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Aspects of the Ecology of Desert-living Rodents in the North–East Badia Region of Jordan

by

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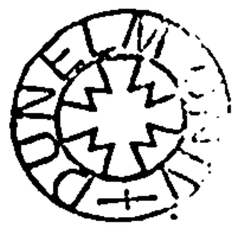
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13 JUL 2001

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ABSTRACT

Several aspects of the ecology of desert-living rodents were investigated in the North-east Badia region of Jordan. Six representative habitats were identified using satellite imagery, within these rodent community composition was investigated using live grid-trapping and spot-lighting techniques. Sixteen environmental variables were recorded in parallel with trapping studies. TWINSPAN and DECORANA analyses revealed three rodent guilds in relation to habitat type: petrophiles, open hammada dwelling species and psammophiles. Habitat preferences and guild composition provided evidence for several mechanisms of resource partitioning suggested to facilitate species coexistence. Temporal variations in community composition were also shown. Canonical correspondence analysis showed that vegetation parameters and soil properties were important in determining rodent community composition.

Within two study sites, spatial and temporal differences in resource abundance and habitat structure were assessed in four habitat types. Habitats were described using vegetation composition and cover, rock and stone cover, and loose soil depth. Jaccard's similarity index revealed that the vegetation composition of a habitat was more similar within sites than between sites, particularly for annual species. Temporal changes in vegetation cover were assessed using twenty $1m^2$ quadrats and followed at 10-day intervals over one spring period (March-May, 1998). Fresh and dry biomass of green vegetation was measured at monthly intervals and revealed differences in water content of vegetation between sites, but not within sites. During spring, seed abundance (density and biomass per m^2) within the different habitat types was assessed at monthly intervals. Seed production was measured by following the timing and output of seeding, seed rain using ten, 7.5 cm diameter seed traps and the seed bank by extracting five, $100cm^3$ soil cores. Analysis revealed differences in the composition, seed size distribution, and the spatial and temporal variability of these three seed 'sources'.

Small mammal trapping studies conducted in parallel with resource assessment revealed that neither density nor breeding parameters directly correlated with natural fluctuations in abundance of seeds or vegetation. Supplementary feeding experiments were conducted at one site, in which three treatments were applied to five grids, two grids receiving an 'early' seed supplement (22kg/ha), two grids a 'late' supplement and a control grid. The addition of food caused an increase in breeding in female *Meriones crassus,* but had no effect on male sexual activity, litter size or juvenile growth rate.

The environmental control of breeding was investigated using a laboratory colony of *Meriones crassus*. Animals were separated into two groups, one of which received a dietary supplement of vegetation (30g fresh weight/week). Photoperiod was manipulated so that both groups of animals bred under long days (16:8) and short days (8:16), once in parallel and once opposite to the natural photoperiod. Copulation attempts were used to assess breeding activity and analyses showed that supplementary vegetation increased breeding only during long days, suggesting that the timing and extent of breeding in *Meriones crassus* is influenced by several interacting environmental factors. Investigations of the resting metabolic rate of *Meriones crassus*, using open flow-respirometry, demonstrated that diet had no effect on metabolic rate, but there were significant sexual and individual differences between animals.

The results of the study are discussed in the context of land management and wildlife conservation in arid regions.

AKNOWLEDGMENTS

My deepest gratitude goes to my mother Christine and my sisters, Pamela and Nicola for their continual support and encouragement no matter which path I choose. Hence, I dedicate this thesis to them. I would especially like to thank Tom Maddox for his tireless advice, encouragement and inspiration.

Nigel Dunstone gave me the initial opportunity and has provided support, advice, friendship and grammatical corrections throughout my research. I am much in dept to Professor Peter Evans for his support and expert advice in all fields, irrespective of fact there was little mention of birds. I am also grateful to Professor Malcolm Todd who managed to secure the majority of funds to enable me to undertake the PhD. The research was partially funded by The Darwin Initiative, The Marion Zunz Award, The Trevelyan Trust, The British and Foreign School Society, Department of Biological Sciences, Durham University and The Access Fund, to all I am in great debt.

