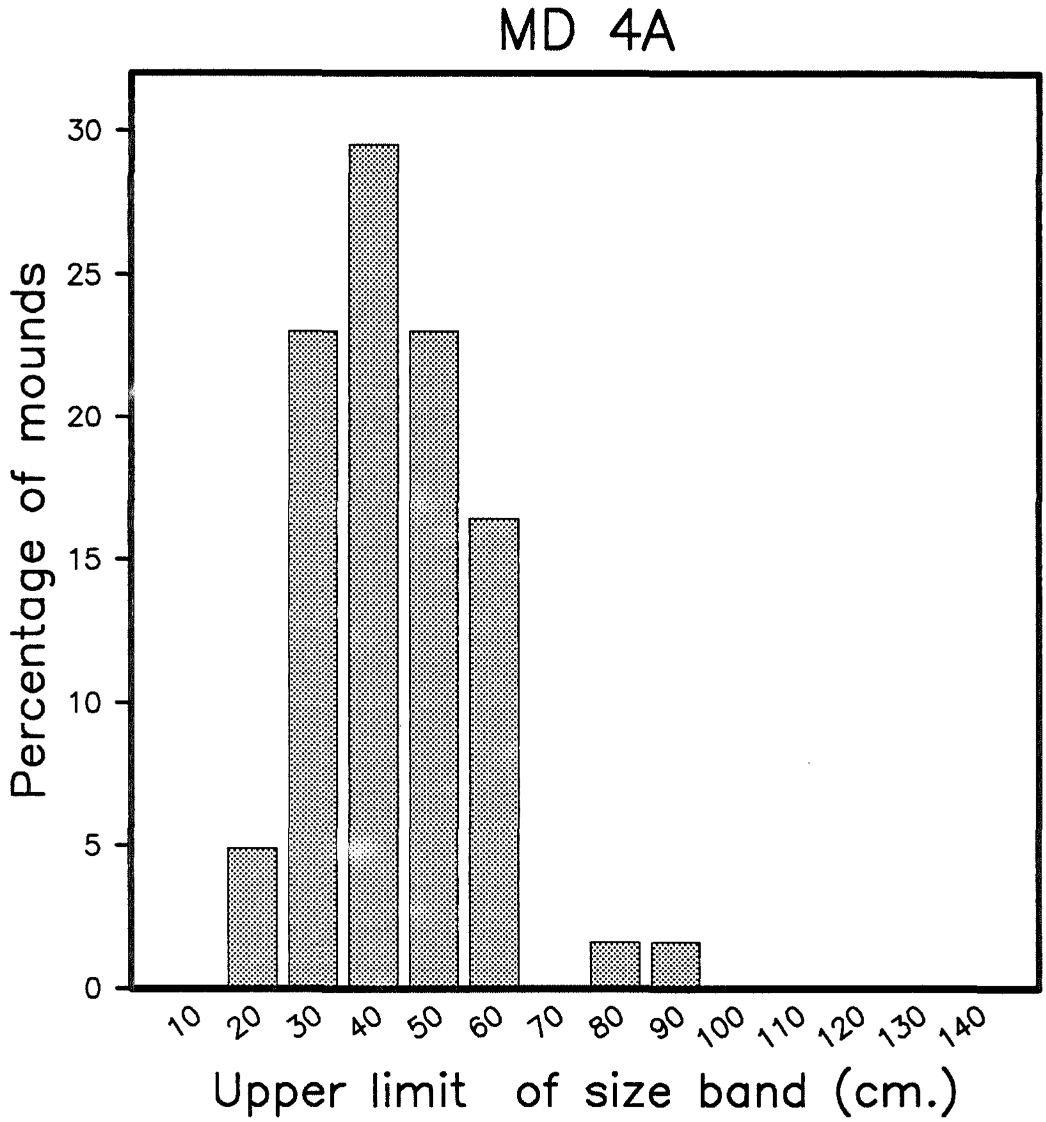
A view of quadrat 17, MD 4A.

The photograph was taken facing south-east. The sample quadrat was positioned in middle distance of the area shown. The vegetation in this area is typically in the sort of condition shown here. Bromus erectus is present at a high density, but not as dominant as in MD 7B (see Figure 10.48.).

Electric sheep fencing is shown in the foreground of the photograph. The use of this fencing has enabled reserve managers to graze precise areas, without permanent fencing being present.

Figure 10.54.

The distribution of mound sizes in MD 4A.



A total of 61 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

appeared to be more than one centre of activity of this colony.

The colonies in this area were highly productive. Colony 3 produced more males than any colony in any of the quadrats in any of the three years; colony 5 produced more gynes than any other colony.

10.20.2. Management. In 1979 this area was dominated by rank *Bromus erectus* with large patches of *Brachypodium pinnatum* also present. Grazing has since reduced these to some extent and a richer flora is developing, as evidenced by the number of species of plant recorded. There is though still a problem with *B. pinnatum* and this is occasionally cut mechanically using a large tractor mounted mower. Grazing is generally carried in winter at a low stocking rate (approximately 50 sheep/hectare for 3 weeks), followed by a short period in spring to remove the first flush of growth of *B. erectus*.

In the three years prior to the examination of the ant mounds in the sample quadrats grazing had averaged 1,205 sheep days/hectare/year. Prior to that, in order to reduce the coarse grass growth, grazing had been more intense with, a mean of 1,635 sheep days/hectare/year from the restart of grazing in 1979 to 1981. The most recent grazing period in this area had been in January to March 1984 with a total of 1,260 sheep days/hectare grazed. Since 1984 grazing has been reduced.

In the more distant past this area, along with MD 4B was the site of a rifle range (Ordnance Survey 1:25,000 map).

The aim of management in this area is to produce a medium height vegetation (intermediate to MD 4B and 7B) where the species of butterfly which are found in this area of the reserve can flourish. These species of butterfly, the Marbled White (*Melanargia galathea*) the Dark Green Fritillary (*Argynnis aglaja*) and the Meadow Brown

(*Maniola jurtina*) all prefer such taller vegetation.

10.20.3. The physical environment.

Altitude - 104 metres.
Slope - 6°, facing 320° (NW).
Mean soil depth - 18.3 +/- 0.72 cm.
Mean soil core density - 0.704+/-0.017 g/cm^3
Mean soil pH - 7.54

The maximum mean water content recorded from the cores was 40.1% on 26/4/89 and the minimum 17.1% on 2/8/89. The changes in water content of the cores throughout the year are shown in Figure 10.55. Only OWH SS 11 had a lower minimum recorded water content, and the low maximum figure would suggest that this was quite a dry area.

The mean annual temperatures are presented in Figure 10.56. The temperature regime was similar to that in MD 4B.

10.20.4. The biological environment.

The flora. The flora in this sample area is dominated by *Bromus erectus*, with large patches of *Brachypodium pinnatum* also present. The vegetation is thus generally quite coarse and tall. At the time of the examination of the ant mounds it appeared that the vegetation was a little less tall than when the flora was examined.

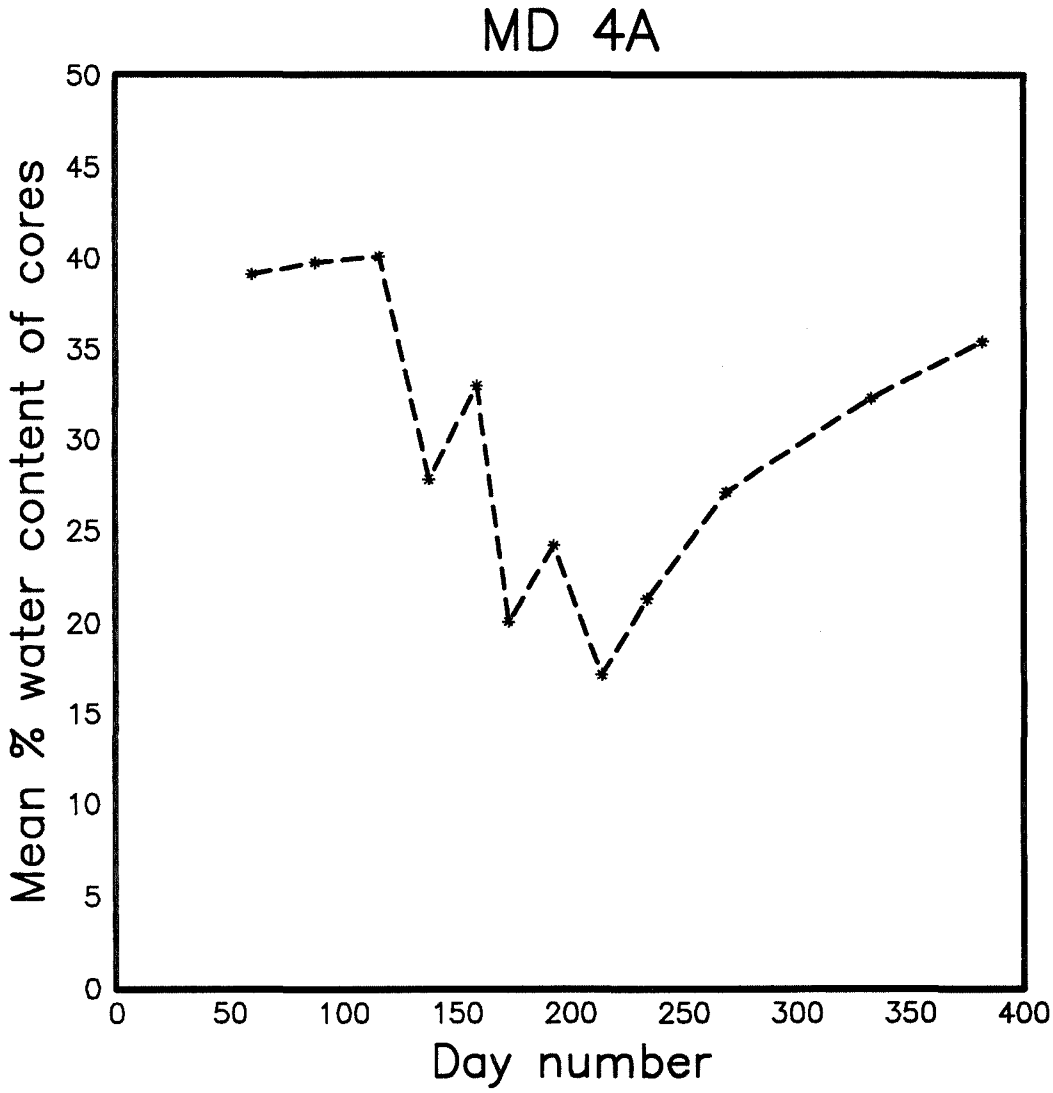
As with MD 7B the taller herbs and grasses dominated in this sample area although *Filipendula vulgaris* was absent. The flora is slightly richer than 7B with for example *Origanum vulgare*, *Achillea millefolium* and *Campanula rotundifolia* coming in.

In all 54 species of plant were recorded in this quadrat.

Rabbit droppings The maximum mean number of rabbit droppings found on the mounds was 58.8 on 22/8 and the minimum 1.6 on 23/3. Off the mounds the maximum was 6.7, although this was an erratic figure due to the location of a single sample quadrat in a rabbit scraping full of droppings. The next highest mean number of droppings found off the

Figure 10.55.

Water contents of soil cores collected in MD 4A.



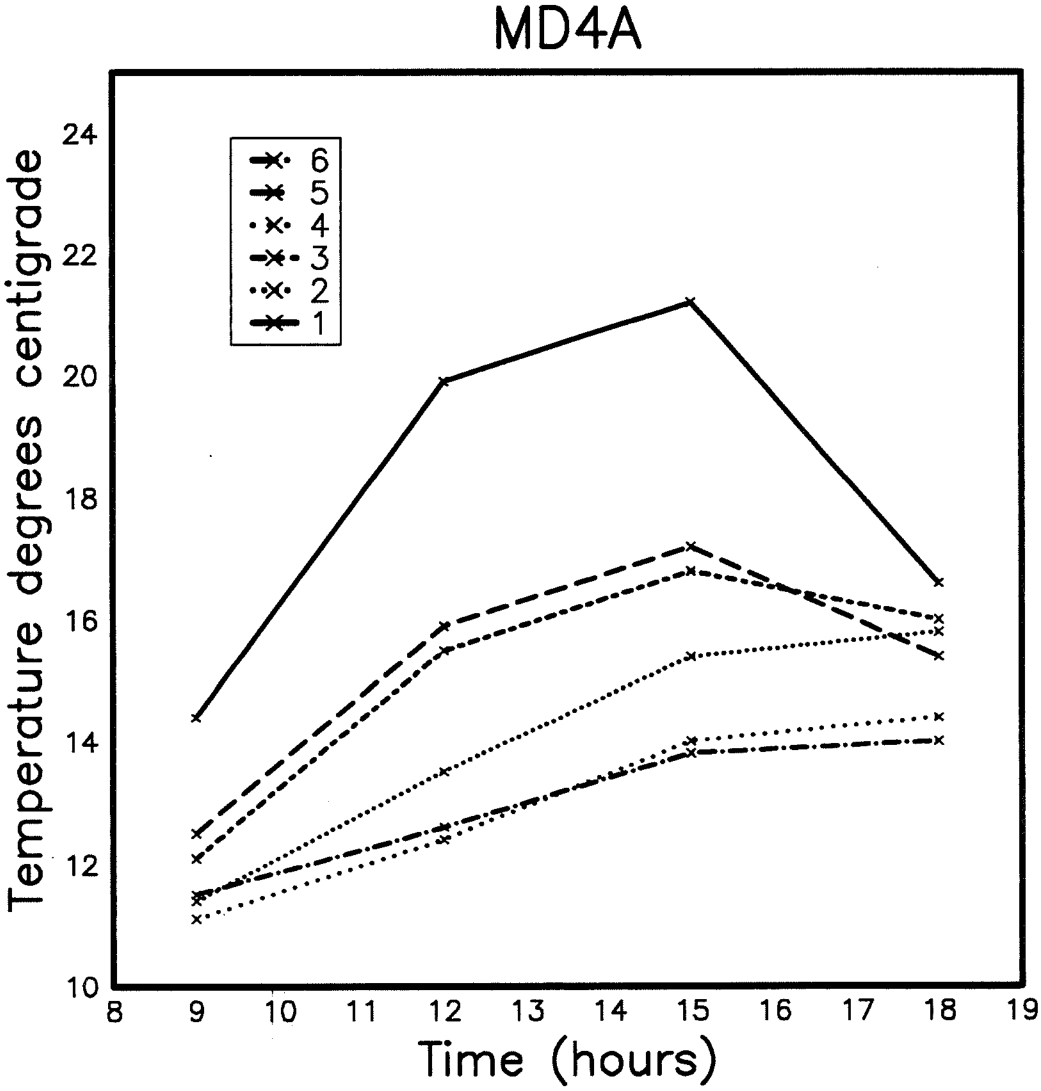
Day number 1 = 1/1/89.

Each point represents the mean water content of a sample of cores collected on that day. The dates of sampling, sample size, mean water contents and standard errors are given in Appendix 4.

Figure 10.56.

Summary of the annual mean temperatures in MD 4A.

The mean annual temperatures at four times of day are shown. Times are British Summer Time. In the table below the graph, the mean figures are shown, together with the mean annual air temperatures. 1 - 6 refer the locations as follows.
1, south side of mound, top 1 cm. of soil. 2, same location 10 cm. deep. 3, north side of mound top 1 cm. of soil. 4, same location 10 cm. deep. 5, ground, top 1 cm. of soil. 6, same location 10 cm. deep.



	1	2	3	4	5	6	AIR
9.00	14.4	11.4	12.1	11.1	12.5	11.5	11.7
12.00	19.9	13.5	15.5	12.4	15.9	12.6	14.9
15.00	21.2	15.4	16.8	14.0	17.2	13.8	15.9
18.00	16.6	15.8	16.0	14.4	15.4	14.0	14.4

The temperature raw data is given in Appendix Eight. The methods are further explained in section 7.3.2. Each point represents the mean of all the temperatures recorded in that location at that time throughout the year.

mounds was only 0.8 on 1/3. The minimum number was 0 found on several occasions. In Figure 10.57. the changes in the numbers of droppings recorded throughout the year are shown.

Root aphids and other invertebrates.

Root aphids. A total of 35 cores were collected. The mean number of root aphids extracted from the cores was 2.49+/-0.73, the lowest in any of the sample areas. The diversity of species found was also amongst the lowest.

The following root aphids were recorded from the cores taken from this quadrat.

Brachycaudus spp.	2	(2.7%)
Geoica eragrostidis	2	(2.7%)
Neanoecia corni	19	(25.3%)
Neanoecia zirnitsi	9	(12.0%)
Neotrama caudata	16	(21.3%)
Tetraneura ulmi	1	(1.3%)
unidentified	21	(28.0%)

Other invertebrates. The mean numbers per core of the major groups of invertebrates found, was as follows.

Mites	118.03+/- 7.12
Collembollans	47.66+/- 5.46
Platyarthrus hoffmanseggi	0.14+/- 0.07
Geophilomorph centipedes	1.34+/- 0.27
Beetle larvae	0.85+/- 0.21
Ants (excluding L. flavus)	3.29+/- 3.29

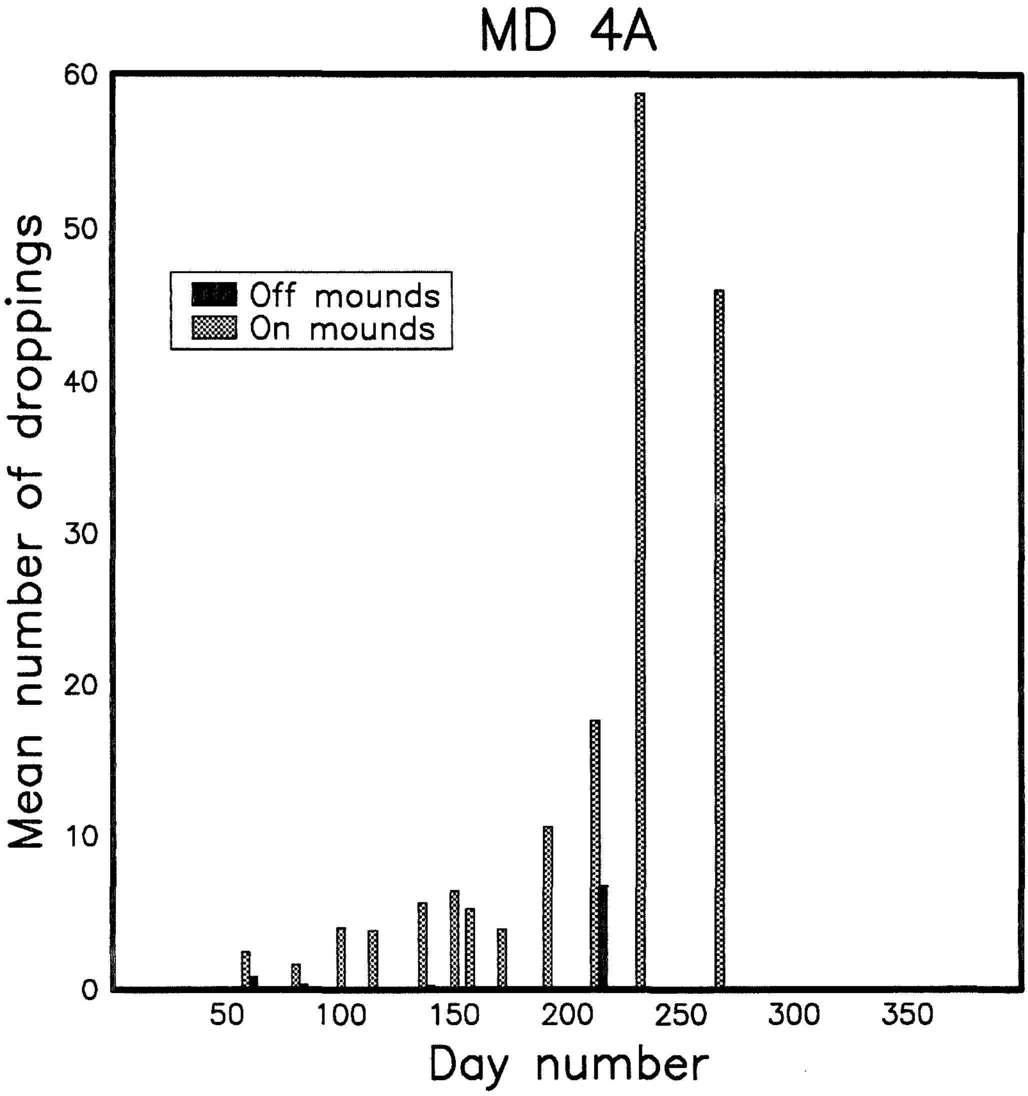
The species of ant found was Myrmica scabrinodis. The mean numbers of ants found per core were the highest of any sample area, but this is misleading as ants were only found in one core, probably a core which happened to pass through a nest of M. scabrinodis.

The number of geophilomorph centipedes was the equal highest (with OWH C10).

The pseudoscorpion Roncus lubricus was extracted from cores collected in this area, as were the Tingids Acalypta parvula and

Figure 10.57.

Rabbit dropping densities in MD 4A.



Day number 1 = 1/1/89.

Each bar represents the mean number of droppings recorded in 5 or 10, 25 x 25 cm. quadrats. The dates of sampling and numbers of droppings recorded in each quadrat are given in Appendix 10.

This area was grazed in November 1989.

Campylosteira verna. The centipedes Schendyla nemorensis and Lithobius duboscqui were also collected.

The beetle Claviger testacea was also present in this area.

10.21. Quadrat 18, MD 4B.

Site - Martin Down.

Location - At the foot of the north facing escarpment slope, adjacent to MD 4A (see Figure 5.5.). A photograph of the area is shown in Figure 10.58.)

10.21.1. The characteristics of the ant population.

The ant mounds.

Number of mounds - 67
Mean diameter of mounds (D) - 41.0 +/- 2.0 cm.
Mean height of mounds (H) - 9.5 +/- 0.6 cm.
Ratio D/H - 4.3
Area of quadrat occupied by the mounds - 2.6%
Mean above ground volume of soil in the mounds - 12.0 litres.
Mean distance to nearest neighbour - 1.37 +/- 0.08 metres.

In Figure 10.59. the percentage of mounds in each 10 cm. diameter band is shown.

The population of mounds in this sample quadrat was very similar to that in OWH SS 4.

Estimates of colony sizes and worker ant density.

Mark-release-recapture.

Set 1. July/August 1985		Set 2. September/October 1985.	
Colony 1.	3,624 +/- 559	Colony 1.	4,816 +/- 1,056
Colony 2.	19,200 +/- 9,540	Colony 2.	23,241 +/- 4,666
Colony 3.	17,400 +/- 10,002	Colony 3.	4,784 +/- 1,480
Colony 4.	19,678 +/- 7,982	Colony 4.	6,833 +/- 1,048
Colony 5.	2,490 +/- 378	Colony 5.	4,680 +/- 849
Mean.	12,478 +/- 3,869	Mean	8,871 +/- 3,615

The means of both sets of estimates were in the mid-range of the sample areas in which estiamtes were made. The second estimates mean was slightly lower than in MD 7B.

Numbers of worker ants found in the core samples. The mean number of worker ants extracted per core was 2.60+/-0.66. A total of 35 cores were collected. This was the lowest number of ants per core in any of the sample areas in which cores were collected.

Figure 10.58.

A view of quadrat 18, MD 4B.

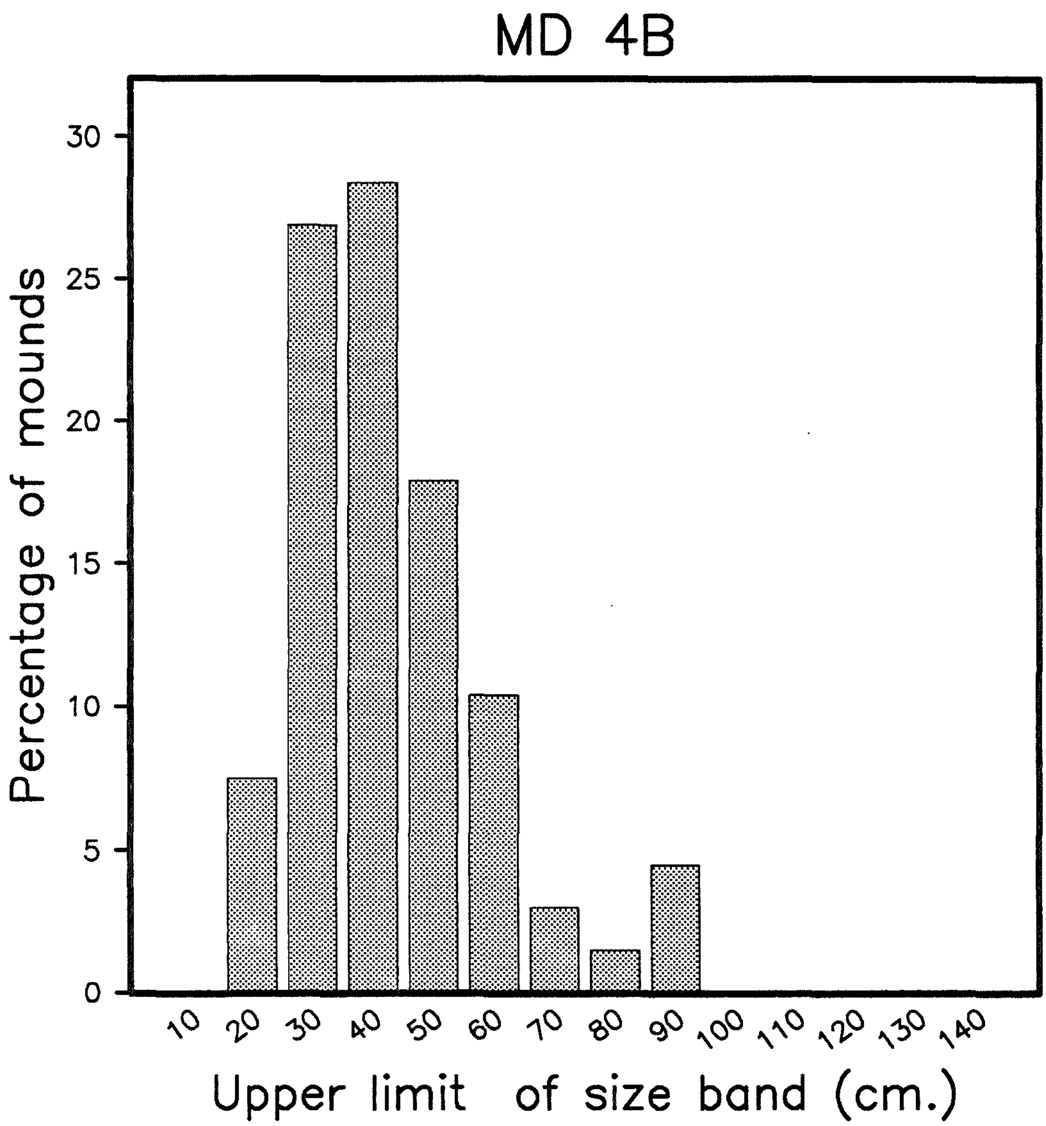
The photograph was taken facing south. The sample quadrat was positioned in middle distance of the area shown, just in front of the person standing in the middle of the photograph.

The photograph was taken in Winter and the vegetation is not as well grazed down as it usually is.

Mole hills can be seen on the right hand side of the picture. Mole activity was more common in the Martin Down sample areas than those on the other reserves.

Figure 10.59.

The distribution of mound sizes in MD 4B.



A total of 67 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

Sexual production of colonies.

The numbers of sexuals.

	1985		1986		1987	
	Gynes	Males	Gynes	Males	Gynes	Males
Colony 1.	16	759	82	400	26	1,403
Colony 2.	0	100	22	2,643	13	2
Colony 3.	11	2,092	256	1,910	494	3,060
Colony 4.	101	1,587	53	2,245	119	2,314
Colony 5.	42	1,664	4	1,132	11	0
Mean	34.0	1,240.4	83.4	1,666.0	132.6	1,355.8
SE	18.1	357.6	45.2	402.3	92.5	612.2

Headwidths of male and gyne samples. All measurements are in millimetres.

	Males	Gynes
Colony 1.	0.70 +/- 0.006 (10)	1.40 +/- 0.006 (10)
Colony 2.	0.68 +/- 0.006 (10)	---
Colony 3.	0.70 +/- 0.009 (10)	1.39 +/- 0.017 (9)
Colony 4.	0.68 +/- 0.008 (10)	1.39 +/- 0.009 (10)
Colony 5.	---	--
Mean	0.69 +/- 0.005	1.39 +/- 0.003

The mean sizes of the males and gynes was the smallest of any of the sample areas in which sexuals were collected in 1985.

Dry weights of male and gyne samples. All measurements are in milligrams. The average dry weight of an individual ant is given with the total sample size.

	Males	Gynes
Colony 1.	0.290 (20)	8.850 (10)
Colony 2.	0.265 (20)	---
Colony 3.	0.353 (19)	9.722 (9)
Colony 4.	0.274 (19)	9.010 (10)
Colony 5.	---	---
Mean	0.300+/-0.020	9.194+/-0.268

The dry weights of the males and gynes were in the mid-range of the sample areas.

Dates of production of sexuals. In this quadrat the first small pupae were seen on 4/6 and the first males on 8/7. The first gyne pupae were seen on 26/6 and the first adult gynes on 8/7.

10.21.2. Management. The aim of management in this sample area is to produce a short herb rich turf.

In 1979 this area was again dominated by rank Bromus erectus. It has since been grazed heavily both in summer and winter to return it to short Festuca dominated grassland. It has become increasingly herb rich since 1979.

The area is generally hard grazed in Winter for approximately three weeks and again in Summer, thus keeping turf height short throughout the year. In the three years prior to the examination of the quadrat there were a total of 3,335 sheep days/hectare grazed. This was slightly reduced afterwards (1985/6) but has since returned to a high level.

Like MD 4A this area too is noted as being the site of a rifle range in the Ordnance survey 1:25,000 map.