Mohammed Shabaz of BRDP allowed me to conduct my studies within the Badia Research and Development Program area. I am grateful to all the staff at Safawi field centre for supplying the logistics to undertake the fieldwork and to the drivers that accompanied me in the field, especially Mohammed for his understanding and assistance, Abu Abdallah for his patience and Hassan for his inexhaustible entertainment. The Higher Council for Science & Technology also assisted in organising logistics and helped me to eventually retrieve my equipment from customs. The Royal Society for the Conservation of Nature in Jordan collaborated with the Darwin initiative project and provided some equipment and transport within the field. I would especially like to thanks Mike Evans for his advice on field techniques and Sultan Mashaqbar for his co-ordination efforts and enthusiasm. Thanks go to all the staff at the British Institute for Archaeology in Amman for allowing me to exploit their resources whilst in Amman i.e. accommodation, camping equipment, e-mail, postal service and beer laden fridge. I am in debt to Darius Campbell for initially convincing me I was capable of undertaking this thesis and for his endless hospitality and entertainment, which made my time in Jordan more bearable. Additionally Karen Jones deserves recognition for all her support, advice and nurse-maiding when I was ill. Vanessa Mitchinson was a highly valued companion during my first year in Jordan and made the field centre a more enjoyable place. I would also like to thank Andrew Besson

for his veterinary assistance in the field and advice on soil samples. Other people in Jordan who provided comments on the research and personal support were Kevin, Marianne, Neil and Alan.

From the field work component I would finally like to thank all the British and Jordanian research assistants who participated with the study and tried to keep me sane/insane whilst undertaking field work; Tom Maddox, Kate Lister, Anne Burrows, Mike O' Connor, Rachel Freer, Karen Taylor, Arabe and Mano. Although brief, I appreciated the accompaniment and assistance of Gill Hinchcliffe, Bob Elliott and Rick Lockwood during the 1997 spring field session. Apologies to you all for the suffering you endured in the desert, but I couldn't have done it without you! Finally in Jordan I would like to thank the Border Police at Hashad and Hazim, and all the Bedouin I met for their overflowing hospitality. Roderick Dutton, Bob Allison, Rodney Stobbs, Alistair Kirk and Kevin Brown from the Centre for Overseas Research and Development (C.O.R.D., Durham University) helped to organise pre-visit arrangements including budgets, freight, logistics and transportation. I am additionally grateful to Alistair for allowing me to use some of his weather data and to Kevin for his valuable scientific and cultural advice. The Darwin Vegetation Team supplied information to aid in plant identifications. Other collaborations with C.O.R.D. include the Royal Geographical Society and the Institute of British Geographers.

During my time in Durham I was fortunate enough to share my laboratory with Yia-Yah Liao, Steve Willis, Liam Simms, Panos Giannokos, Laura Bonesi, Marcelo Mazzolli and Nathalie Walker, who provided entertainment, friendship, comments and advice. Extended gratitude goes to another laboratory companion Julian Mallinson, for his loyal friendship, understanding, support and valuable comments on my work. Throughout my research I have periodically utilised the expertise of members of Durham University Biological Sciences Ecology Section. Both Phil Hulme and Tom Sherrat provided useful statistical comments and I am especially grateful to Professor Brian Huntley for his time and effort in helping me apply and understand multivariate analysis. Tusi Butterfield and Rus Hoelzel provided useful comments on the draft publication manuscript of Chapter 2. I am financially grateful to Mike Stacey, who allocated me enough demonstrating to enable me to continue to fund the research. Mark O'Connell, Claire McSorley, Martin Souter, Andy Dean, Jackie Hay, Matt Davey, Anna Topf,

Chris Coles, Robin Ward, and Kate Lewthwaite are all valued friends who have provided comments and advice.

I am grateful to Mike Jordan for the loan of the *Meriones crassus* breeding colony, Mansour Al Mansor for his expert demonstrations in use of the respirometery equipment, Eric Henderson for providing space and equipment to enable me to process samples, Martin Christmas for demonstrating techniques in pH and electrical conductance and Derek Coates for demonstrating soil sample preparation and the use of the granulometer. Phil Gates helped me in my to attempt to locate *Atriplex halimus* and along with Jackie Spence showed me how to use the microscope set-up to take seed photographs. Judy Allen advised me on seed identification. I am especially grateful to the Biological Sciences technicians, John Summerill and Peter Hunt for looking after my rodents when I was away. Thanks also go to Chris Thomas for providing satellite imagery, Michael Bone for his amazing craftsmanship in constructing a rodent respirometry box, and the Biology Photographic Unit, Paul Sidney and David Hutchinson. Appreciation goes to all the undergraduate ecology project students for whom I sort a better understanding of ecology to enable me to advise them, Kate Lawton, Paul Headon, Jenny Knight, Lucy Skyes, Hannah Soulsby, Dawn Scott, Charlie Mead, Alex White and Rachel Kay.

I would like to thank the staff at Harrison Zoological Museum, David Harrison and Paul Bates for training in specimen collection and identification, and later confirming species identifications. I am much in debt to Irina Khokhlova and Boris Krasnov at the Jacob Blaustein Institute of Desert Research, Israel, for advice on captive breeding and supplementary feeding of *M. crassus* and their encouragement.

On a final and personal note I would like to thank all my other friends, particularly Sarah, Angela, Claire, Jenny, Alex, Hannah and Anthony, who remind me that there is more to life than chasing small furry things in the desert.

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CHAPTER 1
GENERAL INTRODUCTION

1.1 Overview

The focus of this thesis is an investigation of several aspects of the ecology of desert rodents of the north-eastern Badia, Jordan, a semi-arid predominantly basaltic area in which no previous mammalian ecological studies have been undertaken. Desert environments are characteristically hostile and unpredictable in terms of resource abundance and therefore provide particular challenges to animals that inhabit them. Although desert rodent communities have been the focus of many ecological investigations, there are still several aspects of desert ecosystems that are poorly understood, more specifically the temporal and spatial fluctuations in rodent communities and the factors that determine them. This thesis reports the results of investigations of the community composition of the species inhabiting the Badia region and attempts to identify which environmental factors may be influencing them. The variations in abundance of two food types, vegetation and seeds, were examined in space and time and their role in determining the timing and output of breeding in one species of desert rodent (*Meriones crassus*) assessed through field and laboratory experiments. In this thesis I aim to provide 'baseline' data, comparable to previous studies, on several aspects of desert ecology to enhance understanding of ecological processes governing this particular basaltic region and other desert ecosystems globally.

1.2 Why study desert ecology in Jordan?

The increasing demands on natural resources of the world's growing human population coupled with poor land management practices are causing an increase in global desertification. Jordan has a human population of approximately 4 million, with an estimated growth rate of 3.4% p.a. (Dutton *et al.*, 1998). Its more severe environmental problems arise where the demands of the rapidly increasing human population exceed the local natural resources (Abu-Taleb & Salameh, 1994). Overgrazing by livestock and detrimental land management practices have been identified as the major causes of land deterioration and desertification, the term used to define an area in which productivity has decreased dramatically to uneconomic levels (Sankary, 1981; Khresat *et al.*, 1998). Conservation and land management have become primary interests of recent projects in Jordan. However, many of these studies have focused solely on rare and endangered species (Qumsiyeh, 1993) or short-term effects of grazing prevention in national nature

reserves (Hatough *et al.*, 1986; Abu-Irmaileh, 1994). To enable exploitation and sustainable utilisation of arid land resources, and to conserve the rich diversity of endemic animal and plant species that inhabit these areas, there is an urgent need to increase our understanding of the ecological processes governing desert ecosystems.

1.3 The desert environment

Globally, deserts are diverse and are found from subtropical to Polar regions, varying in terrain from the more typical sand dunes to rocky deserts and gravel plains. However, they all share one common feature, aridity. The definition of a desert is still debated. Classifications of deserts may be based on the mean annual rainfall they receive: semi-arid (600–400mm); arid (400-100mm); and hyper-arid (<100mm) (Wilson, 1989). However, aridity is not derived solely from levels of annual precipitation, but also from environmental factors such as temperature, wind and solar radiation which influence evapotranspiration (Meigs, 1953 in Degen, 1997). Rainfall in deserts is characteristically unpredictable in the amount, time of year and location (Evenari, 1981 in Degen, 1997). In most low-latitude deserts, water scarcity is coupled with extreme seasonal temperature fluctuations, with maximum values commonly exceeding 40°C (Dutton *et al.*, 1998). Aridity and extreme temperature fluctuations provide major physiological challenges for the organisms that inhabit deserts.