10.21.3. The physical environment.

Altitude - 104 metres.
Slope - flat (3.5^{o}).
Mean soil depth - 14.15 +/- 0.65 cm.
Mean soil pH - 7.51
Mean soil core density - 0.711+/-0.013 g/cm^3

The maximum mean water contents recorded from the cores were 40.07% on 1/3/89 and 40.19% on 29/3/89. The minimum water content was 17.16% on 2/8/89. The changes in water contents of the cores throughout the year are shown in Figure 10.60. Again, these figures would suggest this was quite a dry area, comparable with MD 4A and OWH SS 4, but not as dry as OWH SS 11.

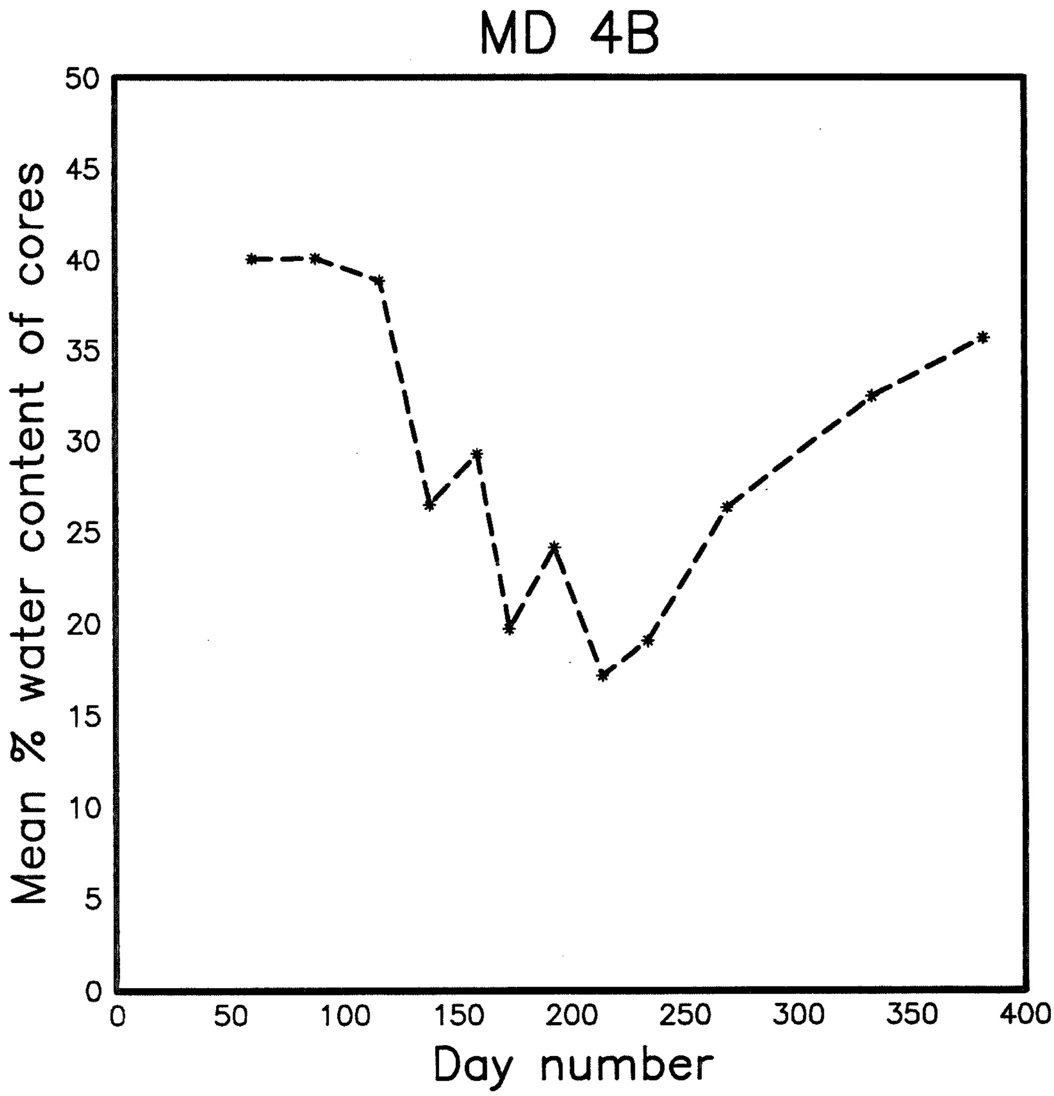
The mean annual temperatures are presented in Figure 10.61.

10.21.4. The biological environment.

The flora. This quadrat was heavily grazed in June 1989 and so as a result no small 1 metre quadrat with estimates of percentage cover were examined. The grazing removed much of the vegetation and would

Figure 10.60.

Water contents of soil cores collected in MD 4B.



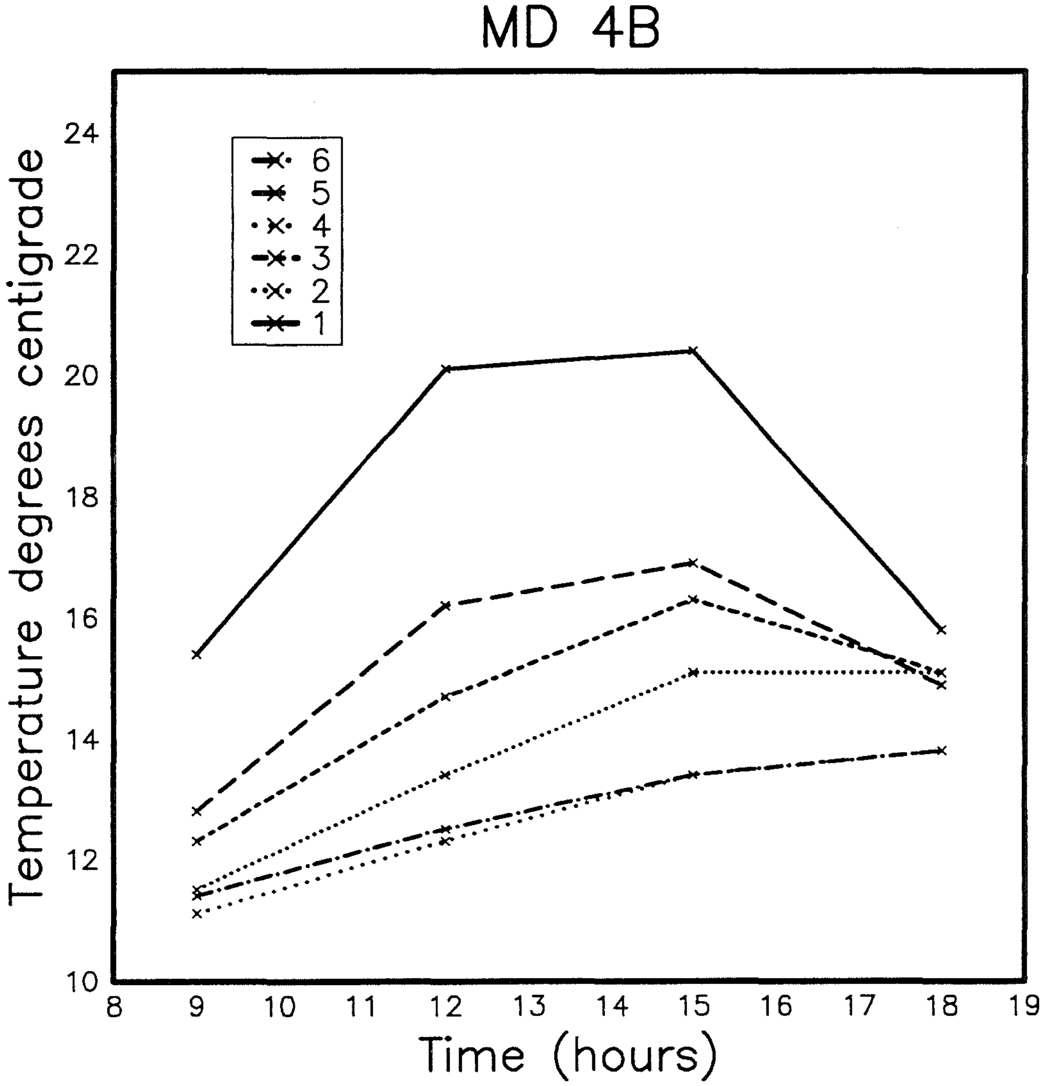
Day number 1 = 1/1/89.

Each point represents the mean water content of a sample of cores collected on that day. The dates of sampling, sample size, mean water contents and standard errors are given in Appendix 4.

Figure 10.61.

Summary of the annual mean temperatures in MD 4B.

The mean annual temperatures at four times of day are shown. Times are British Summer Time. In the table below the graph, the mean figures are shown, together with the mean annual air temperatures. 1 - 6 refer the locations as follows.
1, south side of mound, top 1 cm. of soil. 2, same location 10 cm. deep. 3, north side of mound top 1 cm. of soil. 4, same location 10 cm. deep. 5, ground, top 1 cm. of soil. 6, same location 10 cm. deep.



	1	2	3	4	5	6	AIR
9.00	15.4	11.5	12.3	11.1	12.8	11.4	11.8
12.00	20.1	13.4	14.7	12.3	16.2	12.5	14.9
15.00	20.4	15.1	16.3	13.4	16.9	13.4	15.8
18.00	15.8	15.1	15.1	13.8	14.9	13.8	13.7

The temperature raw data is given in Appendix Eight. The methods are further explained in section 7.3.2. Each point represents the mean of all the temperatures recorded in that location at that time throughout the year.

thus have produced a distorted picture. This may also have led to the missing of some plant species from the area for the presence and absence analysis.

However, the vegetation consisted of a much shorter turf than the previous two areas with Bromus erectus much less dominant. In all 42 species of plant were recorded in this quadrat, probably less than expected due to the heavy mid-season grazing. The plants recorded were almost all short herbs such as Asperula cynanchica, Crepis capillaris, Thymus serpyllum and Hieracium pilosella. H. pilosella was found here and in MD 3B areas of short turf, but not in the taller vegetation of MD 4A and 7B. There was much less scrub in this area than the others examined, with only a very small amount of Crataegus monogyna and Rubus fruticosus present.

Mosses were well represented in the flora of this quadrat. Possibly the heavy grazing made them much easier to find. Barbula recurvirostra, Bryum capillare and Hypnum cupressiforme were only found in this quadrat at Martin Down.

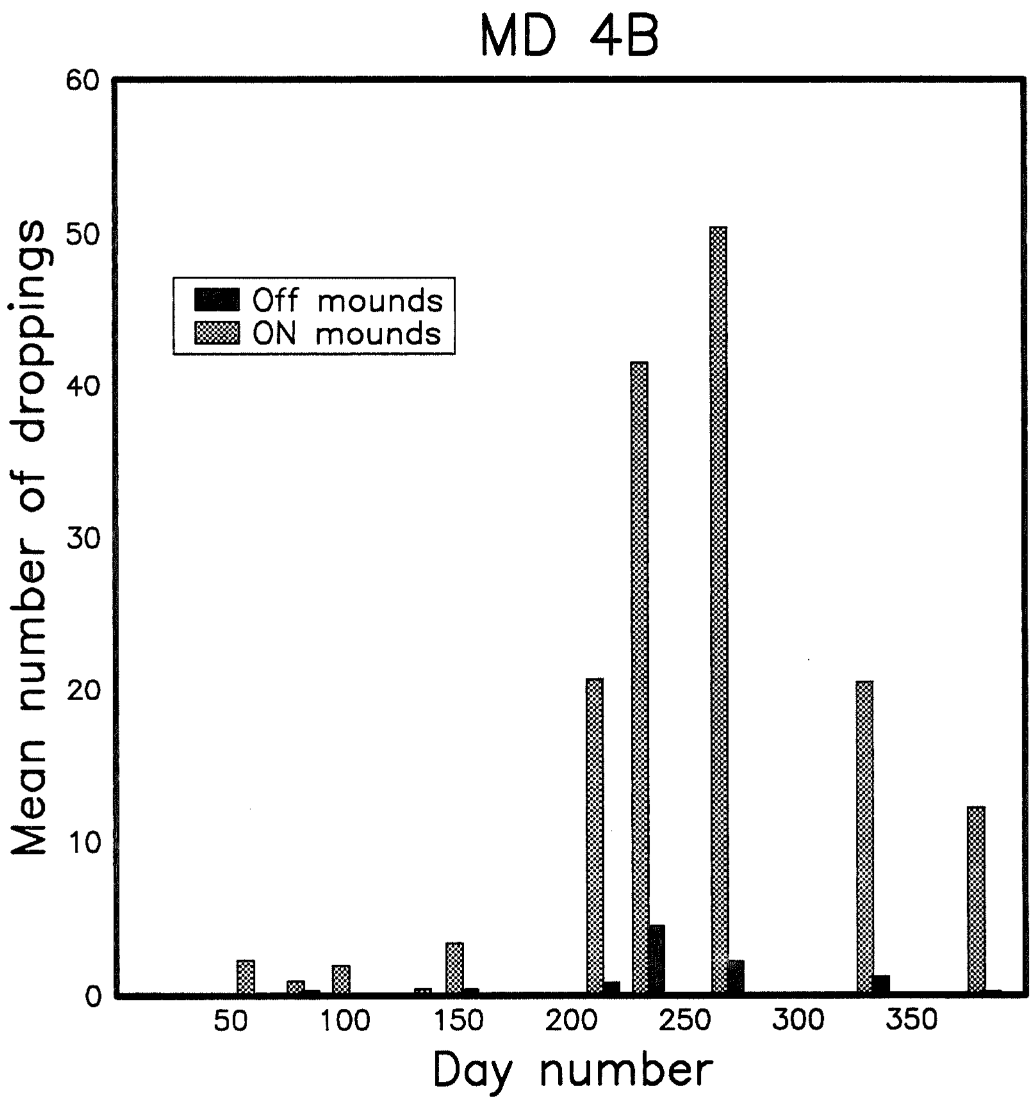
Rabbit droppings. The maximum mean number of rabbit droppings recorded on the mounds was 50.4 on 26/9, while the minimum was 0.9 on 23/3. Off the mounds the maximum was 4.5 on 22/8 and the minimum 0 on 18/5. At the time of the examination of the quadrats the intense amount of rabbit activity was noted in this area. Many of the mounds in the quadrat were damaged by the digging activities of the rabbits. The full data on the rabbit dropping density is presented in graphical form in Figure 10.62.

Root aphids and other invertebrates.

Root aphids. The mean number of root aphids extracted per core was 3.20+/-1.12. The following species of root aphid were recorded in

Figure 10.62.

Rabbit dropping densities in MD 4B.



Day number 1 = 1/1/89.

Each bar represents the mean number of droppings recorded in 5 or 10, 25 x 25 cm. quadrats. The dates of sampling and numbers of droppings recorded in each quadrat are given in Appendix 10.

This area was grazed in June 1989.

this quadrat. Higher than in MD 4A but less than MD 7B.

Aploneura lentisci	1	(0.9%)
Dysaphis spp.	1	(0.9%)
Forda formicaria	1	(0.9%)
Forda marginata	22	(19.6%)
Geoica eragrostidis	1	(0.9%)
Geoica setulosa	1	(0.9%)
Neanoecia zirnitsi	46	(41.1%)
Tetraneura ulmi	3	(2.7%)
Unidentified	36	(32.1%)

Other invertebrates. The mean numbers extracted per core of the major groups of invertebrates was as follows:

Mites	144.00+/-14.94
Collembolans	37.40+/- 4.07
Platyarthrus hoffmanseggi	0.43+/- 0.17
Geophilomorph centipedes	0.86+/- 0.20
Beetle larvae	1.37+/- 0.23
Ants (excluding *L. flavus*)	0.60+/- 0.36

Workers of the ant *Myrmica scabrinodis* were collected here.

The pseudoscorpion *Roncus lubricus* and the Tingid *Acalypta parvula* were extracted from cores collected in this area. As in all of the other areas the centipedes *Schendyla nemorensis* and *Lithobius duboscqui* were also found.

The beetle *Claviger testacea* was also present in this area.

10.22. Quadrat 19, MD 3B.

Site - Martin Down.

Location - Near the top of the escarpment slope facing north, above and east of MD 4A and 4B (see Figure 5.5.). A photograph of the area is shown in Figure 10.63.

10.22.1. The characteristics of the ant population.

The ant mounds.

Number of mounds - 78
Mean diameter of mounds (D) - 47.7 +/- 2.1 cm.
Mean height of mounds (H) - 11.0 +/- 0.7
Ratio D/H - 4.3
Area of quadrat occupied by the mounds - 4.0%
Mean above ground volume of soil in the mounds - 20.6 litres.
Mean distance to nearest neighbour - 1.40 +/- 0.06 metres.

In Figure 10.64. the percentage of mounds in each 10 cm. diameter band is shown.

This area had the largest mean mound size of the Martin Down quadrats, as recorded by all of the statistics measured.

10.22.2. Management. This area survived the period of reduced grazing up to 1979 better than many other areas on the reserve, probably due to an active population of rabbits, which the Warden noted were still active in 1987. This is illustrated by the survival of a population of Silver Spotted Skipper Butterflies (*Hesperia comma*) a species which requires short turf conditions so that its food plants, *Festuca ovina* and *Lotus corniculatus* in this case, will survive. (Other plants found more in acidic conditions also can act as food plants for this species eg. *Aira praecox*, *Deschampsia flexuosa* and *Ornithopus perpusillus*). Despite this, *Bromus erectus* was still the dominant plant species in 1979. It is now very much reduced.

This is an area of low productivity, so comparatively little grazing grazing is required to keep the turf short. In the three years

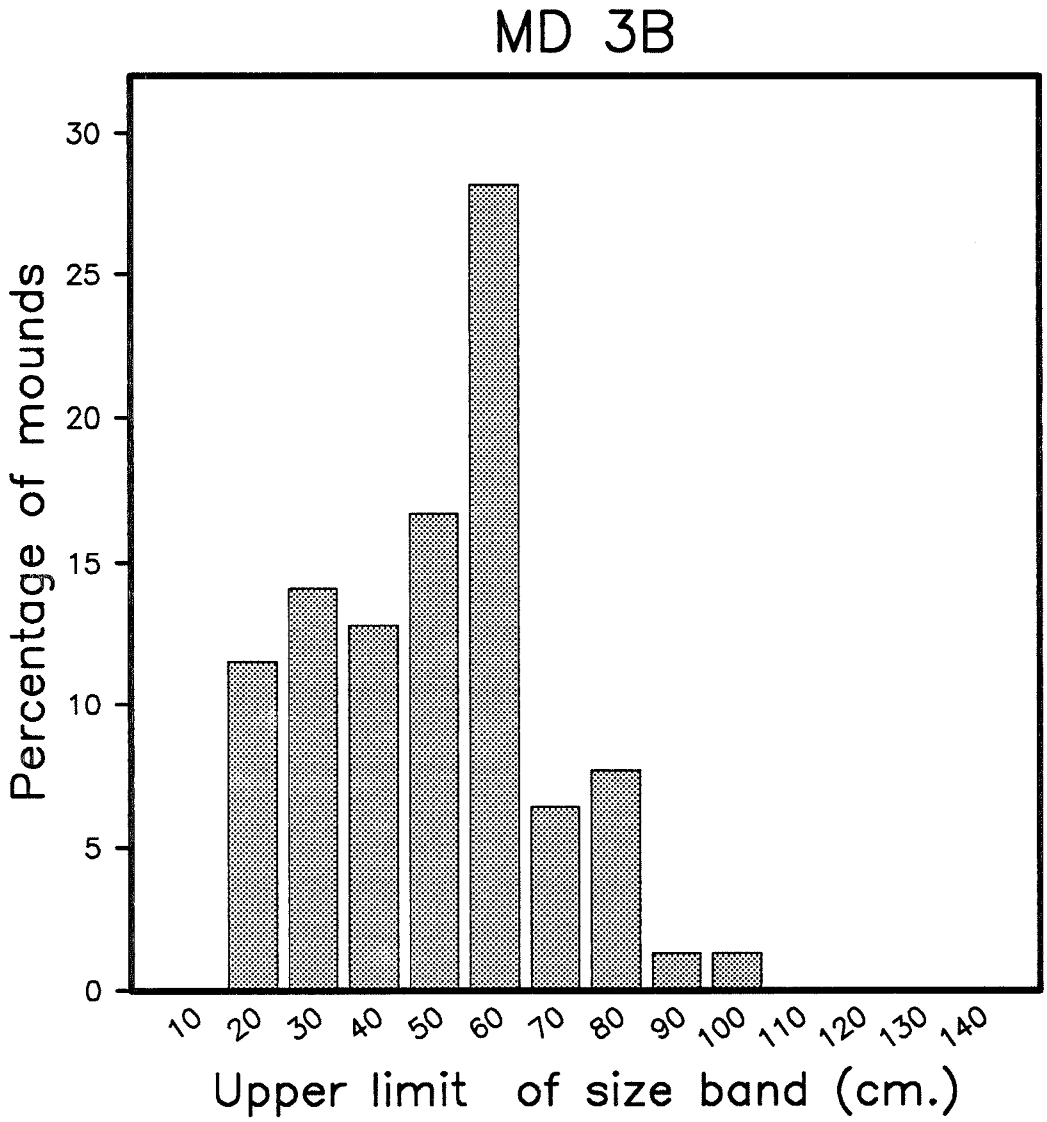
Figure 10.63.

A view of quadrat 19, MD 3B.

The mounds in this area stand out clearly because of the short vegetation. This photograph was taken facing west, towards MD 4A and 4B in the middle distance.

Figure 10.64.

The distribution of mound sizes in MD 3B.



A total of 78 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

prior to the examination of the ant mounds the area had recieved a total of 1,346 sheep days/hectare. Between 1979 and 1984 grazing averaged only 600 sheep days/hectare/year. Since that time a similar pattern has been maintained with an average of 625 sheep days/hectare/year up to 1987. In practice the area is kept under control by rotational winter grazing with some addtional spring and summer grazing.

10.22.3. The physical environment.

Altitude - 122 metres.
Slope - 13^{o}, facing 340^{o} (NNW).
Mean soil depth - 10.8 +/- 0.97 cm.
Mean soil pH - 7.49

This area was at the highest altitude of the Martin Down quadrats and on the steepest slope. It had the thinnest soil and the lowest soil pH of the Martin Down quadrats.

The mean annual temperatures are summarised and shown in Figure 10.65. The mean air temperatures were the coldest of the Martin Down quadrats, except at 18.00PM when MD 7B and MD 4B (the first area to be shaded by the north facing escarpment slope, as the sun goes down) were cooler.

10.22.4. The biological environment.

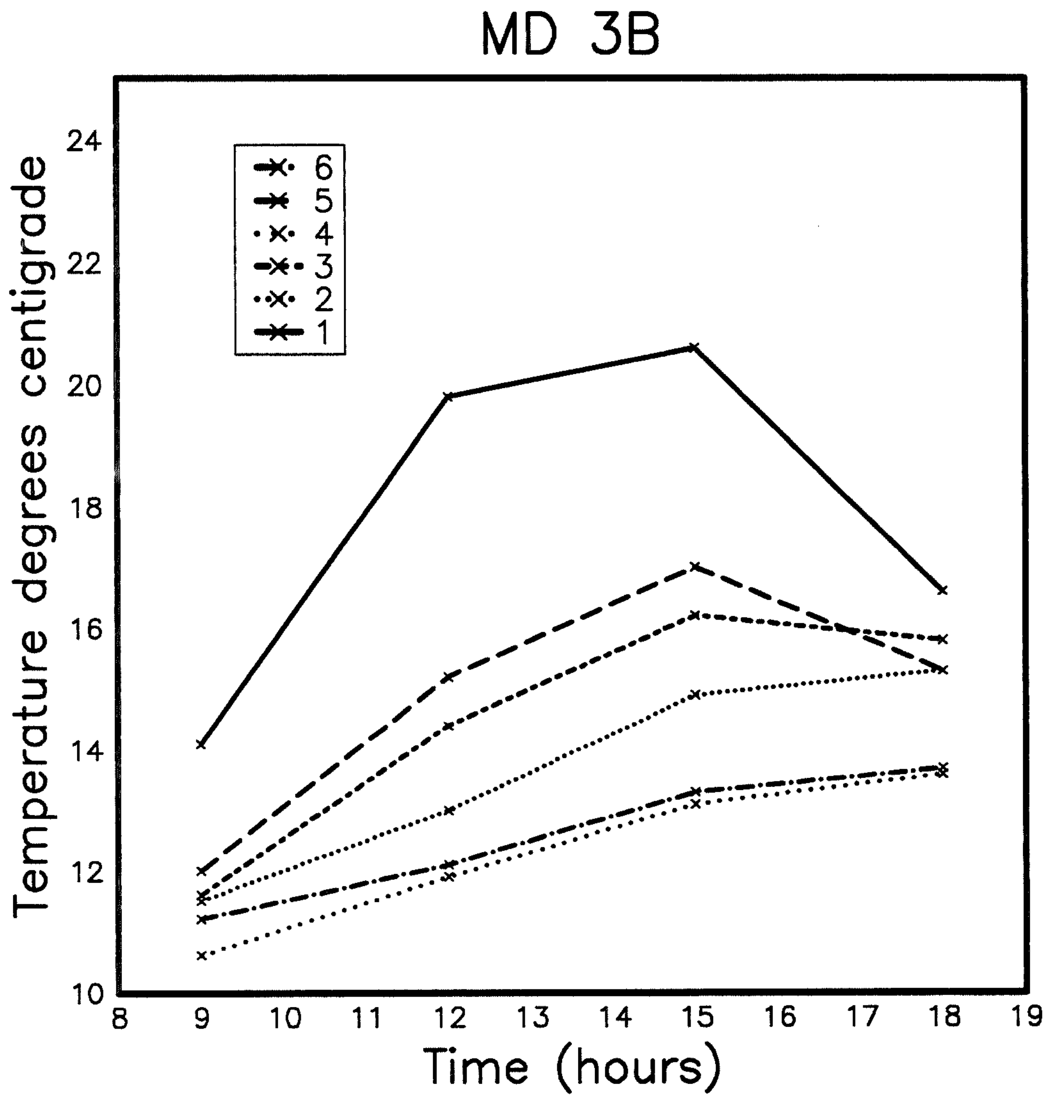
The flora. This area had a short herb rich turf in which *Thymus serpyllum* was extremely abundant. The grass was dominated by the *Carex* spp. and *Festuca* sp. with the tall *Bromus erectus* reduced although stll quite common. There were also some small patches of *Brachypodium pinnatum*.

In all 51 species of plant were recorded in this quadrat including 7 different moss species, with *Dicranum bonjeani* found only in this quadrat of the Martin Down ones.

Figure 10.65.

Summary of the annual mean temperatures in MD 3B.

The mean annual temperatures at four times of day are shown. Times are British Summer Time. In the table below the graph, the mean figures are shown, together with the mean annual air temperatures. 1 - 6 refer the locations as follows.
1, south side of mound, top 1 cm. of soil. 2, same location 10 cm. deep. 3, north side of mound top 1 cm. of soil. 4, same location 10 cm. deep. 5, ground, top 1 cm. of soil. 6, same location 10 cm. deep.



	1	2	3	4	5	6	AIR
9.00	14.1	11.5	11.6	10.6	12.0	11.2	11.4
12.00	19.8	13.0	14.4	11.9	15.2	12.1	14.6
15.00	20.6	14.9	16.2	13.1	17.0	13.3	15.5
18.00	16.6	15.3	15.8	13.6	15.3	13.7	14.4

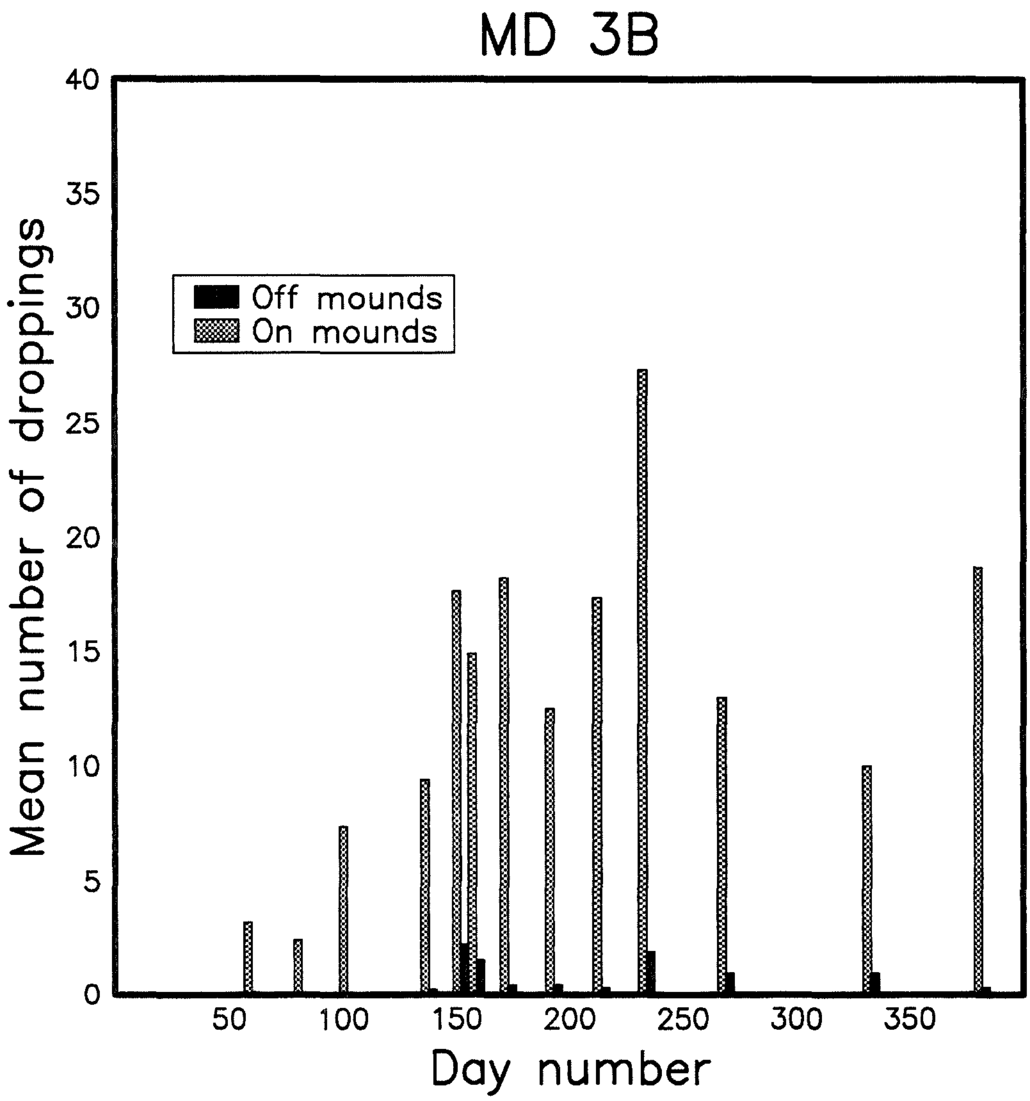
The temperature raw data is given in Appendix Eight. The methods are further explained in section 7.3.2. Each point represents the mean of all the temperatures recorded in that location at that time throughout the year.

Rabbit droppings. The maximum mean number of droppings found on the mounds was 27.3 on 22/8 and the minimum 2.4 on 12/4. Off the mounds the maximum was 1.9 on 22/8 and the minimum 0 on 12/4 and 26/4. The full data is presented in Figure 10.66.

As discussed in the section above, rabbits have been a considerable influence on this sample area in the past, large populations frequently present, although in 1989, the number of droppings recorded was lower than in MD 4A and 4B.

Figure 10.66.

Rabbit dropping densities in MD 3B.



Day number 1 = 1/1/89.

Each bar represents the mean number of droppings recorded in 5 or 10, 25 x 25 cm. quadrats. The dates of sampling and numbers of droppings recorded in each quadrat are given in Appendix 10.

This area was grazed in February 1989.

10.23. Quadrat 20, ST. C.

Site - St. Catherine's Hill.

Location - South facing slope.

10.23.1. The characteristics of the ant population.

The ant mounds.

Number of mounds - 66
Mean diameter of mounds (D) - 45.0 +/- 2.2 cm.
Mean height of mounds (H) - 9.7 +/- 0.7 cm.
Ratio D/H - 4.6
Area of quadrat occupied by the mounds - 3.0%
Mean above ground volume of soil in the mounds - 15.6 litres.
Mean distance to nearest neighbour - 1.57 +/- 0.06 metres.

In Figure 10.67. the number of mounds in each 10 cm. size band is shown.

The area supports a population of mounds very similar in density and size to the quadrats on the south slope at OWH.

10.23.2. Management. Little detail is known of the management of this area. It appears to recieve a small amount of winter cattle grazing each year, at a low density. There are frequent winter scrub cutting operations in order to prevent early scrub succession. Because of its use as a recreational area it is subject to considerable trampling pressure from human activity.

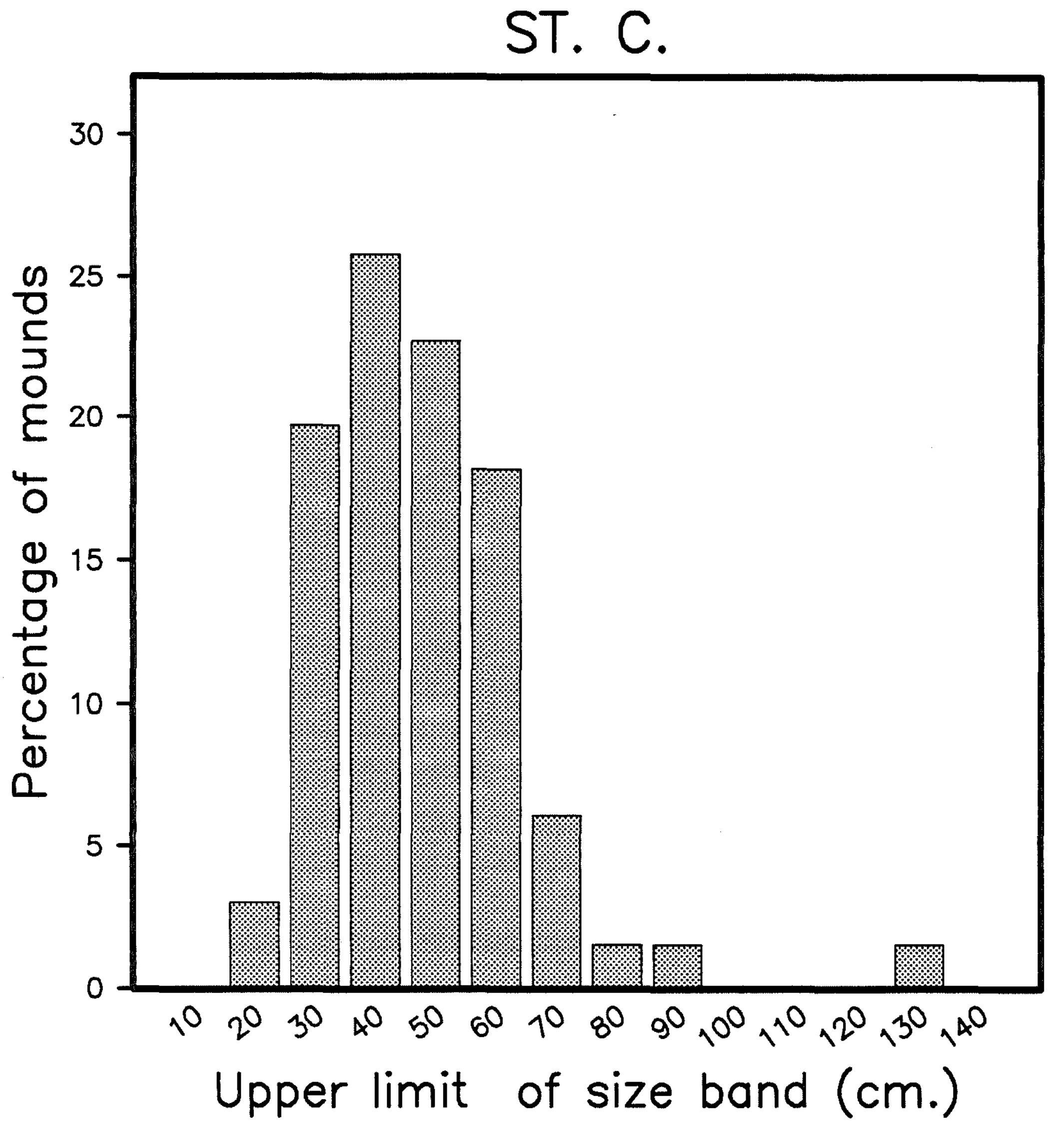
10.23.3. The physical environment.

Altitude - 61 metres.
Slope - 35^{o}, facing 220^{o} (SW).

10.23.4. The biological environment. Details of this were not investigated. The area supports a flora typical of moderately grazed chalk grassland. It is not overly herb-rich.

Figure 10.67.

The distribution of mound sizes in ST. C.



A total of 66 mounds were found in this sample quadrat.

The percentage of the mounds in each diameter band, 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. is shown.

PART FIVE

THE ANALYSIS AND INTERPRETATION OF THE RESULTS, PART ONE

CHAPTER ELEVEN

Comparison of the ant mound populations with those recorded by other authors.

11.1. General characteristics of the ant mound populations of the sample quadrats.

In order to facilitate the comparison of the mound populations recorded in this study, with those recorded by other authors, the results from Chapter Ten are summarised in Tables X and XI. In Table X the number of active mounds located, the average maximum diameters and heights of the mounds in each quadrat, and the ratio of these two figures, D/H, are given for each sample quadrat. In Table XI the density of the mounds, the area of the quadrat covered by the mounds and the mean volume of the mounds are given.

11.1.1 The density of the mound populations.

In the 20 quadrats a total of 1,748 mounds were found, a mean of of 87.4 mounds per quadrat. The quadrat with the most mounds was AR 12 with 273, and with the least was OWH SS7 with only 8. Excepting these, the range was from 57 to 126 mounds. Over 50% of the quadrats had between 60 and 80 mounds in them (see Figure 11.1.). This corresponds to densities of between 0.15 and 0.20 mounds/m^2. The highest density of mounds was that in AR 12 at 0.68 and the lowest in OWH SS 7 at 0.02 mounds/m^2.

11.1.2. The sizes of the mounds.

The smallest individual mounds were only about 5cm. across and 1 cm. high, while the largest were well over a metre across and up to 40 cm. high. The overall distribution of the diameter of the individual mounds found (split into 10 cm. class widths) is shown in Figure 11.2. The distribution is slightly positively skewed. Mounds of 100

Table X.

Numbers and sizes of the mounds recorded from each of the sample quadrats

Quadrat	Number of mounds	Average maximum diameter cm.	Average maximum height cm.	D/H
OWH SS 4	67	40.8 +/- 1.7	10.4 +/- 0.6	3.9
5	64	40.4 +/- 1.9	9.3 +/- 0.8	4.3
7	8	59.1 +/- 8.9	17.9 +/- 4.3	3.3
8	66	46.9 +/- 2.2	13.9 +/- 1.0	3.4
9	99	43.6 +/- 1.4	15.8 +/- 0.7	2.8
11	57	42.9 +/- 2.6	9.6 +/- 0.8	4.5
12	71	42.1 +/- 1.7	11.4 +/- 0.8	3.7
NFS	70	54.6 +/- 3.1	14.6 +/- 0.9	3.7
C10	119	59.9 +/- 2.5	18.2 +/- 0.7	3.3

AR 11	113	45.2 +/- 1.3	12.0 +/- 0.6	3.8
12	273	25.9 +/- 0.8	3.6 +/- 0.2	7.1
15	126	49.8 +/- 1.6	16.3 +/- 0.7	3.1
16	63	43.4 +/- 2.2	11.3 +/- 0.9	3.9
5	75	43.5 +/- 1.5	4.8 +/- 0.3	9.1
NWS	119	21.9 +/- 1.3	4.7 +/- 0.4	4.7

MD 7B	86	38.2 +/- 1.8	6.0 +/- 0.5	6.4
4A	61	40.6 +/- 1.8	9.2 +/- 0.8	4.4
4B	67	41.0 +/- 2.0	9.5 +/- 0.6	4.3
3B	78	47.7 +/- 2.1	11.0 +/- 0.7	4.3

ST. C.	66	45.0 +/- 2.2	9.7 +/- 0.7	4.6

D/H is the average maximum diameter divided by the average maximum height.

Mean and standard errors have been given for the diameters and heights. See section 6.6.2.2. for a description of how the mounds were measured.

Table XI.

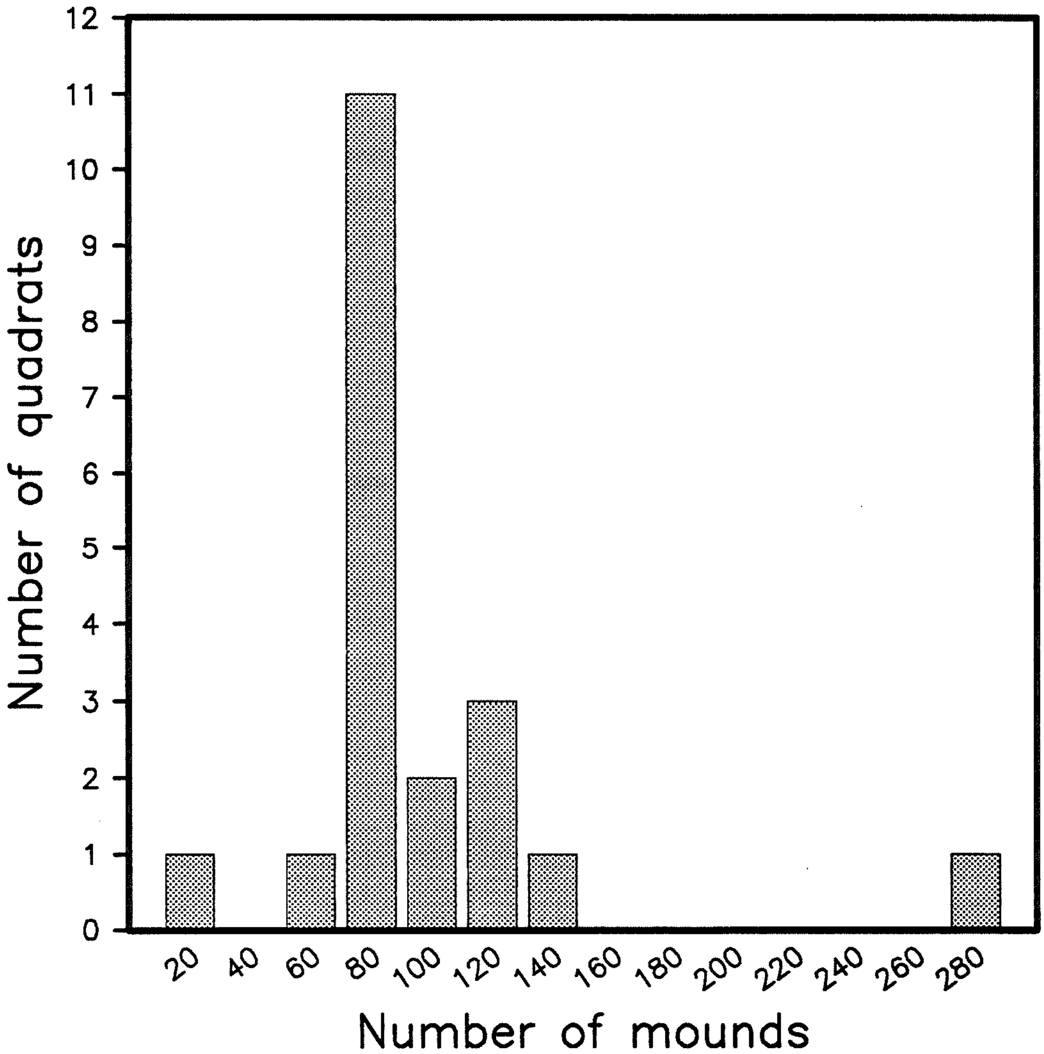
The density of mounds, mean mound volumes and percentage area covered by the mounds in each of the sample quadrats.

Quadrat	Density of mounds/m^2	Mean mound volume (litres)	Percentage of ground surface covered by mounds
OWH SS 4	0.17	12.2	2.4
5	0.16	12.8	2.3
7	0.02	53.1	0.6
8	0.17	23.4	3.3
9	0.25	21.0	4.1
11	0.14	15.7	2.5
12	0.18	15.4	2.8
NFS	0.18	39.9	5.0
C10	0.30	52.0	10.1
AR 11	0.28	17.1	5.0
12	0.68	2.7	4.6
15	0.32	29.7	6.9
16	0.16	16.5	2.7
5	0.19	6.5	3.0
NWS	0.30	3.3	1.6
MD 7B	0.22	7.7	2.9
4A	0.15	11.7	2.2
4B	0.17	12.0	2.6
3B	0.20	20.6	4.0
ST. C.	0.17	15.6	3.0

The area that a mound covered was calculated by using the maximum diameter of the mound as the diameter of a circle. Volumes were calculated for the above ground portion of the mound, with the diameter and height of the mounds used in the formula for a half-ellipsoid.

Figure 11.1.

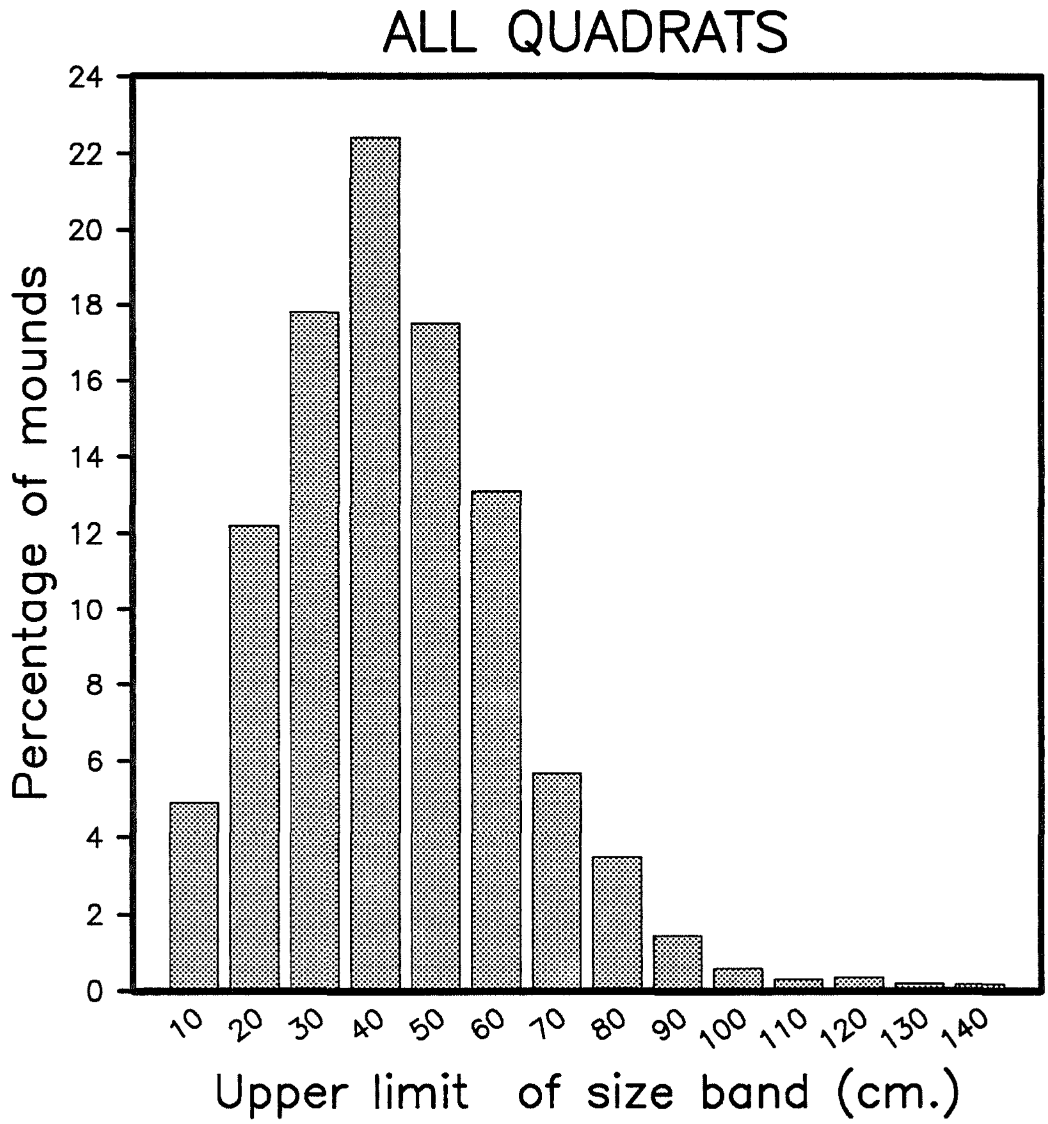
The distribution of mound densities in the quadrats.



A total of 1,748 ant mounds were found in the 20 sample quadrats. Each bar represents the number of quadrats with, 0 - 20 mounds, 21 - 40 mounds, 41 - 60 mounds etc. The two outliers are OWH SS 7 with only 7 mounds found and AR 12 with 273 mounds. Over half of the quadrats (11) had between 60 and 80 mounds in them.

Figure 11.2.

The distribution of mound sizes in all quadrats.



A total of 1,748 ant mounds were measured in the 20 sample quadrats. The percentage of the mounds in each size band, 0 - 10 cm., 11 - 20 cm., 21 -30 cm. etc. is shown. The sizes are those given by the maximum diameter of the mounds.

cm. maximum diameter and above are rare, with over 90% of mounds being in the range of 0 to 80 cm. maximum diameter.

The average size (maximum diameters and heights), of the mounds in a quadrat ranged from only 21.9 cm. in diameter and 4.7 cm. high in AR NWS or 25.9 by 3.6 cm. in AR 12, to 59.9 cm. across and 18.2 cm. high in OWH C10. Calculations of the proportion of the area of the quadrat covered by the mounds gives a highest value of 10.1% in OWH C10. The mean is 3.6% and the lowest 0.6% in OWH SS 7.

How do these figures compare with those produced by other workers looking at the density of *L. flavus* mounds in other areas, both on and off chalk grasslands?

11.2. The density of mound populations recorded by previous workers.

11.2.1. Locations other than chalk grassland. Several authors have previously reported work where the density of colonies of *L. flavus* has been examined. These investigations are summarised in Table XII.

The first three studies are ones in which *L. flavus* was present in low numbers only, and where mixed ant communities were being examined. The densities reported in these studies are low in comparison to almost all of those in the remainder of the Table, where *L. flavus* was the dominant ant species and the only one investigated. The first three studies are those of:

a) Elmes (1974) from limestone grassland ~~grassland~~ in Dorset where there was also a large population of *Myrmica rubra* present,

b) Doncaster (1981) who examined the ant population of the whole of a small island and, where the results are averaged out from the range of habitats available on the island,

c) Pickles (1940) from an area of acidic grassland in Yorkshire, where only a few isolated colonies of *L. flavus* were

Table XII.

Densities of **L. flavus** mounds as reported by previous authors.

a) Habitats other than chalk grassland.

Author/s	Area examined (square metres)	Number of mounds found	Density of mounds, no. per square metre
Pickles (1940)	880	6	0.01
Elmes (1974)	2560	126	0.05
Doncaster (1981)	27900	1038	0.04
Richards and Waloff (1954)	-	-	0.15
Waloff and Blackith (1962)	4047 883 251 410 371	~600 225 76 125 99	0.15 0.25 0.30 0.30 0.27
Blackith et al (1963)	730	84	0.25
Pontin (1963)	-	-	0.26
Nielson et al (1976)	625 625	191 92	0.31 0.15
Pontin (1978)	432	64	0.15
King, Gower data (pers. comm.)	225 600 3,000 1,200 1,000	* 100 * 200 * 400 * 450 497	0.44 0.33 0.13 0.38 0.50

Brief descriptions of the locations on which the ant mound populations were measured are given in the text.

Table XII. continued.

b) Chalk grassland habitats.

Author/s	Area examined (square metres)	Number of mounds found	Density of mounds, no. per square metre
Wells et al (1976)	36 many samples	2 to 18	0.05 to 0.50
King, Miscellaneous data (Pers. comm.	800	* 150	0.18
	500	* 60	0.12
	625	* 80	0.13
	1,875	* 250	0.13
	1,000	* 200	0.20
	1,400	* 300	0.21
	350	* 120	0.34
	1,350	* 70	0.05
	12,000	300	0.03
	375	70	0.19
	14,300	* 650	0.46
	~ 1,400	1,947	~ 0.14

* = figure is an estimate by King.

present.

The habitats in these three studies (possibly barring that of Elmes 1974) may not be as favourable for the presence of L. flavus as those considered in the rest of the studies in Table XII. In the rest of the studies higher densities of mounds were found, ranging from 0.13 to 0.50 mounds/m^2.

The most intensive study into the density of L. flavus mounds has been that by Waloff and Blackith (1961). They have examined a number of populations of the ant on acid grassland in Silwood Park, Berkshire. They reported some variation in the density of the mounds present (see Table XII) but were more impressed by the variation in the size of the mounds in different areas which they related to the prevailing drainage conditions. Mounds were larger in areas that were more waterlogged. The densities they do report are similar to the typical range of densities found for chalk grassland in this study. A study of a similar area in the locality by Richards and Waloff (1954) gave a compatible density.

Blackith et al (1963) recorded a low density of mounds on a damp pasture in Devon at the Eastern margin of Dartmooor. Pontin (1978) measured the numbers of mounds on Staines Moor, Surrey, where the density of mounds was comparable to the less densely populated chalk grasslands examined in this thesis. Nielsen et al (1976) recorded the density of mounds on two areas of a Danish tidal meadow. They found differing mound populations, one area with a high mound density, compared to the chalk grasslands measured in this study, with the other area at half the density.

Pontin (1963) recorded the ant mound populations of two areas of disturbed calcareous grassland (oolitic limestone) at Wytham in

Berkshire. The two populations he gives figures for have densities similar to sample quadrats such as AR 15 and AR 11, two of the more densely populated of the sample areas examined in this thesis.

Wright and Fairney (unpublished data) examined two populations of mounds on limestone grassland near Buxton, Derbyshire and found densities of only 0.11 and 0.10 mounds/m^2, lower than the typical chalk grassland populations measured in this study.

King (pers. comm.) has also passed on data from sites examined in the Gower, Wales (see King 1981a for details of the sites). The densities on these sites are high, up to 0.50 mounds/m^2 and are in excess of the figures from this study, barring AR 12.

11.2.2. Chalk grasslands. There are two data sets available for chalk grassland sites, one of which has been published and one not.

On chalk grassland in Wiltshire (The Porton Ranges), Wells et al (1976) sampled ant mound densities along transects in a range of grassland habitats. They recorded a wide range of densities, but their sample sizes were quite small in comparison to other workers. Wells et al (1976) suggest that the density is related to the time since the last ploughing of the grasslands. Unpublished records of mound populations measured by King (pers. comm.) suggest that in many cases a high percentage of these mounds were, in fact, unoccupied by ant colonies. Thus it is not particularly fair to compare these areas with those studied in this project, where unoccupied mounds were excluded from consideration, although, unnoccupied mounds did not appear to occur in any great frequency in any of the sample quadrats.

King (pers. comm.) has also provided data from a number of grassland sites that he has estimated the density of mounds on. These are summarised in Table XII. They include data from the Wells et al

(1976) study and from a variety of other chalk grassland sites. However, unoccupied mounds were again included, although it is suggested that in most areas these were a negligable part of the population.

11.3. The sizes of the mounds.

The sizes of the mounds can be expressed in two ways, firstly in terms of diameter and height measurements and secondly as volumes of soil. Both methods have been used by various authors. How do the sizes of mounds recorded during this survey of chalk grassland sites compare with mounds on other chalk grassland areas and on other habitats?

The results of other authors are summarised in Table XIII. The results given in Table XIII derive from the same populations of mounds described from Table XII.

As with the density results we can conclude that there are a wide range of sizes recorded. However, it would appear that the use of the volume figures shows up this range to the greatest degree. The smallest volumes from Table XIII are of a similar order to those recorded in the current study, barring the third population of King (1981a) where the mean volume of only 0.7 litres is extremely small. It would correspond to colonies making virtually no mounds at all, perhaps similar to a large proportion of the mound population in AR 12 and AR NWS that were observed in the current study.

The largest mean volumes recorded by other workers are, in fact, exceeded by the populations in OWH C10 and OWH SS 7 although only by a small amount.

11.4. Areas covered by the populations of mounds.

Several authors have used the percentage area of a habitat covered by the ant mounds as a way of expressing the density of a population

Table XIII.

Sizes of ant mounds recorded by other authors.

Author/s	Diameter x Height cm.	Volume (litres)
Haarlov (1960)	100 x 30 maximum	-
Waloff and Blackith (1962)	73 x 22 40 x 15	-
Blackith et al (1963)	43 x 24 69 x 20	-
Nielsen et al (1976)	- -	36.8 40.5
King (1977a)	60 x 26	51.3
King (1981a)	"typical" sizes 50-70 x 15-20	-
King (1981b)	9 areas size unknown	3.0 6.0 0.7 21.0 13.0 10.0 5.0 19.0 4.0
Wells et al (1976)	63 x 26 64 x 28 60 x 30 56 x 36 45 x 23 66 x 30 53 x 29 49 x 21 36 x 22 39 x 17 39 x 14	40.3 46.2 42.0 43.0 18.0 51.6 32.0 19.3 11.5 10.1 8.4

Figures are means unless otherwise stated. King (1981b) further gives sizes of the largest 5 mounds found in 13 separate areas.

of L. flavus mounds.

Nielsen et al (1976) calculated figures of 11.6% and 6.6% for two areas of a tidal meadow on a Danish island and more remarkably a coverage of up to 17.2% is recorded by Nielsen (1982) from a population on a Wadden Sea saltmarsh. Waloff and Blackith (1962) calculated up to 10 or 11% for the areas that they investigated.

Unpublished estimates from the Wells et al (1976) survey of the Porton Ranges, also passed on by King (pers. comm.) give a range of estimates of area covered by the mounds, the smallest being 6%, the largest a massive 28%. However, these estimates do include the unnoccupied mounds, which in some of the areas appeared to constitute a high percentage of the mounds.

The quadrats sampled as part of this thesis do not appear to reach the same level of coverage of ant mounds recorded in many of the areas investigated by other workers. Only in OWH C10 where a coverage of 10.1% was reached does there seem to be a population in any way similar to the larger levels of coverage recorded by other workers. In some cases this may be due to the inclusion of unoccupied mounds, but not always. This seems rather odd when the similarities of the diameter and heights of the mounds and the densities recorded in this survey, to other workers results, are considered. It is possible, though, that in the sample areas in this survey the combination of large mounds and large densities was not reached to the same extent as in some of these other areas.

11.5. Conclusions.

Considering the populations of ant mounds recorded by other authors, as described above, we can conclude that the populations recorded during this survey are not untypical of the normal range of densities and mound sizes of *L. flavus* populations that have been recorded in northern Europe.

The chalk grassland sites recorded in the current study perhaps fail to reach the highest densities recorded by some authors but the sites studied by these other workers may well have been exceptional sites, examined simply because of their large populations of mounds, unlike in this project.

What most of the other authors have generally failed to consider, though, is how the variation in population densities and mound sizes that has been observed, can be explained. Is the environment of the area they inhabit important in determining the density and size of the populations of mounds, or is the management the habitat receives important, or as seems likely, are both? In particular, the recent grassland management does not seem to have been considered in any of the studies described. The data from the current survey can be used to examine the hypotheses posed in Chapter Four, which sets out to examine precisely these points.

CHAPTER TWELVE

Mound sizes, densities, management and the physical environment.

12.1. Introduction.

In all the quadrats examined, the present status of the *L. flavus* population results from many years interaction between management of the grassland and environmental factors. This makes interpretation more difficult as it is not always possible to separate out the importance of these two influences in each sample area. This Chapter will attempt to analyse the various influences, of the physical environment and management of the sample areas, on the ant mound populations.