1.4 Plants in arid environments

Desert-living perennial plants can endure periods of water scarcity by adaptations to prevent water loss. For example, succulents, such as cacti, have a low surface area to mass ratio, which reduces water loss. However, desert annual plants are not usually adapted to withstand extreme arid conditions and are generally short-lived, avoiding the drier periods as seeds in the soil seed bank (Kemp, 1989). As the survival of many desert annuals is dependent on their persistence in the seed bank, they typically invest a large proportion of their energy into seed production (Kemp, 1989). As granivory is common in many desert animals, plant species also employ an array of mechanisms to increase seed survival by reducing predation. Annual plants in deserts tend to demonstrate a rapid facultative response to precipitation in which seeds germinate into adult plants, which reproduce, seed and die soon afterwards (Gutterman, 1993). As precipitation is characteristically sporadic in deserts, variations in the temporal and spatial abundance of annual plants and the yearly seed crop are common (Nelson & Chew, 1977).

1.5 Adaptations of desert dwelling animals

Many desert animals possess morphological, physiological and behavioural adaptations (Brown *et al.*, 1979) to enable them to survive in arid environments, in which temperature extremes, aridity and scarcity of resources all provide potential problems for the inhabitants.

1.5.1 Thermoregulation and water loss

As deserts demonstrate extreme temperature fluctuations, animals inhabiting them must have a great capacity to maintain thermal equilibrium. Homeothermic animals must maintain body temperature, which is affected by the metabolic rate and thermal conductance by regulating heat gain and losses (see Degen, 1997). Rodents inhabiting hot arid environments tend to have lower minimum energy expenditures (i.e. Basal Metabolic Rate, BMR) than those predicted for rodents of the same body size inhabiting other biomes (Degen *et al.*, 1986). This is seen as an adaptation to hot arid environments, as a lower basal metabolism will reduce the amount of water required in cooling (Grodzinski, 1975). When ambient temperatures exceed body temperatures heat loss can be achieved only through evaporation. Many species that must control water loss, uncouple thermoregulation from evaporative cooling by behavioural processes (Bartholomew & Dawson, 1974 in Downs & Perrin, 1990b). Additionally, some deserts can experience low ambient temperatures and the relatively high values of non-shivering thermogenesis exhibited by desert rodents have been suggested as an important physiological adaptation to exploit cooler arid environments (Haim & Izhaki, 1993). Thermal conductance is often lower for nocturnally active desert-living rodents, which regularly experience cold desert nights than for diurnally desert-living species of the same size, which need to facilitate heat dissipation (e.g. *Acomys russatus*, Haim & Izhaki, 1993).

Water is available either from "preformed" water present in the food or from that produced by metabolic processes (Degen, 1997). Therefore in desert-dwelling rodents free water intake is generally low. To balance this, deserts rodents show an enhanced capacity to conserve water by concentrating urine (Kam & Degen, 1992), producing dry faeces (Whittaker, 1975), and minimising evaporative water loss (Degen, 1997). Water balance also depends on the diet of the rodents (see section 1.5.2) and the biotic and climatic features of the environment. For example, Christian (1979) observed that variation in the rates of evaporative water loss in several species of small desert rodents

was greater at low than at high ambient humidity. Actual water loss varies seasonally in association with precipitation and vegetation abundance (Downs & Perrin, 1990).

Problems of heat and water scarcity can be reduced by behavioural means, by adjusting spatial and temporal activity. The majority of desert rodents are nocturnal or crepuscular (see Table 1.5.2), avoiding the heat of the day by remaining within burrows or other refuges which provide a stable microenvironment (Kinlaw, 1999), only emerging at night to forage. Diurnal species show seasonal changes in activity in response to ambient temperature, becoming more crepuscular in the summer and exploiting refuges that provide shade. Several species (e.g. *Jaculus jaculus*, Happold, 1967) control the microclimate within their burrows by blocking the entrances to maintain constant temperatures and high humidity (Degen, 1997). Some rodent species are active throughout the year, whereas others either hibernate or demonstrate facultative torpor (a physiological condition used to minimise energy expenditure), which enhances their survival during periods of food scarcity. Torpor coupled with low basal metabolic rates enable small mammals to inhabit variable and unpredictable environments (Bozinovic & Marquet, 1991).

1.5.2 Adaptations to food scarcity and unpredictability

Rodents that inhabit deserts also have to cope with temporally varying sources and unpredictable quantities of food. Seeds are considered to be continuously available within desert soils and can be harvested when in abundance and stored for times of food scarcity (Brown *et al.*, 1979). Indeed, granivory has been suggested as a dietary adaptation adopted by many animals that inhabit arid environments, i.e. birds (Marone *et al*, 1998), ants (Abramsky, 1983) and mammals (Reichman, 1979). However, flexibility in diet in relation to food availability also enhances survival in desert environments (Degen, 1997).