The results will be considered under four headings, as follows:

1) Mound sizes and management,

2) Mound sizes and the physical environment,

3) Density of mounds and management,

and, 4) Density of mounds and the physical environment.

12.2. Mound sizes and management.

Because of the variation in the management histories of most of the sample areas it is not possible to do an overall analysis, for example correlating the mound density in the sample quadrats to the intensity of grazing over many years. It is simply not possible to come up with a figure for all of the quadrats which represents the intensity of grazing for the past 10 or more years. However, figures for the intensity of grazing over the three years prior to the examination of the quadrats are available for all of the sample areas, except ST.C.

12.2.1. The short term affects of more intense grazing.

Using the estimates of the total number of sheep days/hectare that had been grazed in the three years before the mapping of the sample quadrats, correlations were done with the mean sizes of the mounds (diameters, heights and volumes) in each quadrat. The results of the product moment correlations were as follows. In all cases n = 19 pairs.

diameters	$r = -0.372$,	$P>0.05$
heights	$r = -0.332$,	$P>0.05$
volumes	$r = -0.296$,	$P>0.01$

Thus no significant relationships can be determined between the sizes of the mounds and the short term grazing intensity, using this type of overall analysis.

However, by considering the sample areas in more detail it is possible to observe some degree of consistency in the data.

The south slope at Old Winchester Hill should serve to illustrate the short term effects of variations in grazing intensity, as, before the present management regime was inaugurated in 1981, the area had been grazed as a single unit and it could be supposed that the influences on the ant mounds were the same in all of the sample areas. At the time the quadrats were examined, however, the rotational grazing plan had been in operation for three years and there were thus available for examination areas that had received very different amounts of grazing in the three years prior to the examination of the sample quadrats (see Figure 10.1.).

Considering first the relationship between the ratio of the mean maximum diameter to the mean maximum height (D/H) and the grazing regime, there was a suggestive link between increasing grazing intensity and an increase in the ratio, although, a Spearman rank correlation between the D/H ratio and the number of grazing periods was not significant ($r = +0.545$, $P>0.05$). The data are shown below, with the number of grazing periods of each plot in the period from 1981 to when the sample quadrats were examined.

Quadrat	Grazing periods (since Jan 1981)	D/H	Average maximum height cm.
OWH SS 4	0	3.9	10.4
9	1	2.8	15.8
8	1	3.4	13.9
7	2	3.3	17.9
12	2	3.7	11.4
5	3	4.3	9.3
11	3	4.5	9.6

It is clear that the ratio for OWH SS 4 does not conform to the otherwise consistent pattern of increasing D/H with more grazing periods. This sample area appeared at the time of the mapping to be well grazed down, and it is possible that rabbit grazing, which was not inconsiderable in the area (see Figure 10.5. and Chapter Thirteen) may have been responsible for this. The sample area also had a small pathway running through it, which may have led to more trampling by visitors to the Reserve than in the other south slope sample areas.

The mean height of the mounds in OWH SS 7 also stands out as being higher than in all of the other south slope quadrats. Only a few large mounds were present in this area (see Figure 10.8.) and the absence of smaller mounds meant that the overall mean mound size was much higher than would otherwise have been the case.

A more thorough analysis was done by looking at the diameters and heights of the individual mounds in the quadrats. In a series of t-tests, the results of which are set out in Tables XIV and XV, the heights of the mound population of each of the quadrats was compared with the mounds of each of the other quadrats, and the same was done for the diameters.

Considering first the diameters, the only significant differences

Table XIV.

Summary of the t - tests on the mound diameters of the south slope quadrats.

Quadrat	8	9	11	12	4	5
Diameter	46.9	43.6	42.9	42.1	40.8	40.4
8	X	NS	NS	NS	5%	5%
9	NS	X	NS	NS	NS	NS
11	NS	NS	X	NS	NS	NS
12	NS	NS	NS	X	NS	NS
4	5%	NS	NS	NS	X	NS
5	5%	NS	NS	NS	NS	X

Table XV.

Summary of the t - tests on the mound heights of the south slope quadrats.

Quadrat	9	8	12	4	11	5
Height	15.8	13.9	11.4	10.4	9.6	9.3
9	X	NS	NS	NS	5%	5%
8	NS	X	NS	NS	5%	5%
12	NS	NS	X	NS	NS	5%
4	NS	NS	NS	X	NS	NS
11	5%	5%	NS	NS	X	NS
5	5%	5%	5%	NS	NS	X

NS - no significant difference between the heights of the mounds in that pair of quadrats. $P>0.05$, 2 tailed t-test.

5% - Significant difference between the heights of the mounds in that pair of quadrats. $P<0.05$, 2 tailed t-test.

were between OWH SS 8 and OWH SS 4 and 5 (Table XIV). OWH SS 8 had the largest mean diameters, while OWH SS 4 and 5 had the smallest. There is no explanation for this in the grazing regime and as the sample areas lay at the opposite ends of the south slope it is probable that other factors, possibly involving past management of the area, are responsible. Overall, we can conclude that there is no consistent relationship between diameter of the mounds and the grazing regime.

When considering the heights there are more differences to be seen. A more consistent relationship between them and the grazing regime emerges. The mounds in OWH SS 5 and 11 (3 grazing periods), were significantly different in height from the mounds in OWH SS 8 and 9 (1 grazing period). A significant difference was also found between the mounds in OWH SS 12 (2 grazing periods) and the least tall mounds found in OWH SS 5 (see Table XV).

The mounds in OWH SS 4 appeared to be an exception to this pattern since they had not yet been grazed in the rotation and yet were not as tall as would have been expected. Possible reasons for this have already been discussed when considering the D/H ratios of the quadrats.

The results from the south slope at OWH thus suggest that more intense grazing over three years led to significant reductions in the height of the mounds in some of the sample quadrats, but not the diameters of the mounds.

At Martin Down the grazing regime had been maintained from 1978 to 1984. If the grazing intensity over the three years prior to the examination of the sample quadrats is considered, then in grazing intensity these sample areas would be placed in the middle to lower range of the OWH south slope sample areas, grazing intensity not exceeding a total of 4,000 sheep days/hectare in any of the sample areas. It was thus interesting to find that the D/H ratios in three of the quadrats (MD 4A, 4B and 3B) were similar to those of the most intensively grazed quadrats at OWH (OWH SS 5 and 11) which had been subjected to 3 years of approximately 2,500 sheep days per hectare.

If we recall the histories of these areas before the three year period prior to the examination of them in Summer 1981, the explanation for this difference between the two reserves becomes more apparent. Prior to the starting of the rotation on the south slope at OWH in 1981, the whole area was grazed as one unit and overall grazing intensity quite low, at less than 1,000 sheep days/hectare/year. In contrast, at Martin Down grazing was only re-started in 1978 and in order to reduce the large grass growth that had built up, grazing was initially very intense at over, 1,000 sheep days/hectare/year. The Martin Down mounds had thus been subjected to more intense grazing than the south slope mounds prior to the three year period, ie. from 1978 to 1981.

In contrast to the other sample areas at Martin Down, the mounds in MD 7B were very much flatter in relation to their diameters (D/H = 6.4). This area had had the largest amount of grazing of the MD quadrats, 1,280 sheep days per hectare each year. Even so the mounds were exceptionally flat, but in looking at the area, it appeared that the coarser, taller grasses in the quadrat (*Bromus erectus* and *Arrhenatherum elatius*) acted less well to stabilise the mound soil. The mounds in this area were not covered by short herbs such as *Thymus serpyllum*, as mounds in other areas were. As a result this made them more susceptible to trampling by sheep. After grazing the mounds in this area appeared to have been subjected to more intense trampling than was apparent in other sample areas. This is thus an interaction between the biological environment of the sample area (ie. the flora) and the management of the sample area which leads to the effect of grazing on the mounds being emphasized.

Thus it can be concluded that in the short term, up to three or four years, there is no evidence that the mean diameter of the ant mounds in an area will be reduced, but there is certainly some evidence, from the D/H ratios and the mean mound heights, that the height of the mounds will be reduced, and that as a consequence the mounds become of a flatter shape.

The most probable cause of these reductions in the heights of mounds is simple trampling by the grazing animals, in this case sheep. From observations of mounds after grazing it is clear how much damage can be done to them, particularly in wet conditions, when the loose mound soil is soft. Hoof marks were clearly seen on mounds after grazing. Sheep will preferentially graze ant mounds, probably for the often abundant Festuca rubra on them (King 1977a) and Wardens on the reserves readily confirmed that when sheep are first released into an area the tops of the ant mounds are the first part to be grazed.

Sheep will also frequently stand on top of the mounds, apparently to obtain a raised view of their surroundings. For example on one occasion it was noted that when sheep were disturbed and looked up 8 out of the 10 sheep present (20%) were standing with their front feet on top of mounds. This type of observation was repeated many times.

Thus, the mounds are subject to intense grazing pressure and to being trodden on, when sheep graze an area of chalk grassland.

12.2.2. The long term effects of more intense grazing. Having used the quadrats described above to examine the effects of short term grazing regimes on the mounds, the Barn plots at Aston Rowant can be used to examine the effects of much longer term differing grazing regimes. As discussed in Chapter Ten, the grazing regimes in these quadrats had been maintained for 20 years since the inception of the experimental regime in the early 1960's.

If we first briefly recall the grazing levels discussed in Chapter Ten, and compare them to the mean mound sizes.

Quadrat	Sheep days/ hectare/year	Av. max. diameter	height (cm.)
AR 11	733	45.2	12.0
AR 12	2535	25.9	3.6
AR 15	716	49.8	16.3
AR 16	2006	43.4	11.3

The difference between AR 15 and 16 was very distinctive. The plots lie next to each other, and yet there was a vast difference between them, both statistically and visually (see Figures 10.33. and 10.38.). The mounds in AR 16 had significantly lower heights than AR 15 ($t = 2.274$, 187 d.f., $P<0.02$, 1 tailed test), which is consistent with the OWH south slope results. They were also significantly smaller in diameter ($t = 2.333$, 187 d.f., $P<0.05$, 1 tailed test), which suggests that longer periods of intense grazing lead not only to reduced mound heights but also to reduced diameters.

This was also true in quadrats AR 11 and 12 (diameters: $t = 12.525$ $P<0.01$, heights: $t = 17.158$ $P<0.01$, both 384 d.f., 1 tailed tests). AR 12 was the most heavily grazed plot and had the smallest and lowest mounds of any quadrat so far considered. These replicated plots suggest quite clearly that long term heavier grazing does lead to a reduction in the size, in terms of both heights and diameters, of the ant mounds.

How do the other sample areas not yet mentioned fit into the pattern of grazing effects observed on the south slope and in the AR barn plots?

12.2.3. The other sample areas and management. In AR NWS, which like AR 12 had received continual heavy grazing, the average mound sizes were similarly much reduced compared to the other quadrats. Many of the mounds located in these two quadrats were extremely small, and not mounds in the true sense of the word. It seemed at times as if ants with brood could be found under almost any small bump in the ground. The status of these mounds will be discussed in a section 12.4.

The absence of large mounds, with the enhanced temperature regime that they can bring (see Chapter Seventeen), had clearly not affected the ability of the ants to live in AR NWS or AR 12. The climatic conditions of the English chalk grasslands are not near the more extreme climates that *L. flavus* may face within its range. In a more northerly situation such a position may be more critical. This absence of mounds is also found in southern English garden lawns and recreational areas. These patches of grassland receive excessive amounts of trampling, from both human pressure and frequent repeated grass cutting, and while there are no large mounds to be seen in such areas, *L. flavus* is frequently present. This can be demonstrated if the grass is left unmown in the spring. Small mounds of soil may then be formed by the colonies, (pers. obs.). Normally trampling and grass cutting will prevent their formation. In other areas the formation of mounds is inhibited simply by trampling pressure, see Figure 12.1.

In quadrat OWH C10 there had been no organised grazing at all. The mounds were the largest found in this study. Although other environmental factors undoubtedly contributed to the large size of the

Figure 12.1.

The effects of trampling on the mounds of **L. flavus.**

The photograph shows a pathway at Aston Rowant NNR. Mounds can be seen at the right hand side of the pathway. The effect of the human trampling has been to flatten the mounds. Ants are often also present in the middle of pathways such as this, but the intense trampling pressure means that no mounds at all are built. The only visible signs of colonies are the throwing up of small amounts of soil on damp, warm mornings.

mounds (see following section), the lack of grazing was important. No trampling took place to knock down the large amounts of soil placed on top of the mounds by the worker ants.

In the ST. C quadrat the average height of the mounds and the D/H ratio were most similar to those of the higher grazed areas of the OWH south slope quadrats and this area is a similar south facing slope. It is only lightly cattle grazed in winter and the flatter nature of the mounds could be due to the heavier trampling of the cattle and also possibly to the influence of human trampling, this being a popular recreational area.

Finally, mounds in quadrat AR 5 illustrated the drastic effect that another form of management can have on the mounds. This quadrat had just had the scrub in it cut by a mechanical implement attached to a tractor. As this had been set to operate at a low level, as well as cutting the scrub right down, it had also taken the tops off of all the ant mounds. The average diameter of the mounds was similar to that in other quadrats, but the average height was greatly reduced. Such damage to the mounds could well affect the colonies, perhaps even destroying some of them, if the queen was in the affected part of the mound. If a healthy population of large mounds is desired in an area, scrub cutting must be carefully controlled.

"Topped" mounds were also seen at Martin Down, although in this case this was as a result of tractor mowing in order to control growth of the coarse grass Brachypodium pinnatum (see Figure 12.2.).

In Figure 12.3. the overall effects discussed above are illustrated as a scattergram, each point representing the average maximum height and diameter of the mounds in a quadrat. The dividing lines separate areas of no, light, heavier and very heavy grazing. The lines have

Figure 12.2.

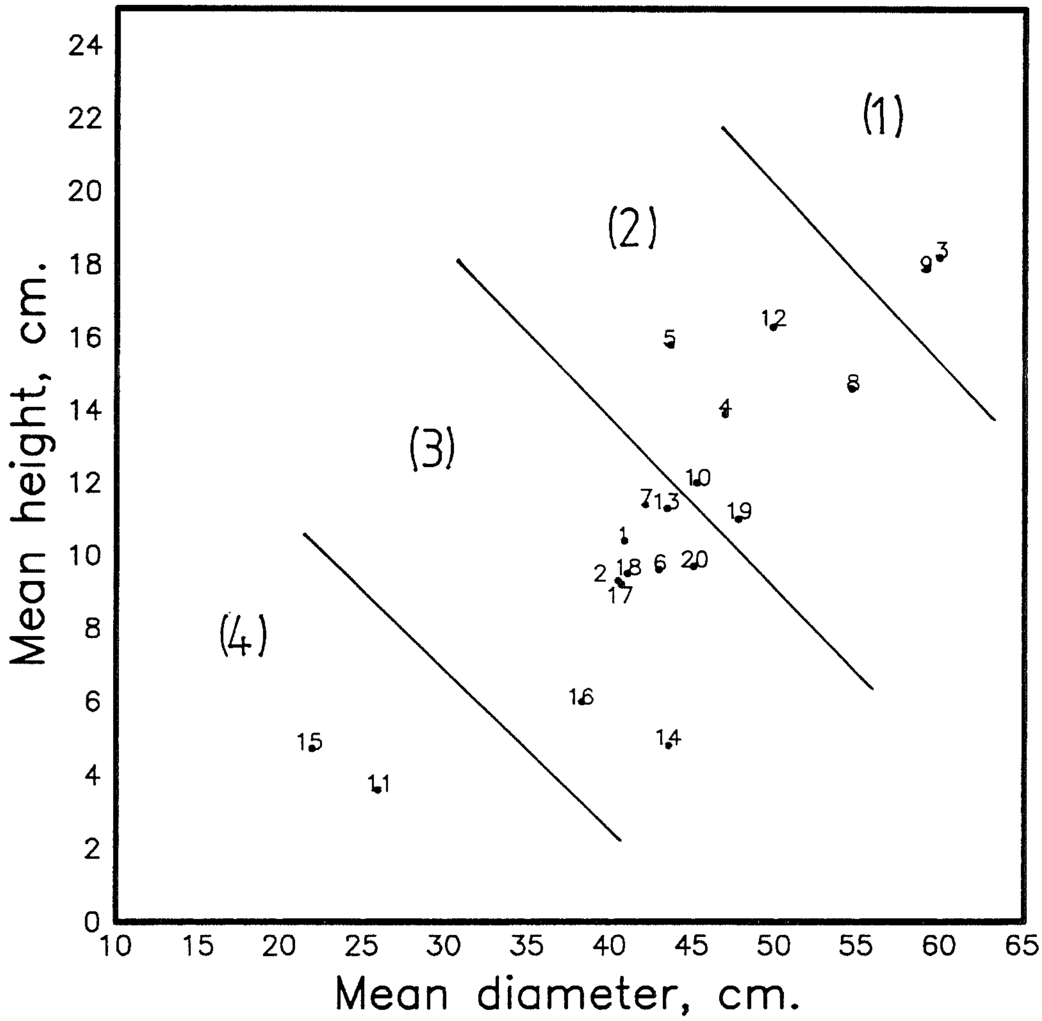
The effect of mowing on the mounds of **L. flavus.**

The photograph shows an area of chalk grassland at Martin Down NNR. The grassland has been cut with a tractor mounted mower in order to control Brachypodium pinnatum. In this case the mower has been set too low and the ants mounds in the area have been "topped". Such damage could kill the colony, if the queen was in the part of the mound removed. Scrub cutting by mechanical means can have the same effect on ant mounds.

Figure 12.3.

Scattergram of the mean diameters and heights of the mounds in each sample quadrat.

1) = no grazing. 2) = light grazing (up to 800 sheep days/hectare/year) 3) = heavier grazing (800 - 1,500 sheep days/hectare/year) 4) = very heavy grazing (>1,500 sheep days/hectare/year.



Some of the quadrats are in anomalous positions for the grazing levels given. For example, OWH SS 7 lies in the no grazing are of the plot, due to its very large mounds. Also MD 7B is placed in level 3) but is presently a light grazed area. See the text for further details of each sample quadrat.

1 = OWH SS 4, 2 = OWH SS 5, 3 = OWH SS 7, 4 = OWH SS 8, 5 = OWH SS 9, 6 = OWH SS 11, 7 = OWH SS 12, 8 = OWH NFS, 9 = OWH C10, 10 = AR 11, 11 = AR 12, 12 = AR 15, 13 = AR 16, 14 = AR 5, 15 = AR NWS, 16 = MD 7B, 17 = MD 4A, 18 = MD 4B, 19 = MD 3B, 20 = ST.C.

been placed on the basis of the grazing figures given in Chapter Ten.

12.3. Mound sizes and environment.

There are a number of environmental factors that can affect the mounds of *L. flavus*. Previous research work would suggest that shading and aspect may be the most important on the study sites. Pontin (1969) and Wells et al (1976) noted that the mounds become taller as shading increases with the growth of vegetation. Thomas (1962) noted how different aspects on a hillside at OWH had different shaped ant mounds on them. Aspect of a slope will also affect the amount of insolation of the mounds. When the mounds are on a north facing slope they receive less direct sunlight than they would on a south facing slope. North facing slopes will also be somewhat damper than south facing ones (Smith 1980). Perring (1959) found a number of soil factors related to the slope and aspect of chalk grassland sites.

The basic physical environmental characteristics that were measured for all of the sample areas (bar ST. C.) were soil depth, soil pH, altitude and slope. Product moment correlation analyses were carried out between these factors and the mean heights, diameters and volumes of the mounds in the sample areas. Significant negative correlations were found between the pH of the sample areas and the mean height and volume of the mounds in the sample areas (volume; $r = -0.587$, $P<0.05$, height; $r = -0.501$, $P<0.05$, $n = 19$ in all cases). The correlation between the pH and the diameter of the mounds was on the borderline of significance ($r = -0.455$, $P=0.05$). This then would seem to indicate that as the soil pH tends to increase the size of mounds present will tend to decrease. However, there is a possibility that this analysis was unduly influenced by 1 or 2 of the data pairs.

In particular the very low pH recorded in OWH C10 where the second largest mounds were found. The pH in this area, at 6.97, was 0.34 lower than the next nearest sample area. In this case the low pH is likely to be due to leaching down of materials from brown earth soils around the area and also it is possible that the Yew trees (Taxus baccata) bordering the sample area are influencing the pH with their acid needles falling into it.

Secondly the high pH recorded in AR 5 where there is a poor underdeveloped soil that has a high raw chalk component. In this sample area the pH was 7.80, 0.12 units higher than the next nearest sample area. Here the mounds were recorded as having very small heights and volumes due to the tops of the largest mounds being removed during scrub cutting operations. Excluding OWH C10 and AR 5 the range of pH is only from 7.31 to 7.66 and the correlations to the size of the mounds are lost.

The wide range of habitats that are occupied by L. flavus colonies (see section 3.4.) with the great range of pH that the habitats clearly have (from acid heathland and peat bogs to alkaline calcareous grassland) would suggest that pH of the habitat is not of major importance to this ant.

A significant negative correlation also occured between the soil depth of the sample areas and the mean diameter of the mounds ($n = 19$, $r = -0.499$, $P<0.05$) and the corresponding correlations to the mean volume and height of mounds were close to significance ($n = 19$, volume; $r = -0.432$, $0.10>P<0.05$, height; $r = -0.430$, $0.10>P<0.05$). This then is indicating that as the depth of soil decreases the size of the mounds in the sample areas tends to increase.

As the size of the mounds increases then more of the soil available in the sample quadrat is locked up in them. In OWH C10 for example, a simple calculation shows that over 20% of the soil in the sample area is locked up in the form of ant mounds. However, the moving of soil by the ants into their mounds is not great enough to significantly affect soil depth in most of the quadrats. It is more likely that the conditions which favour large mounds of L. flavus also favour a loss of soil, perhaps due to water flow erosion.

On chalk grasslands soil will tend to build up on the less steep slopes and be thinner on the steeper slopes, due to soil creep (Harding 1973). However, amongst the sample areas, there was no significant correlation between the soil depth and the slope of the sample areas ($n = 19$, $r = -0.210$, $P>0.10$).

There was no significant correlation between the slope of the sample areas and the mean height or volume of their ant mounds ($n = 19$, height; $r = -0.195$, $P<0.10$, volume; $r = -0.218$, $P>0.10$) but there was a significant negative correlation between the slope and the mean diameter of the mounds ($n = 19$, $r = -0.473$, $P<0.05$). Mean mound diameters tend to be smaller on steeper slopes.

There is thus a somewhat confusing mix of correlations here. Both soil depth and slope of the sample areas show significant negative correlations with the mean diameter of the mounds. Chalk grasslands tend to have thinner soils on steeper slopes, but the sample areas in this study, do not show this characteristic. It is clear that what constitutes a favourable area for L. flavus, in terms of mound sizes cannot be fully explained by the data considered in this section. Other factors, in particular the management of the sample areas will affect the ant populations and other environmental characteristics, not yet considered could also be important.

The slope of the sample areas also showed a significant positive correlation with the altitude of the sample areas ($n = 19$, $r = 0.539$, $P<0.01$) indicating that steeper slopes tended to be found at higher altitudes. No significant correlation was found between slope and pH of the sample areas ($n = 19$, $r = -0.188$, $P>0.10$) in contrast to the results of Perring (1958) who found that lower pH's tended to occur on less steep slopes.

There was no correlation between the altitude of the sample areas and any measure of the size of the mounds ($n = 19$, volume; $r = +0.056$, $P>0.10$, diameter; $r = +0.084$, $P>0.10$, height; $r = +0.082$, $P>0.10$). The altitude of the sample areas was negatively correlated with the soil pH of the sample areas ($n = 19$, $r = -0.576$, $P<0.01$) indicating that the sample areas in higher locations tended to have lower soil pH values.

Moving on to consider the aspect of the slopes on which the sample areas lie, differences are at once apparent. Comparing the mounds on the south slope at Old Winchester Hill to those on the opposite north slope of the reserve, OWH NFS, it was found that the north slope mounds were on average larger than those on the south slope. The average maximum diameter was larger than all the south slope quadrats except OWH SS 7 ($P<0.05$ in a series of t-tests), and the height significantly greater in 4 out of the 7 quadrats ($P<0.05$). The grazing pattern on the north slope has been similar to that on the south slope, although it is grazed as a single unit (J. Bacon, pers. comm.). It is therefore probable that the different aspect is the major factor contributing to this phenomenon.

To examine the effects of aspect on the sample areas as a whole the areas were divided into those facing north and those facing south. Sample areas whose aspects fell into the arc between 135 and 225° (ie.

45^{o}'s either side of 180^{o}) were considered to be south facing. Sample areas whose aspects fell into the arc between 315^{o} and 45^{o} (ie. 45^{o}'s either side of 0^{o} were considered to face north. Areas 45^{o} either side of due east or west were not included. neither were areas that had a slope less than 5^{o} (considered to be flat).

This gave 8 sample areas facing south and 7 facing north. Both the mean diameters and heights of the ant mounds from the sample quadrat were examined for these contrasting aspect groups.

Diameters:	Facing south	Facing north
	40.8	54.6
	40.4	59.9
	59.1	45.2
	46.9	25.9
	43.6	49.8
	42.9	43.4
	42.1	47.7
	45.0	
Mean	45.1+/-2.14	46.6+/-4.07

Heights:	Facing south	Facing north
	10.4	14.6
	9.3	18.2
	17.9	12.0
	13.9	3.6
	15.8	16.3
	9.6	11.3
	11.4	11.0
	9.7	
Mean	12.3+/-1.15	12.4+/-1.79

In both cases the means are higher for the north facing slope mounds. In both cases the largest mounds are found on the north facing slopes. Statistically no significant differences can be demonstrated, either by an F-test or by a Mann-Whitney statistic (diameters $F = 3.16$, $u = 17$, heights $F = 2.13$, $u = 22$, all $P>0.05$).

There does appear to be a trend towards increasing mound size on north facing slopes, but it seems that the small sample size and variability of the sample areas makes it difficult to demonstrate. Management differences are responsible for some of the variation. As has already been discussed above more intense grazing leads to reduced mound sizes. Thus AR 12 and 16 were both heavily grazed and north facing. On the other hand OWH SS 7 had only a few large old mounds yet was south facing.

The fact remains however, that the largest mounds were found on north facing slopes. For example, the largest mounds of any quadrat were found in OWH C10. This area faces north, lies in a valley bottom, surrounded by trees and is thus highly shaded. It is also ungrazed by livestock, with only small amounts of natural rabbit and deer grazing. Scrub is cut periodically to prevent the development of small shrubs. The herbage is, as a result, very tall, frequently overshadowing the mounds. As a result of this combination of environmental and management characteristics the mounds have grown extremely large.

OWH C10 lies close by to OWH NFS which as a result of grazing has much shorter vegetation that does not overshadow the mounds. It is also not overshadowed by surrounding trees as is OWH C10. While the diameters in OWH C10 were not significantly larger than those of OWH NFS, the heights were, ($t = 2.96$, 187 degrees freedom, $P<0.01$ 1 tailed test). Both the lack of grazing and the low insolation probably contributed to the increased size of these mounds. The large amounts of soil 'thrown up' in OWH C10 appeared greater than in any other quadrat.

At Martin Down the largest mounds were also those found on the north facing slope (MD 3B). They had significantly greater diameters than those of the other quadrats on the reserve ($P<0.05$, 1 tailed t-tests).

At Aston Rowant there are no open south facing slopes so that the comparison with a north facing slope could not be made. Furthermore the effects of the different management regimes have obscured the impact of the small differences in aspect that were present.

Observations on the 'throwing up' of soil show that it seems to occur when conditions are wet, ie after rain, or in early morning dew. Dew will persist for much longer on north facing slopes thus giving the workers a longer period to heap soil onto the top of the mound. A similar argument also applies to mounds in tall vegetation, where dew also persists longer. This may be a contributary factor in size differences observed.

In conclusion, the mounds of colonies lying on north facing and more shaded slopes will grow to be larger than those lying on more south facing slopes, providing more intensive grazing or other management procedures do not prevent this.

These conclusions, taken with those of the previous section, show that mound sizes can be greatly affected by both management of the area they are found in, and the environment of that area. The use of size to estimate the age of a mound, based on a single estimate of the amount of soil added to a mound in a year, as proposed by King (1981b) is not likely to be a technique to which much reliability can be attached.

12.4. Mound densities and management.

A product moment correlation between the grazing intensity over the last three years and the density of the mounds in each sample quadrat gave no significant correlation ($n = 19$, $r = +0.127$, $P>0.05$). Again, because of the impossibility of assigning a figure to each quadrat which is a measure of grazing intensity over a longer period, prior to the mapping of the quadrats, it is necessary to look at the sample areas individually and consider their past management in more detail.

There was a very consistent pattern over most of Old Winchester Hill south slope with between 57 and 71 mounds in the sample quadrats. As the variation in the grazing regime here was a recent event, this is reflected in the similarity of the compartments. Only two quadrats OWH SS 7 and 9 do not fit in with this, OWH SS 7 with 8 mounds and SS 9 with 99 mounds. OWH SS 9 had the largest population of mounds found on the south slope. It also had the largest population of Juniperus communis (Juniper) on the slope. From section 5.4.1.3. it will be recalled that the Juniper population on the south slope was substantially damaged when bomb clearing activities were undertaken on the reserve. Juniper is a slow growing and sensitive plant and the large amounts of it in this sample area would thus suggest that this area was much less disturbed than the others. Any disturbance is likely to have affected the ant populations as well. If OWH SS 9 came out of this disturbance better than the other areas it is possible that the ant population, as well as the Juniper population, survived better than in the other areas on the slope. The case of OWH SS 7 will be discussed in Chapter Thirteen.

ST. C., also a south facing slope, had a population of 66 mounds, very similar to the majority of quadrats on the southslope at OWH. All of these quadrats, OWH SS 4, 5, 8, 11 and 12, and ST. C., have around 60 to 70 mounds. They lie on south facing slopes and their grazing is more than heavy enough to ensure that the grass remains short and there is no development of scrub.

At Martin Down the number of mounds per quadrat ranges between 61 and 86. It is, though, more difficult to interpret the results from the quadrats, because of the lack of knowledge of their management before 1978. The situation of *L. flavus* in 1978, before grazing was restarted is not known. Knowledge of how many mounds survived the period of neglected grazing would aid interpretation of the position in 1984.

Many areas of the reserve were covered in dense patches of *Bromus erectus* and *Arrhenatherum elatius* in 1978. In OWH C10 the *L. flavus* colonies have survived in quite tall grass, mainly *A. elatius*, which is ungrazed. *Bromus erectus* was lacking in OWH C10, and this coarse grass, which grew extensively at Martin Down, is much less favourable to the ants, with its thick growth. It is not, of course, known precisely how much of this grass was present in the quadrats at Martin Down in the past, or indeed how far the growth of scrub had progressed, and therefore how many colonies might have survived to 1978. Dense patches of *Bromus erectus* are still present in some areas of the reserve. An examination of one of these areas in 1989, indicated that there were very few colonies of *L. flavus* present. If the density of this grass was in any way similar in the sample quadrats before 1978, it is likely that many colonies would have died. It therefore seems likely that the *L. flavus* population at Martin Down is in the process of building up again from a low level in 1978.

Details of the longevity of colonies of *L. flavus* and their mounds would suggest that they can exist for considerable periods of time. From the studies of other authors it would appear that individual mounds can reach considerable ages. Nests have been observed in continuous occupation for long periods. Pontin (1963) had observed a nest in continuous occupation for 16 years, which he concluded could be 22 years old. King (1977b) estimated from the above ground volume of a mound and his estimate of the maximum accretion rate, that the largest mound he had seen, (at Porton Down, Wiltshire) was 156 years old. Using Kings accretion rate figure, Wells et al (1976) estimated between 80 to 100 years for mounds at Porton Down, Wiltshire, England. Using the same method, but based on Pickles' (1942) acccretion rate figure, Haarlov (1960) estimated between 80 and 90 years for mounds on a tidal meadow in Denmark. King (1981b) has used his own accretion rate figure to attempt to date the age of mounds, using this age as an estimate of the time since grasslands were last ploughed. As noted above these sorts of estimates, based on the size of mounds, may not be greatly accurate, but it is probable that the mounds are long lived.

The life span of an individual queen and colony is not known, although in the laboratory queens can survive for at least 10 years (Pontin 1963). There is as yet little evidence for the adoption of new queens in natural colonies. Crawley and Donisthorpe (1913) and Anderson (1970) managed to observe some queen adoption in artificial nests. Previously Lubbock (1882) found no queen adoption in 5 trials. Gynes are often found in the mound after the sexual flights have taken place (pers. obs.), but it is likely that these are eventually killed by the workers. It seems unlikely that an individual queen could survive for 80 or more years.

The known details on the ages reached by colonies of <u>L. flavus</u> would suggest the brief period since 1978 when grazing was restarted, to the examination of the quadrats in 1984, could well be insufficient for the potential maximum density of mature colonies to have developed. Bearing this in mind, quadrats MD 4A and 4B, having 61 and 67 mounds respectively, are remarkably similar to other areas, such as the OWH south slope quadrats.

Even after being abandoned, L. flavus mounds can survive unoccupied for a long time. For example Grubb et al (1969) found old mounds in Madingly Wood, Cambridgeshire, England, which must have been there since the development of the secondary woodland at least 65 years ago. Similarly at Old Winchester Hill, mounds are still visible in a 40 year old secondary ash (Fraxinus excelsior) wood. Old large abandoned mounds are frequently taken over by new small colonies (pers. obs.). The old mounds are obviously a prime site for a new colony, with warm easily worked soil. Thus in MD 4A and 4B survival of the mounds, without colonies being present, through the period of relaxed grazing, may have allowed new colonies to rapidly occupy the old mounds when grazing was resumed.

The situation in MD 7B was more complex, and demonstrates the need for a thorough knowledge of the past history of an area to understand current ant populations. In the early 1960's the area in which this quadrat lies was harrowed by a local farmer and it is probable that this would have destroyed many, if not all of the ant colonies present.

From that time the grazing was neglected and it is likely that this would have led to ranker grass growth, inhibiting the establishment and growth of new colonies. Some would have undoubtedly established themselves, but probably a reduced number, compared to the other quadrats. When grazing was restarted, it became possible to establish new colonies in the area. Thus in 1984 it probably had a mixture of old and new colonies, a view supported by the distribution of the mound sizes shown in Figure 10.49. where it can be seen that there is a large spread of mound sizes, from small ones (10-30 cm. across) to much larger ones, 50 cm. across and over. As part of the study of the worker populations of individual colonies, five of the colonies in this area were later dug up (see Chapter Ten). Their sizes fell into two distinct groups. Those with greater than 30,000 workers, which were clearly well-established and others which contained a half or less of this number and could therefore be assumed to be more recently founded colonies.

It might be expected that the large number of small colonies in this quadrat (86) would decrease as they grow and competition between them increases. Eventually this might lead to a reduction down to the smaller number of larger colonies as in the other quadrats at Martin Down.

In MD 3B there was a higher density of mounds than in MD 4A and 4B, and they were also larger. As noted in Chapter Ten the area came through the years of neglected grazing better than the other quadrats, with less development of coarse grass and scrub. It seems possible that the population of mounds was able to survive better in this area than in MD 4A and 4B, leading to more being present at the time of the examination of the quadrats in 1984.

The sample area AR 5, in common with many areas of chalk grassland, was ploughed in the Second World War and has never fully recovered. Regular cutting, as shown by the reserve records, has kept the scrub in check, and grazing has been generally light, partially due to the lack of good grass. A surprisingly large population of ant mounds (75) has nevertheless developed despite the bare and slightly scrubby appearance of the ground. The area contrasts with other locations seen on the reserves where severely disturbed grassland has not yet produced any colonies of L. flavus at all. At Aston Rowant there is an area where spoil from the construction of the M40 motorway was dumped in the early 1970's. No colonies were found in this area, even young ones, despite an extensive search in 1984. Similarly, in 1984, there were no colonies visible in an area of Martin Down which was ploughed and used as arable land up until 1956, although a more recent examination (1989) has revealed one or two very small and very widely scattered colonies as present.

There would be no shortage of colonising fertile queens in such areas, where there are many thousands of existing colonies in surrounding areas, and so it must stem from a failure of queens to establish colonies, possibly due to an absence of suitable food organisms. While the ants are very easily spread by the large sexual flights, the food organisms, such as the aphids may not be so easily spread, although, as is later discussed some of the common aphids used by L. flavus would appear to be easily spread. This could limit the ability of the ants to colonise such areas. The extent of the ploughing in AR 5 is not known, but simply turning over the soil would probably not have eliminated the soil invertebrates. Persistent ploughing as in the arable land at Martin Down would probably do so. The soil in the area at Aston Rowant was not downland soil and so, would not have had the same invertebrate fauna to start with. Much more specific evidence would be needed to substantiate a theory such as this, but as the aphids and other invertebrates can be relatively easily isolated from soil samples it should present no great difficulty if attempted.

Another possible reason is a failure to establish colonies due to overwhelming competition from other species of ants. Again it would be possible to investigate this in the future. The work of Pontin (1961b, 1963, 1969) would suggest that competition with other ant species, such as Lasius niger and perhaps more importantly in areas such as this, Myrmica scabrinodis, is important in determining the productivity at least of L. flavus colonies.

The quadrats with the largest number of mounds were AR 11, 12, 15, NWS and OWH C10. Of these quadrats AR 11, 15 and OWH C10 are all on north facing slopes, and were only lightly grazed. It seems that this combination of features leads to the largest populations of mounds of L. flavus. In the AR barn plots, AR 11 to 16, we have a direct comparison between light and heavy grazing. The number of mounds in AR 11 and 15 (113 and 126), was much greater than that in AR 16, (63). The comparison between AR 15 and 16, shown in Figures 10.33. and 10.38. illustrates this large difference.

The very large number of mounds in AR 12 (273) was exceptional. A substantial proportion were very small (see Figure 4.2), and this contrasted greatly with the situation in all of the other quadrats except AR NWS. In fact in AR 12, 45% of the mounds were small diggings under 20cm. across, and in AR NWS the proportion rose to 60%. The examination of some of these 'mounds' in AR 12, (see section 9.2.), demonstrated the difficulty in determining their true status. The mapping of the locations of the mounds in AR NWS showed a patchy distribution. Nearest neighbour analysis also confirmed the lack of overdispersion, (see Chapter Fourteen). Many of these very small mounds, no more than bumps in the ground, were very close to each other. The mounds were overdispersed in AR 12. Both of these quadrats are extremely heavily grazed and it seems possible that the heavy grazing has suppressed the formation of large central mounds, and that the workers have instead moved to a more decentralised organisation. The actual number of true colonies present in these quadrats may have been very much lower than the figures suggest. Without a very detailed examination of the system it is difficult to assess the true situation. A parallel is suggested with the nesting habits of *L. flavus* in garden lawns and recreational areas. Here no mounds are made due to the constant trampling and mowing of the grass.

In conclusion it can be said that the densities found in the sample quadrats, suggest that areas with a more intensive management regime will, after a period of 10 years or more, support a lower density of ant mounds than in areas that have been more sympathetically managed.

12.5. Mound densities and environment.

Using product moment correlation analyses no relationships were found between the soil pH or depth of the sample areas and either the density of mounds present or the area covered by them. Similarly there was no apparent relationship between the altitude or slope of the sample areas and the density of mounds or area covered (in all cases, $n = 19$, $r>-0.43$, $P>0.05$).

The major physical environmental factor that can be simply examined, and does seem to be important, is again the aspect of the sample areas. By dividing the sample areas into north and south facing slopes as in Section 12.3. the following data on the respective numbers of mounds per quadrat is produced.

	South facing slopes	North facing slopes
	67	70
	64	119
	8	113
	66	273
	99	126
	57	63
	71	78
	66	
Mean	62.3+/-8.9	120.3+/-27.2

It is clear at once that the largest densities of *L. flavus* mounds are to be found on north facing slopes rather than south facing ones. An F test shows a significant difference between the two sets of sample quadrats ($F = 8.13$, $P<0.05$).

AR 12 and AR NWS have already been mentioned in the previous section and the odd characteristics of their ant mounds considered. The large size of the mounds in OWH C10 has also been discussed above. A large population of *L. flavus* mounds (119) was maintained in this quadrat and so it can be concluded that this species of ant can survive well here, even in an area of reasonably tall grass, with no managed grazing, on a north facing slope. This is probably only true in the south of England as on more exposed slopes further north the conditions are not as suitable. *L. flavus* mounds are seen only on the warmest south facing slopes in the Derbyshire Dales for example (pers. obs.), and not on north facing slopes at all.

We can thus conclude from this data that north facing slopes on chalk grassland will on average carry a greater density of mounds than comparable south facing slopes.

12.6. Conclusions.

The broad conclusions from this chapter are that the most important factors in determining the density and size of the mounds of *L. flavus* to be found on a chalk grassland, are firstly, the aspect of the slope on which the grassland lies and secondly the intensity of management which the grassland receives.

The highest densities of *L. flavus* with the largest mounds are in general to be found on north facing, sheltered and lightly grazed chalk grassland and the lowest on south facing heavily grazed grassland. More intense grazing can reduce the population density and mound size on north facing slopes, as in AR 16. More favourable environmental conditions can increase the population density and mound size on south facing slopes.

It is clear that appropriate chalk grassland management can improve the density of a population of L. flavus in the long term (perhaps 10 years or more) while inappropriate management (heavy grazing pressure, scrub cutting too close to the ground etc.) can damage the population.

CHAPTER THIRTEEN

Mound sizes, densities and the biological environment.

13.1. Analysis of the floral assessments of the sample areas.

13.1.1. The species richness of the sample areas. This first simple analysis was done to see if there was any relationship between the diversity of the flora of the sample areas and the characteristics of the ant population. Spearman rank correlation analyses were carried out between the number of species recorded in each sample quadrat and the density, mean volume, mean diameter, mean height and area covered by the mounds in each sample quadrat. Only species with a number (1, 2 or 3) and mosses with the status u were included, for the purposes of this analysis. Other categories (see Appendix Nine) were ignored. Lichens were not included as it was felt that they were not searched for with equal effort in all of the sample areas. The number of species found in each sample area is given in Table XVI. The results are as follows, with the value of the correlation coefficient given and N = 19 in all cases.

Density of mounds	+0.222
Volume of mounds	+0.047
Diameter of mounds	+0.390
Height of mounds	+0.060
Area covered	+0.106

None of the correlations were significant.

This simple approach not having yielded any interesting results, further analysis using phytosociological community analysis methods was attempted.

13.1.2. Methods of analysis of floral data. There are two main approaches to the analysis of vegetation patterns, firstly, ordination, where the aim is to produce a spatial arrangement of the samples such that their proximity reflects their similarity (Goldsmith et al 1976, Whittaker 1978) and secondly, classification, where the samples are divided into distinct classes and may be arranged, for example, as a dendrogram. The methods can be complimentary (see Wright 1984 for example).

In this case the aim was not to divide the vegetation of the sample areas into classes but to examine differences between them, which were likely be of a continuous nature, for example, amongst the quadrats on the south slope of Old Winchester Hill. Thus, an ordination of the data was produced, consisting of a two dimensional graphical representation of the similarity of the sample areas.

13.1.3. <u>The production of the ordination.</u> The methods used were simple ones, relying on tried and tested techniques. They are well described by Mueller-Dombois and Ellenberg (1974), Barbour, Birk and Pitts (1980) and Cox (1976). Such techniques were first described and used by Bray and Curtis (1957).

There are several steps involved and these are briefly described below.

1. The calculation of a matrix of index of similarity coefficients (IS's). Whittaker (1978) recommends the use of the index of Sorensen (1948) (which he suggests may have been first derived by Czekanowski 1913) to determine similarity between samples based on presence and absence data, such as the data collected was.

$$IS = \frac{2C}{A + B} \times 100$$

A = The number of species recorded in Sample area 1.

B = The number of species recorded in Sample area 2.

C = The number of species common to both Sample areas.

The species included in the analysis were as described in the previous section. The matrix of the number of species in common is given in Appendix Thirteen as is the matrix of similarity indices.

2. The calculation of a matrix of index of dissimilarity values for the sample areas. The dissimilarity index (ID) for a pair of quadrats is simply 100 - IS. These dissimilarity values can then be used to calculate the figures necessary to ordinate the samples in a polar ordination. The matrix of dissimilarity indices is given in Appendix Thirteen.

3. The first axis. The two most dissimilar quadrats are selected as the ends of the first axis. These were numbers 6 and 9 (OWH SS11 and OWH C10), with a dissimilarity index of 65.5 (see Appendix Thirteen). Thus the first axis is by definition 65.5 units long with sample areas 6 and 9 at its opposite ends.

4. The position of the samples on the first axis. These are calculated by the following formula:

$$X = \frac{(65.5)^2 + (ID\text{-}6)^2 - (ID\text{-}9)^2}{2(65.5)}$$

X = the position on the first axis (the X axis).

ID-6 = the index of dissimilarity between the Sample area and Sample area 6.

ID-9 = the index of dissimilarity between the Sample area and Sample area 9.

The figures calculated are given in Table XVI.

5. The second axis. The calculations so far split the samples in 1 dimension only. To further separate out the sample areas a second axis was calculated. The first step was to determine which sample most

Table XVI.

Values of X, Y and e for the sample areas for the first ordination.

Sample	No. species.	X axis value	e	Y axis value
1	58	10.4	14.8	24.8
2	37	18.5	10.1	27.8
3	42	8.2	21.1	32.9
4	57	14.9	14.5	24.4
5	56	5.0	15.7	27.0
6	47	0	-	28.3
7	57	12.8	14.3	23.2
8	61	52.1	31.9	21.6
9	40	65.5	-	26.0
10	47	26.0	46.4	0
11	60	29.7	34.9	16.6
12	68	25.9	39.1	18.4
13	54	30.6	40.2	18.2
14	48	17.6	34.7	23.2
15	46	12.3	33.3	21.5
16	48	24.3	42.4	47.4
17	54	27.7	37.4	39.6
18	42	27.4	41.2	22.8
19	51	17.8	24.9	27.6

1 = OWH SS 4, 2 = OWH SS 5, 3 = OWH SS 7, 4 = OWH SS 8, 5 = OWH SS 9, 6 = OWH SS 11, 7 = OWH SS 12, 8 = OWH NFS, 9 = OWH C10, 10 = AR 11, 11 = AR 12, 12 = AR 15, 13 = AR 16, 14 = AR 5, 15 = AR NWS, 16 = MD 7B, 17 = MD 4A, 18 = MD 4B, 19 = MD 3B.

poorly fit the first axis. This can be found by calculating the value e for each of the sample areas. This is a measure of the poorness of fit, (Barbour, Birk and Pitts 1980). The value of e is calculated by the following formula:

$$e = (ID-6)^2 - X^2$$

The values of e are given in Table XVI.

The sample with the highest value of e is selected as the first end point of the second axis. Sample area 10 (AR 11) has the highest value of e in Table XVI, and is thus the sample area which has the worse fit to the first axis. In order to select the sample area which will act as the other end point of axis 2, the sample area with the highest ID to sample area 10 was needed, subject to the convention that it should be within 10% of the length of axis 1, in distance from sample area 10, on the first axis, in this case 6.5 units. The sample area which best fit these criteria was number 16 (MD 7B). Thus sample areas 10 and 16 are the end points of axis 2 and the axis is 47.4 units long, the ID between sample areas 10 and 16.

6. The positions of the sample areas on the second axis. These were calculated by the following formula:

$$Y = \frac{(47.4)^2 + (ID-10)2 - (ID-16)^2}{2(47.4)}$$

Y = the position on the second axis, the Y axis.

ID-10 = the index of dissimilarity between the sample area and sample area 10.

ID-16 = the index of dissimilarity between the sample area and sample area 16.

The values of Y calculated are shown in Table XVI.

13.1.4. The results of the ordination. The ordination produced is shown in Figure 13.1.

Examination of the ordination suggested that there are some clear groupings of environmentally similar sample areas. Sample areas 1 to 7, representing OWH SS 4 to 12, are grouped on the left hand side of the ordination. As these samples all come from the same slope on the same reserve it would be expected that they would be similar floristically. In contrast, the other 2 sample areas from Old Winchester Hill (no.'s 8 and 9) are grouped on their own at the opposite side of the plot. These numbers represent the sample areas OWH NFS and OWH C10, located on the opposite north facing side of the reserve. These two areas shared several plants which were not recorded in any other of the sample areas, such as Mercuralis perennis and Cruciata laevipes and were clearly very different floristically to the sample areas on the south slope. However, as would be expected OWH NFS (no. 8) is closer on the plot to the south slope sample areas than OWH C10. It is a more open grazed area, while C10 is ungrazed with much taller grass and a much impoverished flora, only 40 species compared to the 61 of NFS.

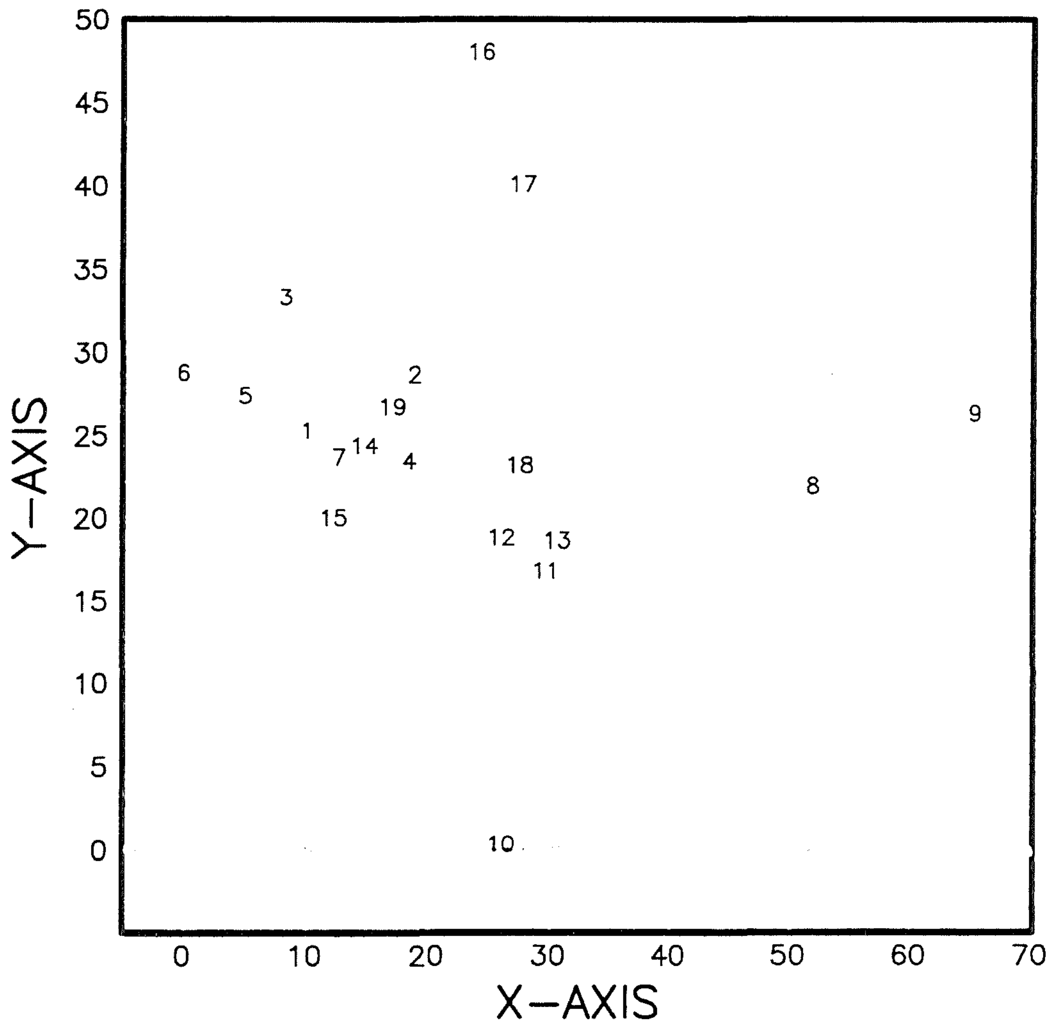
The 'Barn' plots at Aston Rowant, (no.'s 10 to 13) also group well on axis 1 but AR 11 (no. 10) is well separated by axis 2. This was the most species poor of this group of sample areas. Samples 14 and 15 (AR 5 and NWS) fall within the same area of the plot as the OWH south slope samples and these are more open areas than the 'Barn' plots, and thus environmentally more related to the south slope at OWH.

The Martin Down sample areas (no.'s 16 to 19) are also well grouped on axis 1 but again a single area (no. 16) MD 7B is separated well away by axis 2. This was the least grazed plot with the tallest vegetation. It seems possible though, that the separation given by axis 2 tends to exagerate the differences between this plot and the other Martin Down

Figure 13.1.

An ordination of the floras of the sample quadrats.

All plant species were listed for each sample quadrat. Similarity indices were calculated using the Sorensen Index. The ordination was calculated as shown by Barbour, Birk and Pitts (1980).



1 = OWH SS 4, 2 = OWH SS 5, 3 = OWH SS 7, 4 = OWH SS 8, 5 = OWH SS 9, 6 = OWH SS 11, 7 = OWH SS 12, 8 = OWH NFS, 9 = OWH C10, 10 = AR 11, 11 = AR 12, 12 = AR 15, 13 = AR 16, 14 = AR 5, 15 = AR NWS, 16 = MD 7B, 17 = MD 4A, 18 = MD 4B, 19 = MD 3B.

sample areas.

To establish if there was any relationship between the positions on the ordination of the sample areas and the characteristics of the their ant populations, a series of Spearman rank correlations were carried out between the positions of the sample areas on the X and Y axes and the ant population characteristics. The correlation coefficients were as follows.

	X axis	Y axis
Density of mounds	+0.255	-0.492*
Mean mound volume	+0.026	+0.075
Area covered	+0.470*	-0.431
Mean mound diameter	+0.107	-0.025
Mean mound height	+0.014	-0.004

* Significant correlation at the 5% level.

Two significant correlations were found. On the X axis there was a correlation with the area of the quadrat covered by the mounds. As noted above the extremes of the X axis are the south and north slopes at Old Winchester Hill and the importance of aspect to the ant mound populations has already been noted in the previous Chapter. On the Y axis there was a significant negative correlation between the positions of the sample areas and the density of the mounds. On this axis there was a significant correlation between the position on the axis of the sample areas and the soil depth of the sample areas (Spearman rank correlation, $r = +0.69$, $P<0.01$, $n = 19$). Thus soil depth is important to the flora of the sample areas. In Chapter Twelve it was also noted that there was a significant correlation between the soil depth of the sample areas and the volume of the mounds. This analysis indicates that there are links between the soil depth, floras and ant populations of the sample areas

The most important factors affecting the ant mounds were determined in Chapter Twelve, to be the management of the sample area and aspect of the sample area. These factors will also be of great importance to the flora of the sample areas. However, it is probable that the flora of the sample areas is also of importance to the ants. Different plant assemblages may support different invertebrates which form the food of the ants. There may also be differences in productivity of the different floras which may affect the ants. These points will be considered further in Chapter Eighteen.

One aspect of the flora of the sample areas not covered by the above comments, is the situation in OWH SS 7. The sample quadrat in this area had only 8 mounds found in it. It lies on the south slope at OWH, where the other quadrats examined had between 57 and 99 mounds in them. There was a simple difference between OWH SS7 and the rest of the slope, because it was dominated by the grass _Tricetum flavescens_, while the rest of the slope had a more typical chalk grassland _Festuca-Helictotrichon_ sward. OWH SS 7 also had a thick matty ground layer of vegetation, and this could well be the reason for the relative reduction in the ant population. The few mounds in the area were large ones, and it is possible that due to the thick matted layer it had been difficult for new queens to initiate new nests and colonise the area. It has also been suggested to me (J. Pontin, pers. comm.) that _T. flavescens_ is not a good grass for the root aphids that _L. flavus_ relies on for such a large part of its diet (see section 3.9.). In other areas where _T. flavescens_ was common there was not the same thick matted ground layer of vegetation and litter.

13.1.5. _Conclusions._ We can conclude from this analysis that the sample areas have different floras which group together on the ordination quite well according to the reserve on which they are located, their physical environmental characteristics (particularly their aspect) and their management or lack of it. There are also significant relationships between the flora and the ant mound populations. L. flavus can be found in large numbers in a wide variety of very different areas (see section 3.5.) with very different floras. In comparison the minor floristic differences found here are relatively insignificant but may be produced by management and physical environmental factors which have also been shown to affect the ants. The different floras may be a link between the management and the environment and the effects on the ants.

13.2. General comments on the bryophytes.

While the higher plant floras of chalk grasslands have been extensively investigated, the bryophytes are less well known, and so some general comments on the bryophytes found during this survey seem appropriate.

Because of the time of year in which the bryophytes were examined it is possible that some species were missed. During the dry Summer the bryophytes are less conspicuous. However, some interesting points were noted.

Watson (1960) considered the bryophytes of OWH in detail when he surveyed the bryophytes associated with the transect which Thomas (1960, 1963) set up on the reserve. While several species that Watson (1960) lists were not found in the current survey, probably because the bryophytes were looked for in a limited number of areas only on the reserve, ie. the sample areas, several species were found which Watson (1960) does not record as present on the reserve.

Eurhyncium swartzii found on the south slope was recorded by Watson (1960) on other chalk grasslands (Kingsley Vale and Lullington Heath) and so it is not surprising that it was found here on the south slope. Bryum capillare is in the same situation. Other mosses were not found by Watson (1960) on any of the chalk grasslands he examined. These species are Calliergon cuspidatum, Phascum cuspidatum, and Rhyncostegium confertum.

Aside from Calliergon cuspidatum these species were all found on the south slope. One of the interesting things about the south slope was the number of mosses that were found to be associated with the ant mounds. The ant mounds of the south slope appeared to provide a major microhabitat for the mosses. As in other areas which have been investigated, the moss Pseudoscleropodium purum was a common feature of the north side of ant mounds. This feature has been recorded by King (1977a) and Thomas (1962). Also of interest was the presence of another community of mosses on the south facing sides of the mounds. These were typified by the moss Weissia microstoma. This is a small acrocarpous species, described by Watson (1981) as locally common in calcareous places. It was extremely common on ant mounds, not only on the south slope at OWH, but also on mounds on the other reserves.

This species of moss grew best on areas of bare soil that were to be found on the steep south facing side of the mounds. These areas seemed to provide an otherwise almost unavailable niche on chalk grasslands for such mosses to grow in. Also found with W. microstoma, in such situations, were Bryum capillare, Barbula spp., Tortula spp. and Phascum cuspidatum. Another species which could expected to be found in such circumstances is Pottia lanceolata, which was noted by F. Rose on ant mounds in Kent (Watson 1981).

Watson (1960) does record the presence of W. microstoma at Lullington Heath and Aston Rowant, but not at OWH. This seems quite remarkable considering its apparent abundance during the current survey, not only at OWH, but also at AR and MD, unless the moss has increased in frequency since that time, or the survey by Watson (1960) specifically ignored ant mounds.

It is possible that there was less of the moss at the time that Watson (1960) was recording, as this was during the period that grazing of the reserve was much reduced, due to the reduction of rabbits by myxomatosis. It was observed during this survey that W. microstoma was much rarer in areas of taller vegetation. Watson (1960) notes that the presence of this moss was much decreased on sites of taller vegetation that he studied.

One species that it was expected to find was Hylocomium splendens. Watson (1960) records its presence at OWH and also says that it was particularly associated with mounds found in these areas. He suggests, which seems likely, that the mounds were of ant origin. The other moss which was particularly found on the north side of ant mounds was Pseudoscleropodium purum. However, despite extensive searching, no H. splendens was found on any of the sample areas at any of the study sites.

Only one species of liverwort was found during the whole survey, this being Lophocolea bidentata in AR 5. Dry chalk grasslands are not a particularly good habitat for liverworts but Watson (1960) did find some Frullania tamarisci and Watson (1981) suggests that Leiocolea turbinata and Scapania aspera may be found on chalk grasslands. Lophocolea bidentata was not included amongst these but it is a common component of grasslands (Watson 1981).