Examples of morphological adaptations to granivory in rodents can be seen in the North American heteromyids, which possess fur-lined cheek pouches for collecting and transporting large numbers of seeds, and in the family Dipodidae, which exhibit bipedal locomotion to facilitate economic travel between widely spaced seed aggregations. As a result of physiological adaptations, many granivorous rodents can subsist on a diet of dry seeds (Bar *et al.*, 1983), in which their water requirements are satisfied from water in food and from water produced during metabolic processes (Frank, 1988; Degen *et al.*,

1997). Granivorous rodents tend to have a lower metabolic rate in comparison to omnivorous and herbivorous species (Degen & Kam, 1992; Degen, 1994). This allows them to tolerate extremely arid environments (Kam & Degen, 1993).

Diet can have a profound effect on energy and water balance by causing differences in "preformed" water content and digestive assimilation efficiency. Tolerance to water deprivation is also related inversely to assimilation efficiency (Withers, 1982). Dietary adaptations shown by *Meriones crassus* include a low metabolism, a high capacity to digest dry plant feed and low nitrogen requirements, enabling this species to cope with periods of food shortages (Yahav & Choshniak, 1989). Diet selection is also important in water conservation (Degen *et al.*, 1986). For example, *Psammomys obesus* lives solely on saltbush (*Atriplex halimus*), a perennial desert plant with a high water content (Degen *et al.*, 1997). Several desert rodents have been shown to shift their diet in relation to vegetation (supplementary water) availability (Krasnov *et al.*, 1996b). Rodents can also obtain water from food through their hoarding behaviour, as the seeds stored in burrows absorb water from the humid air of the burrow system, increasing seed succulence before ingestion (Nagy & Gruchacz, 1994).

Many rodent populations are influenced by variations in the quality and quantity of available food (Akbar & Gorman, 1993a). It would be expected that this variation would be more prominent in arid areas where extreme fluctuations in resources can occur. As in temperate-dwelling small mammal species, the timing of breeding and the output of breeding, which will directly affect the population density, should be related to the fluctuations in food abundance. Seed abundance has been shown to influence the density, biomass and species diversity of several desert rodent populations (Abramsky, 1988). Rapid increases in population density have been recorded following a large seed crop (Whitford, 1976), and supplementary feeding experiments using seeds tend to lead to an increase in population numbers (Akbar & Gorman, 1993a). Hence, environmental factors that influence seed production may have direct affects on rodent populations. This is supported by evidence from a study on African rodents which suggested that prolonged periods of rainfall might generate excess food and cover resulting in an extended breeding season (Taylor & Green, 1976). Annual productivity, in relation to precipitation, has been positively correlated with rodent species diversity in deserts (Brown, 1973; Abramsky, 1988; Brown & Heske, 1990b) thus fitting Tilman's (1982) predicted productivity-diversity relationship (Abramsky & Rosenzweig, 1984). An

increase in resources may facilitate co-existence of more species and therefore temporal fluctuations in resources may also influence community composition.

Vegetation abundance has also been suggested to be an important determinant of rodent densities, as supplementary water, available in the form of vegetation has been suggested as an important factor in the reproduction of desert rodents (e.g. Bradley & Mauer, 1971). Availability of vegetation has been shown to increase the number of pregnancies and the proportions of lactating females, and extended the breeding season in several desert rodent species (Christian, 1979).

1.6 The role of rodents in desert ecosystems

Rodent granivory can have a dramatic effect on the abundance and distribution of seeds (Brown *et al.,* 1979); for example, in North American deserts, rodents were reported to consume up to 75% of all seeds produced (Nelson & Chew, 1977). Rodents are also selective in terms of seed size and species taken (Reichman, 1975) and the spatial distribution of their foraging efforts (Reichman, 1979). Therefore rodents can play an important role in determining the abundance and community structure of plants (Brown & Heske, 1990a). As potential prey, rodent populations may in turn exert important influences on both the population dynamics and the inter-specfic interactions of their predators (Brown *et al.,* 1979). From preliminary dietary investigations, small mammals predominate in the diet of both avian (*Bubo bubo* & *Athene noctua*) and terrestrial predators (*Vulpes vulpes*) in the Badia region (Burrows, Lawton, Lister and Maddox, pers. comm.). Predation pressure has been shown to greatly influence many aspects of desert rodent ecology, such as, foraging behaviour, species coexistence and the evolution of specialised morphology (e.g. Kotler, 1984).