13.3. Rabbit grazing in the sample areas.

13.3.1. Introduction. The influence of rabbits on the growth and composition of vegetation has long been appreciated (Thompson and Worden 1956, Thomas 1960, Sheail 1971), although perhaps it is not generally realised that this importance is of a fairly recent origin. Thomas (1960) concluded that rabbits had little or no effect on British vegetation (except in very localised areas, around warrens, where they were protected) until the 1840's or 50's. From the early 1800's up to 1950 rabbit populations rapidly increased, due to a variety of factors, with the most important being climatic amelioration, predator reduction and agricultural changes (Southern 1956, Sheail 1971, Lloyd 1975, Sumption and Flowerdew 1985).

The economic damage caused by rabbits, as they rapidly increased in numbers during the nineteenth century, quickly became clear (Buckley 1934) but it was not until the second half of this century that the importance of rabbits in the maintenance (or indeed the destruction) of 'natural' habitats was realised (Thompson and Worden 1956, Costin 1960, Sheail 1971). Several authors then speculated on the effects, in these habitats, of the release of the myomatosis virus in Britain, and indeed, in other countries (Gillham 1955, Ratcliffe 1956, Thomas 1956 for example).

Watt (1957, 1960) conducted an experimental study on the effects of excluding rabbits from acidic grassland in the Breckland of East Anglia. Other researchers conducted observational work in order to observe the effects of loss of rabbit grazing as it occurred. The spread of myomatosis was documented by several authors (Mead-Briggs 1977 for a more recent example). The infection was first introduced into Europe, in France, in June 1952, from where it spread to many

European countries. The first report in England was on 13th October 1953 in Kent (Amour and Thompson 1955). It had reached the farthest corners of mainland Britain by 1955. Kills of rabbit populations were commonly over 99%, under favourable conditions for the spread of the virus (Lockley 1956).

Ranwell (1960) observed the effects on the vegetation of the reduction in rabbit grazing, caused by myxomatosis, on a dune system in Anglesey but of more interest to this study is the work of Thomas (1960, 1963) who observed the effects on the vegetation of the loss of rabbits on chalk grasslands. Thomas (1960) concluded that after the loss of rabbits (in 1954) turf increased greatly in height and there was a spectacular increase in abundance of flowers, especially orchids in some places. However, even at this stage there was an indication that the long term loss of grazing was leading to a loss of botanic density and diversity. There had been an increase in woody plants such as brambles (Rubus fruticosus) and gorse (Ulex europaea).

13.3.2. Rabbits and ant mounds. Thomas (1963) confirmed his previous observations (Thomas 1960) on the effect of cessation of rabbit grazing on the flora of areas, and went on to discuss the relationship between rabbits and ant mounds. He observed that rabbit "latrines" were often located on ant mounds. Thomas (1963) also noted that while ant mounds grew in the absence of rabbits, growth was much faster in their presence. He concluded that one of the reasons for this was the incorporation of rabbit pellet material into the structure of the mound. In Spring, he observed that mounds in areas where rabbits were present, showed up dark green, in contrast to the brown of surrounding grassland. This was said to be due to the fertilizing effects of rabbit urine and droppings on the mounds. The grasses on the mounds (often dominated by Festuca rubra) were also noted to be grazed shorter than the surrounding grassland by the rabbits.

13.3.3. Comparisons with the results of Thomas (1963). The results of this study on the whole support the observations of Thomas (1963) as detailed below.

1). Firstly in all of the sample areas, on all occasions, the number of rabbit droppings found was far greater on the ant mounds than on the surrounding grassland (see Figures in Chapter Ten). Ant mounds are used as the primary site for defecation by rabbits.

2). Ant mounds were clearly seen in Spring to be darker green than surrounding grassland, in several areas where rabbits were present (see Figure 13.2.).

3). Droppings were seen in all states of decay on the mounds and often were partially, or almost completely, covered by soil that had been thrown up by the worker ants. Therefore it seems likely that they do contribute to mound growth, but the importance of this, as opposed to the throwing up of soil by the ants themselves, is not clear. Several authors have estimated the amount of soil excavated by the worker ants and have concluded that there is sufficient to account for the size of the mounds (see section 3.5.4.). However, in the data from this study, is there a relationship between rabbit dropping density on the mounds and mound size?

In order to test this the maximum recorded mean density of rabbit droppings on the mound for each sample area were ranked in order. This was also done for the size measures of the ant mounds. Spearman rank correlations were then done to see if there was any relationship between mound size and rabbit dropping density.

The maximum figures were used because of the build up in the numbers

Figure 13.2.

Ant mounds in Spring at Old Winchester Hill.

The ant mounds in the ungrazed area, on the right of the fence line, show up much greener than their surroundings. This is due to an early season burst of grass growth, possibly induced by the nutrients in rabbit faeces and urine, and also to rabbits grazing the top of the mounds, so that the tall dead grass material from the previous seasons growth has been removed, making the green more visible.

The area on the left of the fence line is OWH NFS.

of droppings found in the sample quadrats throughout the year. This was due to the pellets not decaying in the dry Summer conditions. The first sign of the pellets breaking down did not occur until September, when slugs appeared to be feeding on them. Later on in the year two species of fungi were also found on the droppings, both Ascomycetes. The first produced small orange ascocarps, 1 - 2 mm. across, and the fruiting bodies of the second species were small spindles, similar to those of Calocera cornea, but bright red in colour. Neither species has been identified as yet. The droppings thus build up throughout the year and a maximum figure reflects the amount of rabbit activity through the year.

There was no significant correlation between the maximum mean number of rabbit droppings on the mounds recorded in a quadrat and the diameter or height of the mounds, although the trend was for the mounds to be smaller when the number of droppings was higher (see Table XVIII) which is the reverse to what would be expected from Thomas's (1963) theory.

13.3.4. Further analysis of the data.

In order to investigate the hypothesis posed in Chapter Four, ie. that rabbit activity does not influence any of the measured characteristics of the ant population, it was necessary to assess in some way the differences between the measured rabbit dropping levels in the sample areas.

To do this the dropping density both on and off the mounds had to be taken account of. Just taking the on the mound dropping density might underestimate the influence of rabbits in areas where there were large numbers of droppings off the mounds. The data on the maximum and minimum mean number of droppings recorded both on and off of the mounds is summarised in Table XVII.

A series of Spearman Rank correlations were then carried out with the ranked orders of the mound characteristics. The results of these correlations are summarised in Table XVIII.

Firstly, as noted above, there was no significant correlation between the maximum mean number of droppings recorded on the mounds and the height, volume or diameter of the mounds in the sample area. However, there were significant negative correlations between the droppings and the density of mounds and the area covered by those mounds.

There were no significant correlations found between the minimum mean number of droppings recorded on or off of the mounds or the maximum mean number of droppings recorded off the mounds and any of the ant mound characteristics.

When the four figures shown in Table XVII were added together, significant correlations were found between the sum for each sample area and the mean height and volume of the mounds in the sample areas. There were no significant correlations with the density, diameter or area covered by the mounds.

One of the problems of these correlations is that it is difficult to establish any degree of causality between the parameters. For example with the final correlations several interpretations are possible:

a) More rabbit droppings indicate a higher rabbit grazing level which has caused the mounds to be smaller in volume and less tall. The trampling effects of rabbits may inhibit the growth of ant mounds. Watt (1960) noted from his experimental exclusion of rabbits from an area of Breckland that,

Table XVII.

The maximum and minimum mean numbers of droppings recorded in each quadrat both on and off the mounds.

Quadrat		On mounds		Off mounds	
		Maximum	Minimum	Maximum	Minimum
OWH	SS 4	40.1	2.0	2.2	0
	5	30.7	0.3	1.5	0
	7	42.4	2.9	3.6	0.2
	8	41.0	1.4	0.2	0
	9	27.6	6.1	1.0	0
	11	52.3	4.5	1.9	0
	12	55.1	4.2	1.0	0
	NFS	49.7	0.7	1.0	0
	C10	27.2	1.2	0.7	0
AR	11	35.9	7.9	6.8	0.7
	12	49.0	8.6	4.2	0.5
	15	26.9	2.7	1.6	0.2
	16	54.9	5.9	1.3	0
	5	71.7	3.8	4.2	0.2
	NWS	41.3	13.5	1.0	0
MD	7B	0.4	0	0.2	0
	4A	58.8	1.6	6.7	0
	4B	50.4	0.9	4.5	0
	3B	27.3	2.4	1.9	0

Each figure represents the mean number of droppings found in 10, 25 x 25 cm. sample quadrats. Densities of droppings were recorded throughout 1989. The maximum and minimum mean numbers found are thoe given. Full details of the numbers of rabbit droppings found are given in Appendix Ten.

Table XVIII.

Summary of the results of the Spearman rank correlation analyses carried out between the rabbit dropping densities and the characteristics of the ant populations in each sample quadrat.

	On mounds		Off mounds		Total
	Maximum	Minimum	Maximum	Minimum	
Number of mounds	-0.494 *	+0.286 NS	-0.157 NS	+0.345 NS	-0.280 NS
Mean volume of mounds	-0.339 NS	-0.186 NS	-0.288 NS	-0.008 NS	-0.491 *
Area covered by mounds	-0.404 *	-0.005 NS	-0.203 NS	+0.289 NS	-0.320 NS
Mean diameter of mounds	-0.207 NS	-0.132 NS	-0.122 NS	-0.177 NS	-0.337 NS
Mean height of mounds	-0.333 NS	-0.114 NS	-0.287 NS	-0.018 NS	-0.468 *

The Spearman rank correlation coefficients are given for each case together with the significance level.
* = Significant at the 5% level.
NS = No significant correlation shown.

The correlations were carried out using the rabbit dropping figures in Table XVII and the ant mound characteristics summarised in Tables X and XI.

"a consequential effect of the exclusion of rabbits is the appearance of 2 ant heaps. Ants are active in and around tussocks of Festuca ovina into which they bring sand from the soil below."

It is possible that these ants could have been L. flavus, although it is also possible that they could have been a species of Myrmica, such as M. rubra. Either way it is clear that the presence of the rabbits had previously inhibited the development of the ant "heaps".

Also the digging activities of rabbits may be of importance. Rabbits often dig into the mounds causing substantial damage (see Figure 13.3.). Over many years a large rabbit population may be responsible for damage to a high percentage of the mounds within a sample area, certainly reducing their volume. As well as this there is an alternative explanation which seems equally as likely.

b) Flatter mounds allow more rabbit droppings to stay on them. Mounds that are more domed allow rabbit droppings to roll off of the mounds much easier. This was clearly the case in AR 15. Thus taller mounds have less droppings on them and an increase in droppings on the ground was not recorded because the fallen droppings gather around the sides of the mounds and were not recorded by the sample quadrats taken between the mounds. There was a significant correlation between the ranked D/H ratio of each sample area and the added and ranked figures on rabbit droppings (Spearman rank, $n = 19$, $r = +0.446$, $P<0.05$). The higher D/H figures indicate that mounds are less domed in shape. The rabbit dropping ranks are influenced mostly by the large, on the mound, figures. The indication is then that more domed mounds have less droppings on them, although there was not a significant correlation between the maximum number of droppings found on the mounds in each of

Figure 13.3.

<u>Rabbit damage to an ant mound.</u>

This photograph shows typical rabbit damage to an ant mound. The right hand side of the mound has been completely dug away. In some cases damage could be worse than this. The ant mounds are favoured places for rabbits to dig in because of their light easily worked soil.

the sample areas and the D/H ratios of the mounds (Spearman rank, n = 19, r = +0.279, P>0.05).

c) Smaller mounds are caused by a set of environmental and management conditions which coincidentaly encourage either greater populations of rabbits which thus produce more droppings, or the same populations of rabbits which defecate more. In areas of coarser grass, ie. in many cases the lighter grazed areas, such as OWH C10 and MD 7B, rabbits did not seem to be very active. The finer grasses, which it appears the rabbits prefer to feed on, are much less common in these areas.

It also appeared that there was a burst of rabbit activity in an area a short while after sheep had grazed in it. For example OWH SS 11 was grazed in March 1989. Rabbit dropping numbers showed a peak in the quadrat in June 1989 (see Figure 10.18.). This also happened in MD 4B. The quadrat was hard grazed in June 1989 but there was a very rapid build up of droppings after this. It seems that after grazing there was a short period of low activity but as the grass recovered and there was a regrowth of the finer grasses then the rabbits rapidly responded to this. Thus, observations made during the course of this study, suggest that certainly in part, a, b, and c could all be true.

Large populations of rabbits can have significant effects on the production of grasslands. Myers and Poole (1963) estimated that 25 to 50 rabbits per hectare could depress plant production on a sown grassland by 25% and that 17 to 25 rabbits per hectare were equivalent to 2.5 sheep per hectare (equivalent to 912.5 sheep days per hectare per year).

We do not know the exact levels of rabbits present in the sample areas in this study but from the figures above it is clear that even a modest population could have significant effects on the pasture and there is wide variation amongst the sample areas ranging from apparently very low to quite high levels. King (1972) noted that rabbits will preferentially graze the grasses on ant mounds and this may well increase the importance of the rabbits to the biology of the ants and the ant mounds.

13.3.5. Conclusions. The level of rabbit grazing varies in the sample areas quite considerably. It is possible that large populations of rabbits may cause reductions of size in the ant mounds in an area. Whether rabbits may be responsible for variations in the densities of mounds present is less sure. In some areas of unmanaged chalk grassland it is known that rabbits have been responsible in the past for preventing the growth of scrub which would ultimately lead to the loss of the grassland and of the ant mounds. MD 3B may be an example of this. However, analysis of the effects of stable populations of rabbits over many years, ideally on an experimental basis, would be necessary to see the true effects of rabbits. Rabbit populations fluctuate considerably and a single years results are insufficient to provide conclusive evidence of any effects within the sample areas.

13.5. Other animal influences.

Fewmets were only seen in OWH C10 and in this area deer grazing may contribute to keeping the grass growth down slightly. Green Woodpecker droppings were seen frequently in all of the sample areas. However, the degree to which they might predate the ant populations in each of the areas is unknown. It is probable that they are not significant in the determination of the ant characteristics. Pheasant (*Phasianus colchicus*) damage to a mound was seen in OWH C10, the mound being used as a dust bath, possibly also in a form of anting (Ehrlich, Dobkin and

Wheye 1986). Pheasant damage is only important in artificial conditions, such as those described by Pontin (1963). Thus, as far as is known, the influence of other vertebrate animals in the sample areas is minimal.

CHAPTER FOURTEEN

The spatial analysis of the ant mounds.

14.1. Introduction

The aim of this section of work was firstly to examine the hypothesis posed in Chapter Four, that variation in management and environment do not significantly affect the characteristics of the ant population, in this case the spatial distribution of the mounds, an indication of the intensity of intraspecific competition between colonies.

A secondary aim was to critically examine the types of analysis used and to determine the most appropriate way to analyse the data obtained.

14.2. The analysis of spatial distribution.

14.2.1. The aims of spatial analysis. Spatial analysis aims to examine the null hypothesis that populations of objects are randomly distributed in space. If not, the alternative hypothesis is that they may be either aggregated in groups (such a distribution is also described as contagious or clumped or underdispersed) or may tend towards overdispersion (also known as a regular distribution). This terminology has led to some confusion (Southwood 1978) and, for example, Thompson (1956) reversed the above meaning of overdispersion and underdispersion. In this thesis the types of distribution will be referred to as aggregated, random or overdispersed. Southwood (1978) gives a visual representation of what the different types of distribution look like.

There are a large number of methods of analysing the spatial distributions of populations of individual objects, organisms or colonies of organisms. Reviews of many of the methods are given in

Bartlett (1975), Hodder and Orton (1976), Ripley (1981), Diggle (1983) and Upton and Fingleton (1985) for example. Such methods have been used in a wide variety of scientific fields other than biology, for example in archaeology (Hodder and Orton 1976), astrophysics (Peebles 1974) and geography (Theakstone and Harrison 1970, De Vos 1973).

14.2.2. Spatial analysis by biologists. The first biologists to look for such distributions of organisms were plant ecologists. Methods were developed to examine whether populations of plants, recorded in quadrat analysis of stands of vegetation, showed aggregated distributions. These methods were based on examining deviations from the random distribution of points in space as described by the Poisson distribution. Such methods are described in Clapham (1936) and Greig-Smith (1952).

The nearest neighbour group of methods are those which rely on measuring the distance from a point, or an individual in the sample area, to the nearest neighbouring individual of the population. These methods were also primarily developed by plant ecologists, in particular those interested in the density and distribution of forest trees. The most widely used of these methods are as follows.

14.2.2.1. The closest individual. This is a simple method and relying on measuring the distances from a sample of random points in the sample area to the nearest individuals in the population being studied (Cottom, Curtis and Hale 1953, Morisita 1954). Underwood (1976), for example, used this method to examine the spatial distribution of 4 species of intertidal prosobranch molluscs.

14.2.2.2. The random pairs method. This is a more complex method in which a random point is first selected. The nearest individual is then located and an exclusion line set up on either side of the sample point at an angle of 90 degrees from the line to the nearest individual. The distance measured is then that from the selected nearest individual to the nearest individual in the 180 degrees arc on the other side of the exclusion line. This method was originally described by Cottam and Curtis (1949) but modified by Cottam and Curtis (1955) in the light of their work with it (Cottam, Curtis and Hale 1953).

14.2.2.3. Point-centred quarter method. This is a method that has been used for many years to estimate forest tree densities (Stearns 1949) but was adapted for ecological use by Curtis (1950). Each random sampling point is considered to be the centre of 4 quadrants. In each of the quadrants the nearest individual to the point is located and the distance measured. Cottam, Curtis and Hale (1953) and Morisita (1954) examined this method.

The methods detailed above are adequately described, illustrated and compared in Cottam and Curtis (1956), Lindsey, Barton and Miles (1958) and Mueller-Dombois and Ellenberg (1974). Plant ecologists have since advanced the study of plant distribution by the use of more complex techniques requiring large amounts of computer calculation, such as those requiring the construction of dirichlet tessellations (Rogers 1964, Green and Sibson 1978, Diggle 1983, Hutchings and Discombe 1986).

More simple than these types of analysis, and considered a reasonably robust technique (Ripley 1981) is nearest neighbour analysis, which has been widely used in the past to examine the spatial distribution of a wide variety of organisms including the ant *L. flavus*. For the purposes of this study the measurements required were simply taken, as part of the normal process of measuring and mapping the mounds. This would not have been true of the three methods described above which would have required either, the selection of sample of random points, the required number of which would have had to of been determined by preliminary experiments, or a more time consuming complex set of measurements.

14.2.3. The nearest neighbour method. This method of spatial analysis was originally introduced by Clark and Evans (1954). Morisita (1954) also independently derived parts of this technique. Again, it was originally intended as a method for estimating the density and spatial distribution of forest trees but it is this technique more than any of the others which has been hijacked for use in animal studies. An odd use of the technique was by Newcombe (1970) who used it to investigate the spatial distribution of Cornish hill forts, although this was subsequently criticised by Hodder (1971). Clark and Evans (1979) have produced a modified set of formulae to be used for three dimensional nearest neighbour analysis. White, Lloyd and Zar (1979) have used this method to analyse the distribution of cells of the cicada *Magicicada cassini*.

14.2.4. Uses of nearest neighbour analysis. Some of its earliest uses, with animal populations, were to estimate their density. By rearranging formula 1) (see below), Blackith (1958) used nearest neighbour measurements to estimate the sizes of populations of the grasshoppers *Chorthippus parallelus*, *C. brunneus*, *Omocestus viridulus* and *Stenobothrus lineatus* , and Turner (1960) used it on a population of the Cricket Frog, *Acris gryllus*. Turner (1960) concluded that it was a reasonable method of population estimation for this species. However, this use of the method has not been continued, probably because the assumption of random distribution of the individuals is rarely met, and it as is a measure of spatial distribution that it has been most frequently used.

Nearest neighbour analysis has been employed in several variations on a disparate range of organisms. As already noted it was originally intended for use with forest trees and it has since been used in other plant studies, for example by Yeaton and Cody (1976) who examined the distribution of the desert shrub species Opuntia acanthocarpa, O. ramosissima and Yucca schidigera.

Amongst its uses with animals were the following. Connel (1963) investigated the distribution of a variety of marine invertebrates. Newton et al (1977) used a slightly modified formula (Brown 1975) to demonstrate overdispersion in the spacing of nests of Sparrowhawks, Accipter nisus. Bartlett (1975) used the spacing of gulls nests, Larus spp. as an example in his discussion of the statistics of spatial analysis.

Campbell and Clarke (1971) used nearest neighbour measurements to demonstrate non-randomness in the distribution of populations of the Singing Cricket, Telogryllus commodus. Lamberti and Resh (1983) looked at the dispersal of the larvae of the caddis fly, Helicopsyche borealis on tiles in a stream. Hensen (1961) investigated the distribution of beetles (Conopthorus conyperda) as influenced by thigmotropic aggregation. McClure (1976) and Simberloff et al (1978) looked at the overdispersion of ant-lion pits. Horton and Wise (1983) looked at the distribution of two species of spiders, Argiope aurantia and A. trifasciata.

Amongst the social insects nearest neighbour techniques have been frequently used to demonstrate non-random patterns in the distribution of colonies. Overdispersion of termite mounds has been demonstrated by

Wood and Lee (1971) and Spain, Sinclair and Diggle (1986). Hubbell and Johnson (1977) investigated the dispersion of a number of species of the stingless bee genus Trigona.

Levings and Traniello (1981) have reviewed investigations into the spatial distribution of colonies of ants and give an extensive list of occasions when nearest neighbour analysis has been used, including several on L. flavus. As well as this, they have also subjected the field data of other authors to nearest neighbour analysis when enough detail was available.

14.2.5. Problems with nearest neighbour analysis. One of the problems with the use of nearest neighbour analysis by some authors, is that they have used it as a formula in which numbers are put in at one end and an answer comes out of the other. Little or no thought has been put in to the assumptions that have to be made for the correct use of the method, for example on border areas, sample sizes, size of the individuals, etc.

Many authors have, as a result of this, used the technique in an invalid manner. For example Hubbell and Johnson (1977) used the unmodified Clark and Evans (1954) method to examine the spatial distribution of the nests of a variety of species of stingless bees. Of the species investigated the maximum sample size was only 11 and the minimum 3 nests. For this last species only 2 nests were found in their sample area and for the calculations to be made they had to hunt for a third nest outside of the sample area, to measure another distance. Furthermore, as the nests of these bees were located high up in trees, they were measuring distances in three dimensional space. The basic formulae are only valid for two dimensions and a different method of analysis is necessary for three dimensions (Clark and Evans

1954). Clearly the conclusions of Hubbell and Johnson (1977) that the nests of these bee species were overdispersed, must be viewed with a great deal of suspicion.

While this is an extreme example, it is by no means isolated. Many of the studies mentioned above have failed to be sufficiently critical in their use of nearest neighbour analysis. The results and analysis from this work will help to point out some of the pitfalls of using nearest neighbour analysis.

14.3. Mathematics of the nearest neighbour technique.

14.3.1. The basic fomulae. This technique relies on measuring the distance from a sample of members of a population to each of their nearest neighbours in that population. Clark and Evans (1954) originally described the practical use of the method and Thompson (1956) extended the theory to possible use to the nth nearest neighbour (see Figure 14.1.).

Using formulae derived from the Poisson distribution Thompson (1956) described how to work out the expected mean distances to the 1st to nth nearest neighbouring members of the population. In the following formulae;

A = the area within which the population lies

N = the number of individuals in that area

n = the 1st to the nth nearest neighbour

m = the density given by N/A

d = the mean distance to the nth nearest neighbour

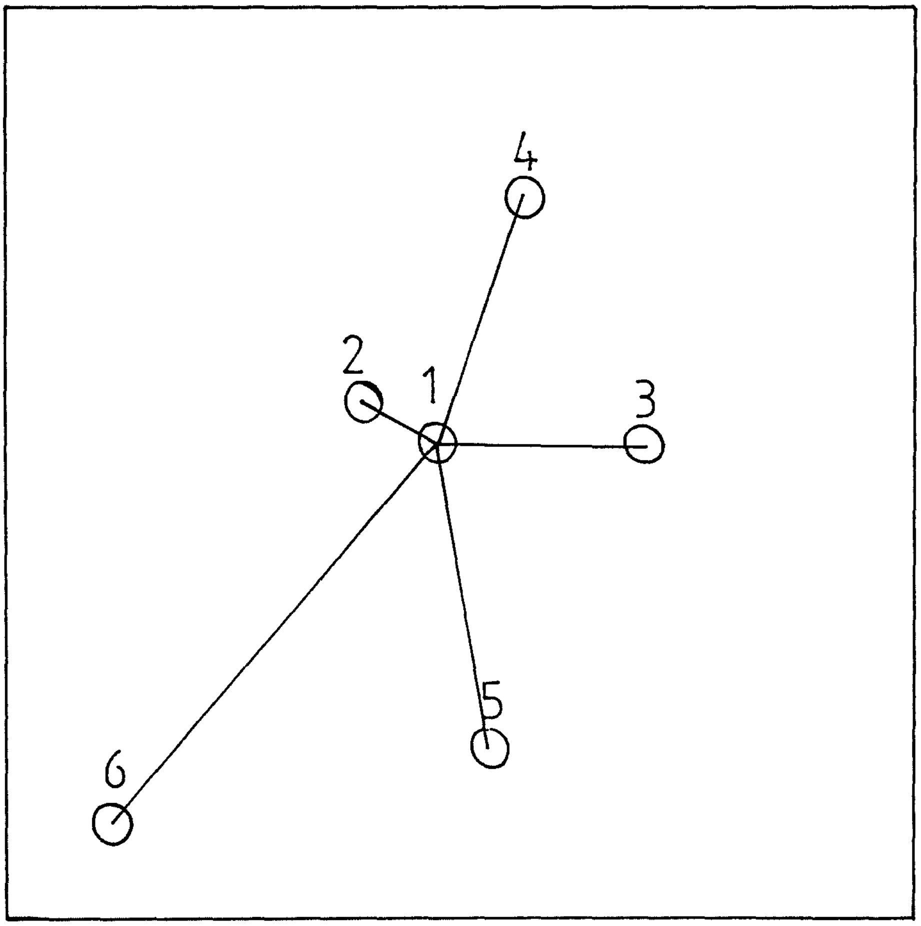
E = expected in a random distribution

O = observed

s = the diameter of a circle

Figure 14.1.

An illustration of neighbouring ant mounds.



The plot area represents a part of the sample quadrat. Mound 1 is the mound whose nearest neighbours are being measured. Mound 2 is the nearest mound to mound 1 and so the distance to the 1st nearest neighbour (ie. n = 1) is the distance between the centres of mounds 1 and 2. Similarly mound 6 is the 5th nearest neighbouring mound to mound 1 and so the distance to the 5th nearest neighbour (ie. n = 5) is the distance between the centres of mounds 1 and 6.

1) $$E(d) = \frac{(2n)!n}{(2^n . n!)^2} \times \frac{1}{\sqrt{m}}$$

For example for the 1st nearest neighbour, n = 1 and the formulae becomes;

$$E(d) = \frac{0.5}{\sqrt{m}} \quad \text{and for } n = 2 \quad E(d) = \frac{0.75}{\sqrt{m}}$$

1)a. By rearangement of equation 1)

$$m = (0.5/E(d))^2$$

Thus the density of a population (assuming it is randomly distributed) can be estimated by measuring a sample of nearest neighbour distances.

2) $\sigma E(d)$ tends to $\frac{0.2821}{\sqrt{(Nm)}}$ as n increases.

However, for values of n below 5, the following constants should be used on the top line of the equation.

n = 1, 0.2614
n = 2, 0.2723
n = 3, 0.2757
n = 4, 0.2774

Two statistical tests were proposed by Clark and Evans (1954) and Thompson (1956) to test the null hypothesis of random distribution. Firstly the statistic:

3) $$2 \pi m \sum (o(d)^2)$$

is distributed as a Chi squared. Small, Wrattan and White (1985) noted a series of errors in the literature describing this method. In particular the number of degrees of freedom associated with this statistic were wrongly described by Southwood (1978) as 2N, when in fact it should be 2Nn. This makes an increasingly large difference to the interpretation of the statistic as higher values of n are investigated. Southwood (1978) further reverses the interpretation of the significance of the probability of the statistic. A probability of less than 0.05 indicates significant overdispersion, while a probability of greater than 0.95 indicates significant aggregation.

Most tables of Chi squared statistics only give values up to 100 degrees of freedom (eg. Neave 1978, Pearson and Hartley 1966). For use in the present study much greater values were needed (because the number of degrees of freedom is given by the formula 2Nn which rapidly escalates in value). For calculation of the critical values of the chi squared statistic at the 0.05 level of probability the following formula is used:-

4) $$\text{Chi squared} = v[(1 - (2/9v) + 1.6649 \sqrt{(2/9v)}]^3$$

v = the number of degrees of freedom

The constant 1.6449 is that given by Pearson and Hartley (1966) for the 0.05 level of probability and can be varied for other probability levels. Short computer programs can be written to ease the calculations.

A second test of significance was also proposed by Clark and Evans (1954). A rough guide to the spatial distribution can be obtained by looking at the Index of dispersion R, calculated by:-

5) $$R = \frac{O(d)}{E(d)}$$

When R is greater than 1, overdispersion is indicated, and when R is less than 1, aggregation is indicated.

A test of significance is also given by the statistic c, which is approximately normally distributed. This is calculated by:-

6) $$c = \frac{O(d) - E(d)}{\sigma E(d)}$$

Where $\sigma E(d)$ is calculated from the formulae given above.

The c values of 1.96 and 2.58 are the 5% and 1% critical levels of significance respectively. Therefore a value of c greater than +1.96 indicates significant overdispersion and a value of less than -1.96 significant aggregation.

14.3.2. Modifications of the formulae. Since the initial work of Clark and Evans (1954) and Thompson (1956) modifications have been proposed to the calculations. Donelly (1978) pointed out that Clark and Evans (1954) had assumed that all of the nearest neighbour points are independent of each other. This is true when a few scattered points are sampled from a large area, but when all of the points in an area are used (ie. the sample is the whole population) then this no longer applies. This was also an observation made by Hamming and Gilbert (1954). Diggle (1976) suggests that the error caused by this assumption is a negligible one.