1.7 Previous investigations of desert rodent ecology

The majority of studies on desert-dwelling rodents broadly fall into two areas: ecophysiology (Degen *et al.,* 1997) and spatial ecology (Shenbrot *et al.,* 1999). The former includes aspects of the adaptations of individual species to desert environments (see section 1.5), and the latter focuses mainly on rodent communities and the mechanisms underlying community structuring. There has also been an emphasis on comparing rodent communities of deserts world-wide in an attempt to identify underlying processes affecting desert ecology. The introduction to each chapter of this

thesis will detail the relevant studies that have contributed to knowledge of the subject in question.

Geographical comparisons have provided examples of evolutionary convergence in desert rodent communities, particularly in habitats of similar climate, vegetation and soil type (Kelt *et al.*, 1996). In these circumstances, coexisting species appear to show comparable patterns of morphology, body size and foraging behaviour (Brown *et al.*, 1979). Differences in species diversity between deserts can be attributed to ecological, biogeographical and evolutionary processes (Brown, 1973). It has been shown that the structure of small mammal communities is strongly influenced by historical factors. Different taxonomic groups with distinctive trophic adaptations have proliferated in different desert regions where they have been subjected to some common structuring processes of community assembly (Kelt *et al.*, 1996).

Identifying structuring processes, such as the mechanisms of resource partitioning to facilitate coexistence, has been the emphasis of many desert rodent ecology studies. Processes examined include competition (Kotler *et al.*, 1993), morphology (Bowers & Brown 1982; Price, 1983), predation (Kaufman & Kaufman, 1982; Kotler, 1984a; Bowers & Dooley, 1993), foraging behaviour (Price & Heinz, 1984; Reichman, 1984; Randall, 1993; Kotler, 1997) diet (Harris, 1986), and macro- (Bowers, 1988) and micro-habitat (Price, 1978) preferences. Attempts have also been made to assess the effects of environmental factors such as resource availability (Price & Heinz, 1984) and productivity (M'Closkey, 1983) on community structure. Co-existing species appear to reduce inter-specific competition via size disparity, differences in morphology and locomotion, and differential microhabitat and resource utilisation (Shenbrot *et al.*, 1999). However, the extent that inter-specific competition determines community composition differs between deserts. In studies of the "morpho-ecological" organisation of four desert rodent communities from Mongolia and Mexico, low convergence was demonstrated between the species of two continents. This led to the suggestion that the importance of different structuring processes may differ amongst deserts, as inter-specific competition played a larger role in community formation in North America than in Central Asia where predators and environmental conditions were more important (Rogovin & Surov, 1990).

Optimal Foraging Theory proposes that an individual attempts to maximise energy intake while feeding and therefore should minimise foraging costs (Cowie, 1977). Foraging behaviour of desert rodents can be influenced by the size, distribution, energy nutritional and water content of seeds; soil properties; ability of individual to locate, recover and cache seeds; inter- and intra- specific competition and predation risk (Randall, 1993). Additionally, environmental conditions may influence many of these factors. Several of the proposed co-existence mechanisms are based on differences in foraging behaviour, such as seed size selection, seed distribution selection and habitat separation.

There has been conflicting evidence that desert rodents select seeds based on seed size in relation to body weight (Brown & Lieberman, 1973; Lemen, 1978), and it is generally considered that this is not the case (Price, 1983). It is also debated whether rodents select seeds based on their distribution. It was suggested that bipedal animals maximise energy returns by specialised on widely distributed patches of clumps of seeds in open habitats, whereas quadrupeds focus foraging efforts on less dense more closely spaced patches under vegetation (Reichman & Oberstein, 1977). However, evidence from studies investigating the energetics of travelling between patches and the utilisation of clumps between bidepal and quadrapedal rodents does not support this hypothesis (Thompson *et al.*, 1980; Trombulak, & Kenagy, 1980).