By use of computer simulations Donelly (1978) has determined that the constant for the first nearest neighbour in equation 2) should be modified to 0.26514 to take account of this.

Clark and Evans (1954) suggested the use of a buffer or border zone around the sample area. This buffer zone should be uniform with the sample area. When the nearest neighbour of a sample point lies outside of the sample area and within the buffer zone it can then be measured. If the uniform sample area is a restricted one, and no buffer zone is possible, then taking a nearest neighbour from inside the zone, when one from outside may be closer, will induce a bias into the analysis.

Donelly (1978) has, again by a large number of computer simulations, calculated modified formulae to be used when no buffer zone has been included. This has only been done for the 1st nearest neighbour analysis equations. The modified formula for the calculation of E(d) is :-

7) $$E(d) = 0.5/\sqrt{(N/A)} + (0.0514 + 0.0412/\sqrt{N})(P/N)$$

P = the length of the perimeter of the sample area

8) $$\sigma E(d) = \frac{0.07(A/N^2) + 0.037[P\sqrt{(A/N^5)}]}{N}$$

This modification only works when the boundary edge is not too convoluted. Squares, rectangles and circles, for example, are fine, while a 4 pointed star shape is not.

Simberloff (1979) has noted, as did Pielou (1960) before him, that on many occasions biological organisms, or their artefacts, should not be treated as points for the purpose of this type of spatial analysis, but as circles, and that this alters the theoretical spatial distribution. Circles in a random distribution cannot be closer together than the sum of their radii. Thus, for circles, the Clark and Evans (1954)/Thompson (1956) formulae will underestimate E(d).

Simberloff (1979) has thus proposed modification of E(d) by interpolation into a curve produced by a large number of computer simulations. Again this is valid only for the analysis of the 1st nearest neighbour. Thus when calculating c from equation 6) the modified values of E(d) and E(d), calculated from the simulated curve, should be used in place of the straight values, calculated from formulae 1) and 2). When using the Chi squared test of significance Simberloff proposes a modified formula to calculate the Chi squared statistic. This now becomes:

9) $$\text{Chi squared} = \sum 2m\pi O(d)^2 - 2Nm\pi(2r)^2$$

r = the radius of the circles

There have been a number of other variations to the technique, for example Brown (1975) has proposed an alternative test using 1st nearest neighbour distances, and this has been used by Newton et al (1977). Called the GMASD test, the geometric mean of the sum of the nearest neighbour distances squared, is divided by the arithmetic mean of the squared distances. A value of over 0.65 means overdispersion is present, 0.65 indicates a random distribution and values less than 0.65 indicate aggregation.

10) $$R = \frac{\mathrm{antilog}((1/N)(\sum \log O(d)))}{\sum O(d)/N}$$

14.4. Preliminary data analysis.

Only the distances to the 1st nearest neighbours were measured in the field (see Section 6.6.2.3.). For the distances to the 2nd to 5th nearest neighbours a computer program was written which in each quadrat used the coordinates of the mounds to examine each mound in turn and determine which were its nearest neighbours. This was done by looking at the difference between the X and Y coordinates of each mound and all of the other mounds in the quadrat and then using the pythagorean equation for calculating the hypotenuse of a right angled triangle (see Figure 14.2.) to measure the distance between each mound and all of the other mounds in the quadrat. These distances were then compared and the smallest 5 selected in order.

The program then calculated the mean nearest neigbour distance for all of the mounds in a quadrat and also the mean squared nearest neighbour distances. The program is listed in Appendix Eleven. Data to be used by the program (ie. the X and Y coordinates of the mounds) has first to be filed using the suite of programs called Statcalc (T. J. Brown and R. B. G. Williams (1985) University of Sussex and McMillan

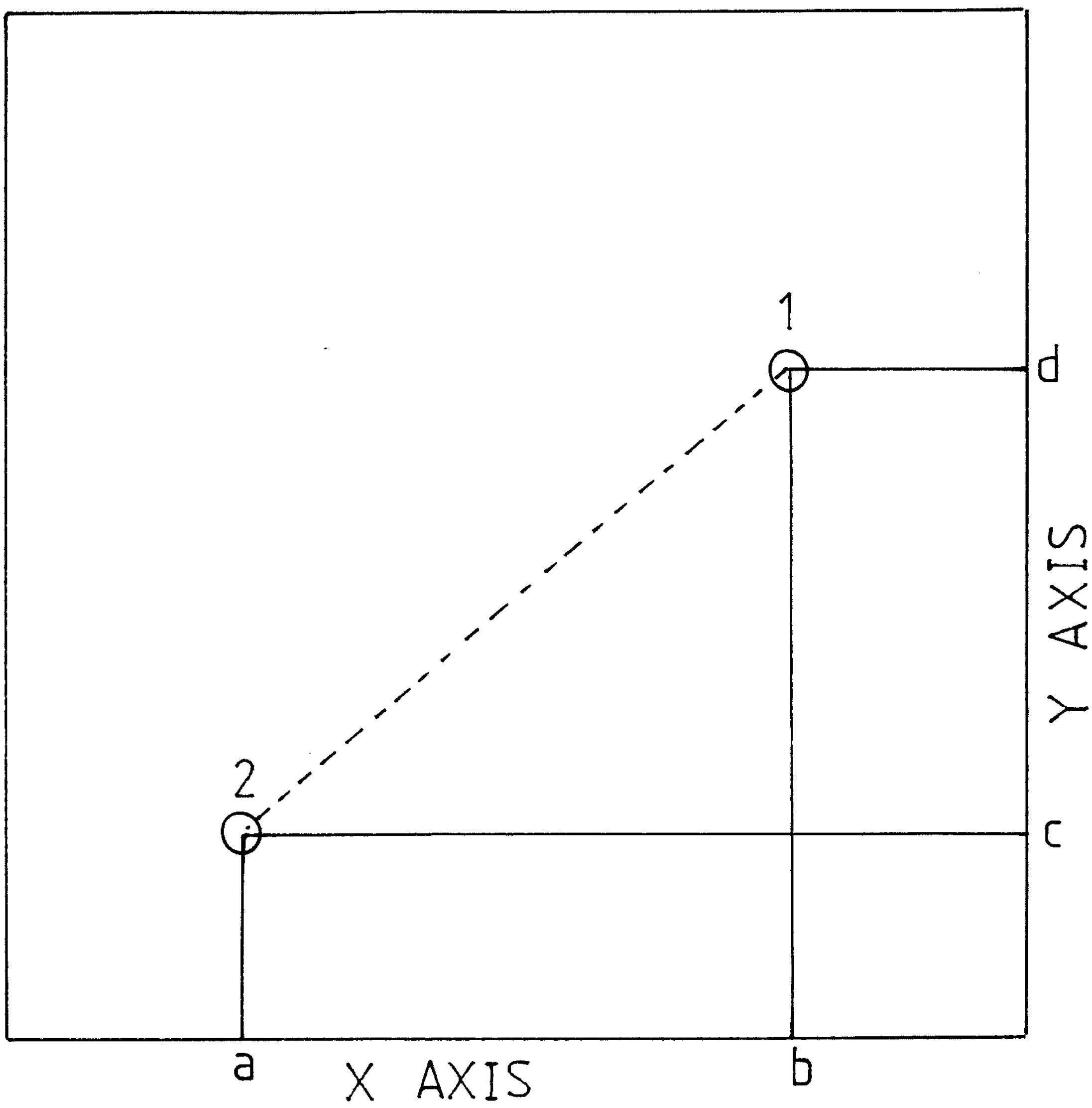


Figure 14.2.

Calculation of the distance between two mounds from their coordinates.

The square plot above is the sample quadrat, each side being 20 metres long. The coordinate of mound 1 is therefore b,d and for mound 2, a,c. The distance between the centres of the two mounds is thus given by:

$$\sqrt{(b - a)^2 + (d - c)^2}$$

The computer program calculates the distance from a mound to all of the other mounds in the sample quadrat and selects the five smallest values.

Education) for use on the BBC b or MASTER microcomputers.

The mean nearest neighbour distances measured in the field for each sample quadrat are given in Table XIX. The mean 1st to 5th nearest neighbour distances calculated by the computer program are given in Table XX and the raw data is given in Appendix Twelve.

14.5. Detailed analysis of the spatial distribution results.

14.5.1. Introduction. As discussed above there are a number of ways to analyse the data obtained in this study, not all of them appropriate. To examine the errors that could arise from using the inappropriate method, all the possible variations in the analysis methods were used. The analysis that was done is descibed below, together with the conclusions, in terms of how many of the sample quadrats showed significant overdispersion of their ant mound populations.

14.5.2. The field measurements on the first nearest neighbours. First the basic formulae of Clark and Evans (1954) and Thompson (1956) were used.

1)The Chi squared test. The sum of the squared nearest neighbour distances, the Chi squared statistics calculated from formula 3) and the significance of these are given in Table XXI. The results show significant overdispersion at the 5% level of significance in 13 out of the 20 quadrats. A table giving the critical levels of the chi squared statistic for the 5% level of probability, calculated from formula 4) is given in the Appendix Fourteen.

2)The Clark and Evans (1954) c statistic. The expected distance to the mean nearest neighbour and its standard error, as calculated from formulae 1) and 2), the index of dispersion R (formula 5), the value of c (formula 6) and the significance level of c, are given in Table

Table XIX.

Mean 1st nearest neighbour distances from the field measurements.

QUADRAT	D(d) (metres)
OWH SS 4	1.40
SS 5	1.50
SS 7	3.40
SS 8	1.51
SS 9	1.28
SS11	1.59
SS12	1.27
NFS	1.52
C10	1.15
AR 11	1.16
12	0.75
15	1.07
16	1.53
5	1.33
NWS	0.87
MD 7B	1.21
4A	1.44
4B	1.37
3B	1.40
ST. C	1.57

This table summarises the results given in Chapter Ten. The distance to nearest neighbour was measured for all mounds in each sample quadrat, as described in section 6.6.2.3. The raw data is contained in Appendix One.

Table XX.

The mean distances to the first to fifth nearest neighbours as calculated from the mound coordinates

QUADRAT	1st	2nd	3rd	4th	5th
OWH SS 4	1.43	1.94	2.41	2.78	3.14
SS 5	1.59	2.19	2.75	3.23	3.57
SS 7	4.92	8.48	10.39	12.50	15.77
SS 8	1.61	2.29	2.79	3.22	3.63
SS 9	1.32	1.72	2.13	2.49	2.83
SS11	1.62	2.25	3.06	3.50	3.98
SS12	1.38	1.95	2.51	2.97	3.31
NFS	1.62	2.22	2.65	3.13	3.48
C10	1.18	1.59	1.98	2.24	2.51
AR 11	1.16	1.59	1.99	2.30	2.64
12	0.74	1.01	1.23	1.43	1.59
15	1.09	1.58	1.90	2.23	2.51
16	1.64	2.25	2.73	3.11	3.40
5	1.38	1.94	2.44	2.89	3.17
NWS	0.88	1.27	1.61	1.90	2.16
MD 7B	1.17	1.80	2.33	2.60	2.94
4A	1.58	2.13	2.59	2.93	3.26
4B	1.49	2.21	2.68	3.23	3.64
3B	1.44	2.04	2.48	2.87	3.23
ST. C	1.62	2.24	2.78	3.10	3.51

All distances given are in metres. The Table summarises the results of the analysis of by the computer program listed in Appendix Eleven. Using the coordinates of each mound in the the sample quadrat, the 5 nearest neighbouring mounds to each mound were located and the distance to them measured (see section 14.4.). The raw data produced by the program is shown in Appendix Twelve.

Table XXI.

Analysis of the field measurements to the first nearest neighbour, using the Chi squared test of Thompson (1956).

QUADRAT	$\sum O(d)^2$	Chi squared
OWH SS 4	154.89	163.01*
SS 5	172.97	173.89*
SS 7	99.06	12.45
SS 8	164.58	170.62*
SS 9	181.39	282.06*
SS11	168.53	150.89*
SS12	128.62	143.44
NFS	187.27	205.92*
C10	176.40	329.74*
AR 11	173.77	324.82*
12	170.56	731.40*
15	157.23	311.19*
16	166.67	164.94*
5	151.67	178.68
NWS	109.13	203.98
MD 7B	147.23	198.89
4A	142.30	136.35
4B	153.16	161.19
3B	176.08	215.74*
ST. C	179.00	185.57*

* Significant overdispersion at the 5% (0.05) level.
O(d) is the observed distance to the first nearest neighbour.
Chi squared figures were calculated from formula 3) in section 14.3.1. The critical values of Chi squared for the 5% significance level are given in Appendix Fourteen. Out of the 20 quadrats, 13 show significant overdispersion at the 5% level.

XXII. The results showed significant overdispersion at the 5% level in 15 out of the 20 quadrats.

3) The Donelly (1978) adaptation for the modification of the standard error of the estimated mean distance to nearest neighbour. The standard error, as calculated from the modified formula 2), is compared with that from the unmodified formula 2), and the thus altered c statistics and significance levels are given in Table XXIII. In total 15 out of the 20 quadrats showed significant overdispersion.

4) Simberloff (1979) adaptation for circles instead of points. The mounds are treated as circles of diameter s, where s is the mean maximum diameter of the mounds in the quadrat, summarised in Table X. Two tests of significance were performed, firstly the chi squared test using the modified formula 9) the results of which are given in Table XXIV, and secondly a modified Clark and Evans c statistic is calculated (using formula 6). For this test the expected mean distance to the 1st nearest neighbour (E(d)) and its standard error, were calculated by interpolation into the simulation curve presented in Simberloff's (1979) paper. The mean mound diameter, the modified expected mean distance to the nearest neighbour, the modified standard error of the estimate, the newly calculated c statistic and its significance are all given in Table XXV. The Chi squared test gave significant overdispersion in 9 of the 20 quadrats and the c statistic test in 12 out of the 20 quadrats.

14.5.3. The 1st nearest neighbour distances calculated from the coordinates of the mounds. Again, the unmodified formulae of Clark and Evans (1954) and Thompson (1956) were used first. These analyses fail to take account of the fact that in this case there was in effect no border area around the sample quadrat.

Table XXII.

Analysis of the first nearest neighbour field measurements by the method of Clark and Evans (1954).

QUADRAT	E(d)	σE(d)	R	c
OWH SS 4	1.22	0.078	1.14	2.23*
SS 5	1.25	0.082	1.20	3.06**
SS 7	3.54	0.653	0.96	-0.21
SS 8	1.23	0.079	1.22	3.48**
SS 9	1.01	0.053	1.28	5.21**
SS11	1.32	0.092	1.20	2.92*
SS12	1.19	0.074	1.07	1.18
NFS	1.20	0.075	1.27	4.31**
C10	0.92	0.044	1.26	5.39**
AR 11	0.94	0.046	1.23	4.70**
12	0.61	0.019	1.23	7.39**
15	0.89	0.042	1.20	4.19**
16	1.26	0.083	1.22	3.29**
5	1.15	0.070	1.15	2.53*
NWS	0.92	0.044	0.95	-1.08
MD 7B	1.08	0.061	1.12	2.10*
4A	1.28	0.086	1.12	1.83
4B	1.22	0.078	1.12	1.88
3B	1.13	0.067	1.24	4.01**
ST. C	1.23	0.079	1.27	4.24**

* Significant overdispersion at the 5% (0.05) level.
** Significant overdispersion at the 1% (0.01) level.
E(d) - the expected mean distance to first nearest neighbour in a random distribution.
σE(d) - the standard error of the expected mean distance.
R - the Index of Dispersion
c - c>1.96 indicates significant overdispersion at the 5% (0.05) level. c is calculated from formula 6) in section 14.3.1.

Table XXIII.

Analysis of the first nearest neighbours from the field measurements using the formulae of Clark and Evans (1954) with the modified constant of Donelly (1978)

QUADRAT	σE(d) CE	σE(d) DON	c
OWH SS 4	0.078	0.079	2.20*
SS 5	0.082	0.083	3.03**
SS 7	0.653	0.663	-0.21
SS 8	0.079	0.080	3.43**
SS 9	0.053	0.054	5.11**
SS11	0.092	0.093	2.89*
SS12	0.074	0.075	1.16
NFS	0.075	0.076	4.25**
C10	0.044	0.045	5.27**
AR 11	0.046	0.047	4.60**
12	0.019	0.019	7.39**
15	0.042	0.042	4.19**
16	0.083	0.084	3.25**
5	0.070	0.071	2.50*
NWS	0.044	0.045	-1.06
MD 7B	0.061	0.062	2.07*
4A	0.086	0.087	1.81
4B	0.078	0.079	1.85
3B	0.067	0.068	3.95**
ST. C	0.079	0.080	4.18**

* Significant overdispersion at the 5% (0.05) level.
** Significant overdispersion at the 1% (0.01) level.
σE(d) - the standard error of the estimated mean distance to nearest neighbour, calculated from formula 2) in section 14.3.1.
c - the result of the normal approximation significance test. A value of c>1.96 indicates significant overdispersion at the 5% level.
CE - the unmodified formula was used.
DON - the modified constant proposed by Donelly (1978) was used.

Table XXIV.

Analysis of the first nearest neighbour distances from the field measurements by the Chi squared test of Simberloff (1979).

Quadrat	mean diameter	unmodified Chi square	modified Chi square
OWH SS 4	0.408	163.01*	151.27
SS 5	0.404	173.89*	163.39*
SS 7	0.591	12.45	12.10
SS 8	0.469	170.62*	155.57
SS 9	0.436	282.06*	252.79*
SS11	0.429	150.89*	141.50*
SS12	0.421	143.44	129.41
NFS	0.546	205.92*	182.97*
C10	0.599	329.74*	249.93
AR 11	0.452	324.82*	283.84*
12	0.259	731.40*	652.87*
15	0.498	311.19*	249.34
16	0.434	164.94*	153.20*
5	0.435	178.68	161.96
NWS	0.219	203.98	193.31
MD 7B	0.382	198.89	181.94
4A	0.406	136.35	126.72
4B	0.410	161.19	149.34
3B	0.477	215.74*	194.00*
ST. C	0.450	185.57*	171.71*

* Significant overdispersion at the 5% (0.05) level.
mean diameter - the mean maximum diameter, in metres, of the mounds in each sample quadrat.
Unmodified Chi squared - the Chi squared test of Thompson (1956) using formula 3) in section 14.3.1.
Modified Chi squared - the Chi squared test of Simberloff (1979) which takes into account that ant mounds are circles and not points, formula 9) section 14.3.2.

The Simberloff test is more critical with overdispersion found in only 9 of the 20 quadrats, compared to 13 by the unmodified test.

Table XXV.

Analysis of the first nearest neighbours from the field measurements by the method of Clark and Evans (1954) modified by Simberloff (1979).

QUADRAT	diam.	E(d)	σE(d)	c
OWH SS 4	0.408	1.28	0.070	1.59
SS 5	0.404	1.31	0.074	2.55*
SS 7	0.591	3.54	0.633	-0.22
SS 8	0.469	1.32	0.069	2.63**
SS 9	0.436	1.10	0.045	4.13**
SS11	0.429	1.39	0.083	2.45*
SS12	0.421	1.27	0.065	0.06
NFS	0.546	1.31	0.063	3.23**
C10	0.599	1.07	0.034	2.72**
AR 11	0.452	1.04	0.038	2.96**
12	0.259	0.65	0.016	5.73**
15	0.498	1.00	0.033	1.96*
16	0.434	1.33	0.074	2.74**
5	0.435	1.22	0.061	1.81
NWS	0.219	0.94	0.041	-1.72
MD 7B	0.382	1.15	0.054	0.98
4A	0.406	1.34	0.077	1.22
4B	0.410	1.28	0.070	1.22
3B	0.477	1.22	0.057	3.12**
ST. C	0.450	1.31	0.071	3.67**

* Significant overdispersion at the 5% (0.05) level.
** Significant overdispersion at the 1% (0.01) level.
diam. - the mean maximum diameter, in metres, of the mounds in each sample quadrat.
E(d) - the expected mean distance to nearest neighbour in a random distribution.
σE(d) - the standard error of that distance.
c - the result of the normal approximation test of significance. c>1.96 indicates significant overdispersion at the 5% level.
Significant overdispersion was found in 12 of the 20 sample quadrats. The test is less critical than the Chi squared test of Simberloff (1979).

1) A Chi squared analysis was run on the results using formula 3). The calculated Chi squared statistic together with its significance are given in Table XXVI. Significant overdispersion was demonstrated in 16 of the 20 quadrats.

2) An unmodified Clark and Evans (1954) analysis was run on the results. The statistics R and c are given (formulae 5 and 6) together with the significance level of c, in Table XXVII. Significant overdispersion was found in 18 of the 20 quadrats.

3) The full Donelly (1978) adaptation, to take account of the absence of a border area, was used to calculate the same statistics as in 2). The modified formulae 7) and 8) were used to calculate E(d) and E(d) (see Table 6). In Tables XXVII and XXVIII the results are presented alongside those using the unmodified calculations done in 2). Table XXVII gives the comparison between the expected mean distance to nearest neighbour and its standard error, as caculated from the unmodified Clark and Evans (1954) and the modified Donelly (1978) formulae. Significant overdispersion was demonstrated in 15 out of the 20 quadrats.

4) The results were then analysed using the Simberloff (1979) adaptations for circles instead of points. This was done as for the measured distances to the 1st nearest neighbour above. The results are presented in Table XXIX. The modified values of E(d) and its standard error are, of course, the same as those used for the analysis of the direct measurements with this method, as described above. Using the Chi squared method significant overdispersion is found in 12 out of the 20 quadrats and by calculating the c statistic in 17 of the sample quadrats.

Table XXVI.

The analysis of the first to fifth nearest neighbours, as calculated from the mound coordinates, by the Chi squared test of Thompson (1956)

QUADRAT	1st	2nd	3rd	4th	5th
OWH SS 4	166.56*	298.40	440.92	577.06	728.93
SS 5	191.73*	345.42*	523.14*	719.40*	871.87*
SS 7	20.24	58.99*	88.89*	126.62*	198.61*
SS 8	193.10*	382.27*	561.16*	734.95*	930.12*
SS 9	306.61*	500.67*	762.98*	1035.47*	1318.16*
SS11	151.48*	269.60*	510.61*	675.10*	844.06*
SS12	170.27	322.94	531.19	739.61*	907.55*
NFS	228.18*	404.35*	572.07*	799.39*	996.44*
C10	349.97*	598.36*	917.27*	1163.85*	1456.59*
AR 11	293.38*	544.31*	832.64*	1107.21*	1440.70*
12	723.83*	1322.15*	1922.27*	2556.13*	3116.29*
15	336.45*	683.73*	964.20*	1297.34*	1610.38*
16	190.01*	343.14*	498.38*	635.81*	757.70*
5	191.36*	364.05*	552.98*	756.96*	918.25*
NWS	208.87	420.05	643.72	870.03	1113.21
MD 7B	194.18	418.66*	672.91*	826.91*	1054.02*
4A	173.93*	291.86*	415.93	524.19	635.21
4B	184.06*	371.65*	526.36*	759.06*	948.40*
3B	231.38*	433.96*	630.88*	841.07*	1060.25*
ST. C	196.82*	349.03*	532.52*	659.30*	855.79*

* significant overdispersion at the 5% (0.05) level.
The Chi squared statistics were calculated from formula 3) in section 14.3.1. The critical 5% levels of the Chi squared statistic are given in Appendix Fourteen. The number of quadrats showing significant overdispersion would be expected to decrease as further nearest neighbours are analysed (Waloff and Blackith 1962). The reasons why the results do not follow this pattern are discussed in section 14.6.1.3.

Table XXVII.

Analysis of the first nearest neighbours, as calculated from the coordinates of the mounds, by the methods of Clark and Evans (1954) and Donelly (1978).

QUADRAT	Clark and Evans			Donelly		
	R	C	S	R	C	S
OWH SS 4	1.17	2.62	0.01	1.11	1.73	NS
SS 5	1.27	4.13	0.001	1.20	2.87	0.005
SS 7	1.39	2.12	0.05	1.17	0.84	NS
SS 8	1.31	4.84	0.001	1.24	3.50	0.001
SS 9	1.31	5.98	0.001	1.26	4.60	0.001
SS11	1.23	3.26	0.002	1.16	2.09	0.05
SS12	1.17	2.68	0.01	1.11	1.60	NS
NFS	1.35	5.64	0.001	1.28	4.22	0.001
C10	1.29	6.02	0.001	1.24	4.68	0.001
AR 11	1.23	4.71	0.001	1.18	3.49	0.001
12	1.22	6.93	0.001	1.19	5.66	0.001
15	1.23	4.88	0.001	1.18	3.66	0.001
16	1.30	4.61	0.001	1.23	3.29	0.002
5	1.19	3.22	0.002	1.14	2.09	0.05
NWS	0.96	-0.83	NS	0.92	-1.51	NS
MD 7B	1.09	1.55	NS	1.04	0.62	NS
4A	1.24	3.53	0.001	1.17	2.34	0.02
4B	1.22	3.47	0.001	1.16	2.56	0.002
3B	1.27	4.57	0.001	1.21	3.30	0.001
ST. C	1.32	4.97	0.001	1.25	3.62	0.001

R - the Index of dispersion (formula 5, section 14.3.1.)
C - the result of the approximation to the normal distribution. A value of $c>1.96$ indicates significant overdispersion, a value <-1.96 indicates significant aggregation, at the 5% level (0.05).
S - the significance level. NS - not significant.
The Clark and Evans (1954) test shows significant overdispersion in 18 out of the 20 quadrats. The Donelly (1978) test, which takes account of the absence of a border area, is more critical, with significant overdispersion found in only 15 of the 20 sample quadrats.

Table XXVIII.

Analysis of the first nearest neighbours, as calculated from the coordinates of the mounds - the estimated mean distance to first nearest neighbour by the methods of Clark and Evans (1954) and Donelly (1978)

QUADRAT	Clark and Evans		Donelly	
	E(d)	σE(d)	E(d)	σE(d)
OWH SS 4	1.22	0.078	1.29	0.080
SS 5	1.25	0.082	1.32	0.093
SS 7	3.54	0.653	4.19	0.874
SS 8	1.23	0.079	1.30	0.090
SS 9	1.01	0.053	1.05	0.059
SS11	1.32	0.092	1.40	0.105
SS12	1.19	0.074	1.25	0.083
NFS	1.20	0.075	1.26	0.085
C10	0.92	0.044	0.95	0.049
AR 11	0.94	0.046	0.98	0.051
12	0.61	0.019	0.62	0.021
15	0.89	0.042	0.93	0.046
16	1.26	0.083	1.33	0.095
5	1.15	0.070	1.21	0.079
NWS	0.92	0.044	0.95	0.049
MD 7B	1.08	0.068	1.13	0.068
4A	1.28	0.086	1.35	0.098
4B	1.22	0.078	1.29	0.080
3B	1.13	0.067	1.19	0.076
ST. C	1.23	0.079	1.30	0.090

E(d) - the estimated mean distance to the first nearest neighbour in a random distribution.
σE(d) - the standard error of the distance.

The Donelly (1978) formulae make allowances for the lack of a border area around the sample quadrat (see Table XXVII). E(d) and σE(d) are both slightly increased by using the Donelly adaptation. This results in the significance test being more conservative (see Table XXVII).

Table XXIX.

Analysis of the first nearest neighbour distances, calculated from the coordinates of the mounds, using the methods of Simberloff (1979).

QUADRAT	R	c	Chi squared
OWH SS 4	1.11	2.04*	154.82
SS 5	1.21	3.73**	181.23*
SS 7	1.39	2.18*	19.89
SS 8	1.22	4.22**	178.04*
SS 9	1.20	5.03**	277.38*
SS11	1.17	2.82**	142.26*
SS12	1.09	1.74	156.23*
NFS	1.23	4.79**	205.23*
C10	1.11	3.39**	270.15
AR 11	1.11	3.02**	252.39
12	1.13	5.23**	645.29*
15	1.09	2.77**	274.60
16	1.24	4.22**	178.37*
5	1.13	2.58**	174.64
NWS	0.94	-1.44	198.20
MD 7B	1.02	0.35	177.22
4A	1.18	3.11**	164.30*
4B	1.16	2.99**	172.20*
3B	1.18	3.78**	209.64*
ST. C	1.25	4.51**	182.97*

* Significant overdispersion at the 5% (0.05) level.
** Significant overdispersion at the 1% (0.01) level.
R - the Index of Dispersion.
c - the result of the normal approximation test, using interpolation in the curve given by Simberloff (1979).
Chi squared - the Chi squared value given by formula 7), section 14.3.2.
The Chi squared test is more conservative than the normal approximation. However, neither method is as conservative as when used with the field data. See section 14.6.1.2. for further explanation.

14.5.4. Analysis of the results for the 2nd to 5th nearest neighbours.

1) The results were first analysed using the unmodified formula 3) of Thompson (1956) to calculate the appropriate Chi squared statistics. The sums of the nearest neighbour distances squared for the 1st to the 5th nearest neighbours, as calculated by the computer program, are given Appendix Fourteen. The Chi squared statistics and their significance are presented in Table XXVI. The critical 5% levels for the Chi squared statistics are given in Appendix Fourteen. For the 2nd, 3rd and 4th nearest neighbours, 17 out of the 20 quadrats show significant overdispersion, and for the 5th nearest neighbour, 18 show significant overdispersion.

2) The c statistics were then calculated for each of the quadrats, using formulae 1), 2) and 4). The values of E(d) are given in Appendix Fourteen. The standard errors of those expected means are given in Appendix Fourteen. The values of R are given in Appendix Fourteen and finally the c statistics and their significance are presented in Table XXX. For the 2nd and 3rd nearest neighbour 18 of the 20 quadrats show significant overdispersion, and 1, significant aggregation. For the 4th and 5th nearest neighbours 17 quadrats show significant overdispersion and 1, significant aggregation.

14.6. Interpretation of the analyses.

14.6.1. The effect of the method of analysis. As can be seen from the analysis of the results there is considerable variation in the conclusions obtained from the different analyses.

14.6.1.1. The field measurements of the 1st nearest neighbour. Thompson (1956) recommends the Chi squared method for the analysis of nearest neighbour results, as it is more accurate than the

Table XXX.

Analysis of the nearest neighbour distances for the first to fifth nearest neighbours, as calculated from the mound coordinates, using the normal approximation test of Thompson (1956).

QUADRAT	1	2	3	4	5
OWH SS 4	2.62**	1.34	1.47	1.31	1.60
SS 5	4.13**	3.75**	4.74**	5.67**	5.60**
SS 7	2.12*	4.67**	5.46**	6.86**	10.03**
SS 8	4.84**	5.32**	5.83**	6.24**	7.08**
SS 9	5.98**	3.87**	4.55**	5.28**	6.19**
SS11	3.26**	2.80**	5.97**	6.19**	7.27**
SS12	2.68**	2.19*	3.66**	4.79**	4.87**
NFS	5.64**	5.52**	5.18**	6.44**	6.68**
C10	6.02**	4.79**	5.72**	5.07**	5.45**
AR 11	4.71**	3.78**	4.64**	4.96**	6.56**
12	6.93**	5.35**	4.77**	5.39**	4.84**
15	4.88**	5.67**	5.27**	6.31**	6.98**
16	4.61**	4.14**	4.16**	4.06**	3.36**
5	3.22**	2.91**	3.78**	4.88**	4.41**
NWS	-0.83	-2.31a	-2.27a	-2.24a	-2.94a
MD 7B	1.55	2.92**	4.79**	3.79**	4.32**
4A	3.53**	2.34*	2.04*	1.46	1.13
4B	3.47**	4.56**	4.68**	6.74**	7.49**
3B	4.57**	4.91**	5.10**	5.53**	6.07**
ST. C	4.97**	4.78**	5.63**	4.81**	5.62**

* Overdispersion at the 5% (0.05) level of significance
** Overdispersion at the 1% (0.01) level of significance
a Aggregation at the 5% (0.05) level of significance

The c statistics calculated from formulae 1), 2) and 6) in section 14.3.1. are given. The results tend to increase in significance as further nearest neighbours are considered. See section 14.6.1.3. for an explanation of this.

approximation to the normal distribution used in calculating the c statistic. However, this has usually been ignored (Simberloff 1979) or often misused (see section 14.3.1. above). It has been suggested that one of the reasons that the use of the c statistic has been preferred is because of the ease of the calculations required. The power and simplicity of modern hand held calculators and computers now invalidate that argument.

Are there, though, any differences in the results of the two types of analysis? The Chi squared method (Table XXI) resulted in significant overdispersion being demonstrated in 13 out of the 20 quadrats, the c statistic (Table XXII) in 15 out of the 20. The two quadrats in which the results of the analysis are changed are AR 5 and MD 7B, which are the most borderline cases. Thus it seems that the Chi squared test is slightly more conservative. The c statistic may tend towards a type 1 error.

In Table XXII there is also a demonstration that the Index of Dispersion, R, should not be relied upon as the best indication of overdispersion. For example in OWH SS 4, an R value of 1.14 has an associated c statistic indicating overdispersion at the 5% level of significance. In AR 5 the larger R value of 1.15 suggests a greater tendancy towards overdispersion but in fact the c statistic is less than the critical 5% level.

The effect of the modification of Donelly (1978) to the constant in the equation to calculate the standard error of the estimated mean distance to nearest neighbour, thus taking account of the effect on the calculation of having reciprocal pairs, can be seen in Table XXIII. The modification has had the effect of slightly increasing the standard error. As a result the c statistics are slightly reduced but in no quadrats has this affected the conclusion. It is possible though, that in a borderline case, this modification could prevent the false rejection of the null hypothesis of random distribution, another type 1 error, and thus should always be used.

Ants mounds are, of course, not points and the analyses discussed above use theory related to the distribution of points of infinitesimal diameter in space. The analyses of Simberloff (1979) which take account of this have a considerable effect on the results.

Using the Chi squared tests, in the standard point analysis 13 of the 20 quadrats show significant overdispersion but using the Simberloff (1979) analysis this is reduced to only 9 of the 20 quadrats. The quadrats in which the conclusion of significant overdispersion is overturned can be divided into two categories. Firstly OWH SS 4 and 8 which have quite a low diameter (s) to estimated mean nearest neighbour distance E(d) ratio. Of these OWH SS 4 is very much a borderline case of significant overdispersion. Secondly OWH C10 and AR 15 which have a high s to E(d) ratio and where there were dense populations of large mounds. Simberloff (1979) recommends that when the statistic s/E(d) is greater than 0.5 the Chi squared analysis is not used and is replaced by interpolation into his simulation curve. As this ratio, increases the Chi squared analysis becomes more unreliable.

This would explain why these two quadrats (OWH C10 and AR 15) are somewhat surprisingly considered to have a random distribution of ant mounds by this method, while in all of the others they are amongst the most clearcut cases of overdispersion. Using the simulation curve to calculate modified c statistics this anomaly is corrected and these two quadrats are restored to showing significant overdispersion. With this method 12 out of the 20 quadrats showed significant overdispersion, AR 15 and OWH C10 amongst them, although AR 15 is in fact very close to the critical level (Table XXV).

14.6.1.2. <u>The coordinate data, the first nearest neighbour.</u>

By examining the analysis of this dataset the importance of the modifications proposed by Donelly (1978) can be seen. The results were first analysed by the straightforward Clark and Evans (1954) c statistic and the Chi squared test. As with the direct measurements the Chi squared test is more critical, with overdispersion found in 16 quadrats compared to 18 using the c statistic.

This compares with 13 and 15 quadrats out of 20 respectively for these two methods when used on the direct measurements. By examining the Tables XIX and XX it will be seen that in 17 out of the 20 quadrats the mean distance to nearest neighbour O(d) is larger when calculated by the computer program from the coordinates, than when measured directly. Part of this may be due to small measurement errors in the field work but it is likely that the chief cause of this discrepancy is the absence of a border area around the quadrats.

With the direct measurements, if the nearest neighbour to an ant mound lay outside of the quadrat, the distance to it was measured anyway, as recommended by Clark and Evans (1954). Since the quadrats were postioned in theoretically uniform areas, the areas outside the quadrats could be considered as a border zone. By using the computer analysis to calculate the nearest neighbours and the distances to them, mounds from outside the area, whose coordinates were not measured, were not included. There is in effect no border zone.

The consequences of this are, that for some mounds, whose nearest neighbour would have lain outside the quadrat, the distance to their nearest neighbours would be overestimated, as the distance to a mound further away but lying inside the quadrat, would be recorded instead. This would lead to the observed mean distance to the nearest neighbour O(d) being slightly exaggerated, thus biasing any calculation on spacing towards overdispersion being produced as a result (another type 1 error).

The Donelly (1978) modifications to the formulae are designed to counter precisely this problem when a c statistic is being calculated. No method yet exists to correct this problem for the Chi squared test. The Donelly (1978) formulae have the effect of increasing both the expected mean distance to nearest neighbour and its standard error by a small amount. This has the result, seen in Table XXVII, of reducing the statistics R and c, and thus reducing the number of quadrats in which significant overdispersion is found to 15 out of 20, exactly the same as for the direct measurements using the unmodified Clark and Evans (1954) test. This would indicate that the modifications to the formulae have had the desired effect.

Unfortunately the different methods do not aggree on which of the quadrats showed, or did not show overdispersion. In the original Clark and Evans (1954) analysis on the direct measurements, the quadrats OWH SS 4 and MD 7B were found to show significant overdispersion. Using the Donelly (1978) formulae on the coordinate data these two quadrats are found to be not significantly different from a random distribution. Similarly on the direct measurements MD 4A and MD 4B were found to be not significantly overdispersed, while on the coordinate data using the modified formulae they were overdispersed. Thus it is possible that while the Donelly (1978) adaptations go some way towards improving this nearest neighbour analysis, they cannot be considered perfect. However, Donelly (1978) did suggest that his analyses were accurate for very small sample sizes (as small as 7) while for the Clark and Evans (1954) analysis, at low sample sizes there is some inacuracy.

The Donelly (1978) calculations are designed to overcome the lack of a border area in the field sample. Using the data from this study it is also possible to predict what size of border area would be necessary to ensure an accurate representation of the true field situation. The nearest neighbour distances are distributed normally. It is thus simple to establish a 95% confidence limit for a border area that would contain 95% of the nearest neighbours of all mounds that lay on the edge of the sample area.

It is done by using the z transformation, where u is the mean of the distribution, z can be obtained from standard statistical tables, and is the standard deviation of the distribution.

$$z = \frac{x - u}{\sigma} \qquad \text{or} \qquad x = z(\sigma) + u$$

If the value of z that corresponds to a 1 tailed distribution, with 95% of it less than z, is found from tables (eg. Neave 1978) we can calculate the corresponding value of x, or the nearest neighbour distance of which 95% of nearest neighbour distances will be less than, as both the mean and standard deviation of the distribution are known. By using this as the width of the border area we can guarantee that at least 95% of the mounds to be found on the border of the sample area will have their nearest neighbour within the border area. It will in fact be higher than 95%, as this would refer only to mounds that have their nearest neighbours outside the inner sample area (theoretically 50%) and where the nearest neighbour is located at 90^{o}

to the border line. As these are quite rare conditions this can then be considered an extremely safe border area to use.

This border size has been calculated for all of the quadrats and is shown in Table XXXI. It is clearly strongly reliant on the density of the mounds in the first place. It is clear, however, that a border area of between 2 and 3 metres would more than sufficient for all of the quadrats and probably for any other similar distribution of mounds.

Finally, using the Simberloff (1979) analyses on the coordinate data, in exactly the same way as on the direct measurements, the use of the coordinate data again results in significant overdispersion being much more readily demonstrated. On the direct measurements overdispersion was found in 9 quadrats using the Chi squared test and 12 using the normal approximation. With the coordinate data the comparable figures are 12 and 17 quadrats respectively.

Using the Simberloff modification of the c statistic test produced only one altered result compared with the unmodified test, with OWH SS12 being altered to non-significance. This is in strong contrast to the same results on the direct measurements where the use of the Simberloff (1979) methods greatly reduced the number of quadrats in which significant overdispersion was described (see section 14.6.1 above).

In the calculation of the c statistic it is possible to see a reason for this. The method involves calculating the statistic s/E(d). This is then used to interpolate into the simulation curve. As s/E(d) increases the consequent reduction in E(d) is greater. Thus as the coordinate results show an artificially increased E(d) the ratio s/E(d) is reduced and the effect on the modification of E(d) reduced.

Table XXXI.

Estimated size of border area necessary in each of the sample areas.

(Size in metres).

QUADRAT	Size
OWH SS 4	2.40
SS 5	2.61
SS 7	5.02
SS 8	2.30
SS 9	2.00
SS11	2.67
SS12	1.99
NFS	2.53
C10	1.80
AR 11	1.90
12	1.17
15	1.61
16	2.43
5	2.16
NWS	1.53
MD 7B	2.04
4A	2.29
4B	2.38
3B	2.30
ST. C	2.41

See section 14.6.1.2. for full details of how the border area size was calculated.

It thus becomes harder to decrease E(d) by a significant amount and a type 1 error is more likely. Using the Chi squared test the calculations are again biased towards overdispersion by the increased E(d).

The Chi squared test was much more conservative, although it did not fully make up for the problem of not having a border zone. Again the quadrats with a high s/E(d) ratio, OWH C10 and AR 15 were wrongly shown to have a random distribution of mounds.

14.6.1.3. <u>The coordinate data, the second to fifth nearest neighbours.</u> Neither the Donelly (1978) or Simberloff (1979) analyses have been extended in theory to the second or greater nearest neighbours. Therefore it was only possible to use the unmodified c statistic and Chi squared analyses on the data.

It has already been discovered, from the discussion of the first nearest neighbour analysis of the coordinate data, that the calculations are biased towards the demonstration of significant overdispersion, due to the lack of a border zone causing an increase in O(d). The results of the analyses on the second to fifth nearest neighbours clearly demonstrate that this problem is exacerbated as n increases.

Using the Chi squared test of significance, the degree of overdispersion appears to increase as n increases, in most of the quadrats. For example in OWH SS 12 the analysis of the first, second and third nearest neighbours does not indicate significant overdispersion while that of the fourth and fifth does. As discused by Waloff and Blackith (1962) we would expect that the degree of overdispersion would in fact decrease as n increases due to heterogeneity in the environment. Similarly, the analysis using the c statistic shows, in most quadrats, increasing significance as n increases.

This feature can be simply explained as a product of the same distortion in the estimation of O(d) as discussed for the first nearest neighbour coordinate analysis. Clearly if there is a small probability of the first nearest neighbour of a mound lying outside of the quadrat and thus being ignored, this probability is increased as n increases. In order to take account of this effect it would be necessary to have a large border zone around the actual quadrat in which nearest neighour distances would be measured. As n increases then so the size of border area necessary also increases. Field measurement of more than the first nearest neighbour is clearly desirable, if possible. If this is not done then the results must be viewed with a great deal of suspicion, if some allowances are not made.

Bearing this in mind, the analysis of the quadrat AR NWS is quite revealing in that it indicates aggregation of the mounds is present. This suggests that in this quadrat the habitat may certainly be somewhat patchy.

14.7. Conclusions on the methods of analysis.

It is clear that for ant mounds a straightforward use of the Clark and Evans (1954) method is not valid. Ant mounds are better represented as circles, not points, and thus the modifications proposed by Simberloff (1979) should generally be used. When the ratio s/E(d) is large the use of the c statistic test of significance is better than the Chi squared test. If at all possible, a border zone should be used, in which the distance to nearest neigbour may be measured if the nearest neighbour lies outside of the sample area. If this is not possible, then, providing the Donelly (1978) adaptations are used, then some degree of reliability in the calculations will still be present. This should always be used when nearest neighbour distances are calculated from the coordinates alone.

It is not possible in the described methods in the literature at the moment, to combine the adaptations of both Simberloff (1979) and Donelly (1978). An examination of whether this could be done, presumably using simulation methods, would be a great advance in nearest neighbour analysis.

Analyses when n is greater than 1 should always be done from field measurements. Modifications, such as those of Donelly (1978) and Simberloff (1979) are not yet available for n>1 and again would be an advance in this sphere. As n increases, larger and larger border areas should be used. It is suggested from the work described above that a preliminary set, of measurements of distances to the largest n required, will assist in deciding the size of the border area necessary.

When using the Simberloff (1979) method the diameter of the circle used to calculate the theoretical E(d) was taken as the mean diameter of the ant mounds in the quadrat. Use of this figure ignores the individual variation in the mound size. A way of overcoming this problem, and many of the others associated with nearest neighbour analyses, may be to use Monte Carlo simulation methods to analyse the data. In this technique, described by Spain, Sinclair and Diggle (1986), the populations of mounds would be placed in repeated random simulated distributions and the O(d) of these distributions measured. The real O(d) is then compared against the O(d)'s measured from a large number of random simulated distributions.

Such methods would of course be much more time consuming than some of the simple nearest neighbour analysis already described but on the other hand might be more reliable. Again, experimental tests would be valuable.

Above all it is clear that field measurements are likely to be more accurate than any other techniques.

14.8. The distribution of mounds of L. flavus.

14.8.1. Spatial distribution of ant colonies. Work on the spatial distribution of ant colonies has been summarised by Levings and Traniello (1981) who concluded that most ant species show overdispersion of colonies.

Since their paper the spatial distribution of ant colonies ahas continued to be investigated, and in the following cases nearest neighbour analysis has been used. Ryti and Case (1986 1988) on the harvester ants *Veromessor pergandei*, *Pogonomyrmex californicus* and *Myrmecocystus flaviceps*, Harrison and Gentry (1981) on *Pogonomyrmex badius*, Chew (1987) on *Novomessor cockerelli*, *Myrmecocystus mexicanus* and *M. depilis* and Cushman, Martinsen and Mazeroli (1988) on *Formica altipetens*. These studies have also concluded that overdispersion is present, generally as a result of competitve interactions between the colonies.

14.8.2. Previous studies on L. flavus. Previous studies on populations of *L. flavus* mounds have concluded that they are generally overdispersed. These studies are summarised in Table XXXII. The most thorough examination as been by Waloff and Blackith (1962). They examined four separate populations of mounds at Silwood Park in Berkshire, England, with two populations showing significant overdispersion, one on the borderline and one randomly distributed.

Table XXXII

Previous examinations of the spatial distribution of the mounds of *L. flavus*.

Author/s	Method	N	Result	Significance
King (1977a)	H	25	O	P<0.01
King (1977a)	H	50	O	P<0.01
Waloff and Blackith (1962)	CE	21	B	P=0.05
	CE	46	O	P<0.03
	CE	11	R	P=0.60
	CE	60	O	P<0.01
Elmes (1974)	CE	50?	R	P>0.05
Pontin (1978)	CE	64	O	P<0.01
Pontin (1961)	CE	10	O	P<0.05
Blackith et al (1963)	CE	84	O	P<0.01
	CE	19	O	P<0.01

Methods: CE - unmodified Clark and Evans (1954).
H - Hopkins (1954).

Results: O - significant overdispersion demonstrated.
R - randomly distributed.
B - borderline case.

However, the sample sizes for the latter two populations were very small, 21 and 11 mounds respectively. In all, in the examples shown in Table XXXII, of 11 cases, 8 showed significant overdispersion.

From this Table we can also see that all of the authors, bar King (1977) used the unmodified technique of Clark and Evans (1954). However, as we have seen from the discussion of the methods of nearest neighbour analysis, it is possible that erroneous conclusions could have been arrived at by use of this method.

Simberloff (1979) demonstrated that the conclusion of overdispersion, by Waloff and Blackith (1962) in case 2 in Table XXXII, was wrong. If the mounds are considered as circles of diameter of 30cm. then using the modified calculations, the conclusion is one of a random distribution. In case 4, though, the conclusion is upheld. In the other cases it is not possible to examine the validity of the conclusions because insufficient data is given as to the size of the sample area and of the mounds themselves.

Thus we might conclude that the suggestion of mound populations of _L. flavus_ being generally overdispersed is not proved. What about the populations in this study, where all the required information is available?

14.8.3. _Conclusions from the results of this study._ Having discussed the methods of analysis above the sample quadrats were divided into three categories.

1) Significant overdispersion is clearly demonstrated.

2) No overdispersion present.

3) Borderline cases.

The quadrats were divided into these categories mainly on the results of the analysis of the field measurements of the first nearest neighbours, using the Simberloff (1979) adaptations (Tables XXIV and XXV).

1	2	3
OWH SS5	OWH SS7	OWH SS4
OWH SS9	OWH SS12	OWH SS8
OWH SS11	AR NWS	
OWH NFS	AR 5	
OWH C10	MD 7B	
AR 11	MD 4A	
AR 12	MD 4B	
AR 15		
AR 16		
MD 3B		
ST. C		

Despite all of the variations of the different methods of analysis it is quite clear that when considering the first nearest neighbours at least 11 out of the 20 quadrats show significant overdispersion and that we can conclude that it is a common feature of populations of mounds of L. flavus on chalk grassland. However, it certainly can not be assumed that L. flavus mounds are always overdispersed.

We can now look for common characteristics present in quadrats in each category to see if any particular characteristic of the management or environment of the sample areas, is linked to a random distribution, or indeed to an overdispersed one. There is no obvious correlation with the number of mounds found in each of the quadrats. A t-test of the numbers of mounds in categories 1 and 2 shows no significant difference ($t = 1.29$, $P>0.20$). Similarly there appears to be no correlation with the amount of grazing in each of the categories. In both groups there are highly grazed quadrats (eg. AR 12 and 16 in category 1 and AR NWS in category 2) and lightly grazed quadrats (eg. OWH C10 and AR 15 in category 1 and MD 7B in category 2). No relationship was found to any aspects of the environment either.

What does come out of this analysis is that the quadrats in category 2 seem to be those with a disturbed past history. For example category 2 contains MD 7B, 4A and 4B. As discussed in Chapter Five, Martin Down has only recently had grazing properly restarted, prior to which there was a period when it was allowed to become overgrown and dominated by coarse grasses. In addition the area in which MD 7B lies was harrowed in the early 1960's. AR 5, also in this category, lies in an area which was ploughed during the war, and has not had a stable grazing regime since. OWH SS 7 has been overgrown by the grass Tricetum flavescens.

Other quadrats on the south slope at Old Winchester Hill are scattered among the categories. It will be recalled that this area too had an unstable period of history in the 1970's when cattle grazing was necessary to reduce coarse grasses. Before this there was considerable disruption on the south slope due to bomb clearance activities (see section 5.4.1.3.). It was suggested that OWH SS 9 was less disrupted in this process (section 12.4.) and this sample quadrat is placed in category 1.

In category 1 all the quadrats with the most stable past history are to be found. All the Aston Rowant quadrats in the experimental set up (AR 11 to 16) with a consistant pattern of grazing for 20 years, are here. The quadrat MD 3B which is in this category is the one that best survived the unstable period on Martin Down (see section 10.22.2.).

There is an apparent relationship between a stable past history of a quadrat and the development of an overdispersed distribution. As discussed previously, (section 12.4.), the individual ant colonies appear to be extremely long lived and it might therefore take quite a long period for an equilibrium distribution of colonies to be established. Any disturbance to an area would disrupt this process.

14.9. The causes of overdispersion.

It is generally assumed that overdispersion of organisms is due to competitive interactions between individuals, or in this case individual colonies. As L. flavus is an underground ant it is not possible to make direct observations on any interactions between colonies. However, Anderson (1970), in some unpublished work, demonstrated, in a series of laboratory behavioural experiments, that there was aggression between the workers of different colonies. Workers were able to recognise members of their own colony from chemical cues and differentiate them from 'foreign' workers.

Pontin (1963) observed that queens landing on the mounds of colonies after the nuptial flight were attacked if discovered by the 'home' workers. This would thus prevent the founding of new colonies in the immediate vicinity of established ones. Waloff and Blackith (1962) and King (1977b) found the mortality of small immature colonies was high. It may be possible that older larger colonies are responsible for the death of small colonies in their area, thus leading in the long term to more spacing out.

This evidence suggests that the aggressive responses of workers in established colonies may inhibit the founding of new colonies close by and thus eventually lead to the overdispersion commonly observed for L. flavus mounds. If so, this would mean that in 'defending' an area against members of another colony, the workers are setting up a true territory, as it is defined by some authors (Baroni-Urbani 1979, Holldobler 1974), in that there is defence of an area involved.

Similar lines of evidence have been advanced in other ant species (Wilson 1971, Holldobler 1976, Mabelis 1979, Brian 1983). Cushman, Martinsen and Mazeroll (1988) concluded that the same mechanisms were responsible for the overdispersion observed in colonies of the ant Formica altipetens. They also suggested another possibility, namely that existing colonies may so deplete the important resources in an area that new colonies coming into the area fail to establish themselves. There is no available evidence for this in populations of L. flavus.

One of the original aims of this section was to establish whether overdispersion was present, in order to examine the presence of intraspecific competition between the colonies. The evidence discussed above suggests that intraspecific competition is present in the majority of the quadrats. There are, however, other methods of looking at this using the nearest neighbour data.

Nielsen et al (1976) demonstrated that the size of the nest mound of L. flavus could be correlated with the worker population of the colony. This was also found in the colonies that were dug up at Aston Rowant and Martin Down in the current study. A product-moment correlation between the maximum diameters of the mounds and their worker populations gives a significant result ($n = 15$ pairs, $r = +0.816$, $P<0.01$). Thus we can conclude that these chalk grassland mounds show a degree of correlation between mound size and worker population as well.

Wood and Lee (1971) argued that larger mounds of the termite Nasutitermes exitiosus should contain larger colonies, which would exert a larger influence on their neighbours. They found a positive correlation (product moment correlation $r = +0.88$ $P<0.01$, $n = 32$) between the size of the termite's mound and the distance to the nearest neighbouring termite mound.

Waloff and Blackith (1962) did not find a relationship between mound diameter and nearest neighbour distance of 60 L. flavus mounds from Silwood Park, Berkshire. In contrast, the data from this study did show a significant correlation (see Table XXXIII). When all the quadrats were combined, thus giving a sample size of 1,748 mounds, the correlation was highly significant. Significant correlations were also found for the mounds in 14 out of the 20 quadrats when examined separately.

This relationship is graphically illustrated in Figure 14.3 Here the mound diameters have been grouped into size bands of 10 cm. each and the average nearest neighbour distance calculated for each band. It shows the steadily increasing nearest neighbour distance as the diameter enlarges. This relationship becomes less clear for the very large mounds, but it will be recalled that the sample size is much smaller (see Figure 11.2.).

14.10. Conclusions.

Overdispersion of L. flavus populations that has been demonstrated in the past may not be reliable. Recalculation using the more recent adaptations of the basic nearest neighbour analysis formulae, is necessary.

The results of the spatial analysis of the ant mound populations of the sample quadrats demonstrate that populations of L. flavus tend towards overdispersion, but that significant disturbance to the sample area can destroy this. A relatively long stable past history (greater than 10 years) is necessary for the population to develop to a degree where overdispersion is clearly present.

Table XXXIII.

The relationship between mound diameter and nearest neighbour distance in all quadrats.

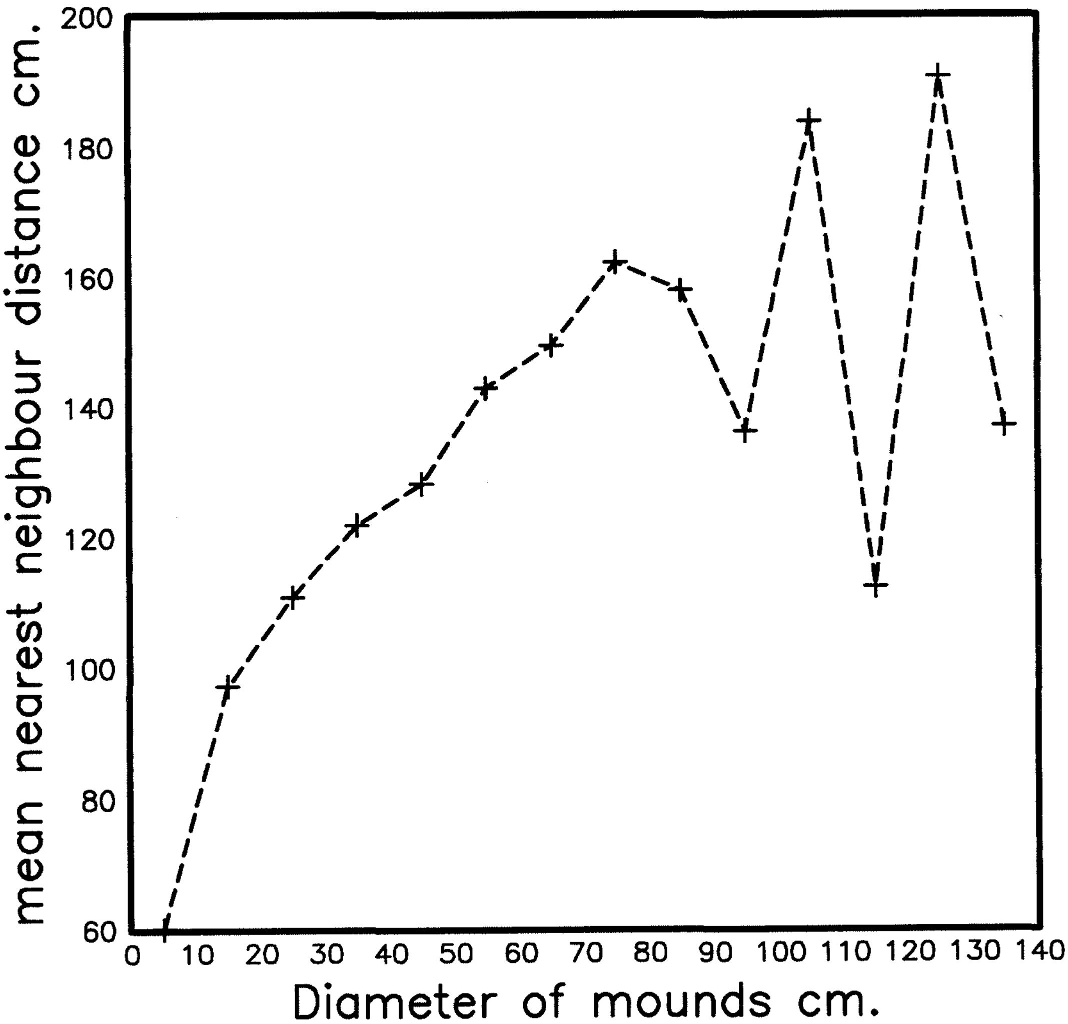
QUADRAT	NO. MOUNDS	r	SIG. LEVEL
OWH 4	67	0.1666	NS
5	64	0.2957	0.05
7	8	-0.5648	NS
8	66	-0.0506	NS
9	99	0.1399	NS
11	57	0.1449	NS
12	71	0.2920	0.02
NFS	70	0.3561	0.01
C10	119	0.2077	0.05
AR 11	113	0.4674	0.002
12	273	0.3243	0.002
15	126	0.2993	0.002
16	63	0.0849	NS
5	75	0.3093	0.01
NWS	119	0.3563	0.002
MD 7B	86	0.2419	0.05
4A	61	0.3543	0.01
4B	67	0.3582	0.01
3B	78	0.3982	0.002
ST. C	66	0.3306	0.01
TOTAL	1748	0.3515	<<0.002

r is the product-moment correlation coefficient. The mound diameters and distances to first nearest neighbours were those measured in the mapping of the sample quadrats, the raw data of which is given in Appendix One. Out of the 20 quadrats, 14 show significant correlations at the 5% (0.05) level. When all the data is added together the result is highly significant.

Figure 14.3.

The relationship between mound size and distance to nearest neighbour.

A total of 1,748 mounds were measured. The size of the mounds was assessed by their maximum diameter (see section 6.6.2.2.).



The mounds were split into 10 cm. diameter bands, ie. 0 - 10 cm., 11 - 20 cm., 21 - 30 cm. etc. The mean distance to nearest neighbour, as measured in the field, was calculated for each group of mounds. The numbers of mounds in each size band is shown in Figure 11.2. At the larger sizes of mounds the sample size is small. The raw data for this analysis is contained in Appendix One.