The vertical distribution of seeds will also be of importance in determining foraging economics. It has been suggested that rodents will harvest seeds from the surface of the soil (seed rain) before taking buried seeds (seed bank) (Price & Joyner, 1997) and harvesting rate decreases with increasing soil depth (Lockard & Lockard, 1971). Desert rodents are thought to use a combination of olfactory cues and tactile discrimination to locate and harvest seeds from desert soils (Lawhon & Hafner, 1981), therefore soil properties can potentially influence foraging efficiency. It has been demonstrated that soil particle size in relation to seed size effects harvesting efficiency (Hughes *et al.*, 1995) and increased soil moisture content can facilitate seed detection by olfaction (Vander Wall, 1995).

There has been substantial evidence that predation risk has been a selective pressure in the evolution of anti-predator behaviour and morphology. Morphological examples include, hyper-inflated auditory bullae in rodents, allowing enhanced predator detection

(Webster & Webster, 1971) and bipedal locomotion, conferring ability to avoid predators by fast sprint speed and erratic escape patterns (Kotler *et al,* 1994). Cryptic coloration, i.e. the dorsal pelage corresponding to that of the predominant habitat (e.g. Harrison & Seton-Browne, 1969), is also thought to be anti-predatory adaptation.

Brown *et al.,* (1994) determined the relative contributions of predation risk to foraging costs of two desert rodent communities. They showed that predation risk varied between seasons and microhabitats, i.e. open areas were more risky than areas with cover and therefore it was important in determine foraging decisions. The risk of detection by predators varies with levels of lunar illumination and both temporal and spatial shifts in foraging activity of desert rodents have been observed with change in moonlight (Kaufman & Kaufman, 1982; Price *et al.,* 1984). Anti-predatory behaviour is also considered to be dependant on predator type, i.e. snakes, birds and carnivores (Kotler *et al.,* 1993), the perception of predation risk (Lagos *et al.,* 1995) and the presence of other predators, which may result in predator facilitation (Kotler *et al.,* 1993). Predation risk can lead to a shared preference for 'safe' habitat types and therefore result in increased competition within these (Hughes *et al.,* 1994). However specialisation in predatory avoidance can also promote coexistence (Kotler, 1984a).

1.8 Further information required

Even with the large number of studies that have been undertaken on desert rodents there are still many gaps in current knowledge of the basic biology of desert-living species and desert ecology as a whole. Shenbrot *et al.* (1999) called for further research on deserts that have previously been understudied, particularly with regards to community ecology, to fill in gaps in knowledge of these systems and to allow ecological comparisons between deserts world-wide. Although community composition and the factors influencing structure appear to have been well studied, temporal and spatial fluctuations in rodent community composition and abundance, in relation to changes in resources have been relatively overlooked. Yet, it is imperative to consider these in studies of deserts, where spatial and temporal fluctuations in resources result in highly dynamic communities. Additionally there is also a need to identify and assess what resources are available to rodents, how they fluctuate and how fluctuations in availability may influence population parameters, such as breeding output.

1.9 The mammals of Jordan

Distribution records and studies on the fauna of the Arabian Peninsula have been collated in 'The Mammals of Arabia' (Harrison & Bates, 1991), which indicates a paucity of information on the distribution, biology and ecology of the mammalian fauna of Jordan. The first descriptions of mammal specimens in Jordan were by Allen (1915, in Harrison & Bates, 1991), who collected data from the southern coastal region of Aqaba. In the 1966 'International Jordan Expedition', species lists and systematic notes were made for mammals of the Azraq Basin (eastern Jordan) and El-Jafr (southern Jordan) (Atallah, 1967). This resulted in a list of 22 mammal species, including clarification of ambiguous subspecies and identification of a new species of spiny mouse (*Acomys*). Notable publications since have included the description of new small mammal species (Bates & Harrison, 1989), regional records of species presence in the north-east Syrian desert (Searight, 1987), distribution patterns of mammals throughout Jordan (Amr *et al.*, 1987), the compilation of an inventory list for mammals acquired by the Jordan museum and a study of small mammal karyotypes (Qumsiyeh *et al.*, 1986).

To date only Nelson (1973) has reported on the ecology of small mammals of the Badia region, providing comments on the behaviour and ecology of some of the common rodent species found in the area, particularly the lesser jerboa (*Jaculus jaculus*). It is thus evident that little is known of which species inhabit this area and many aspects of their biology and ecology. Table 1.1 summarises the current information on species found within the region, and which are relevant to this investigation.

1.10 The Study Area

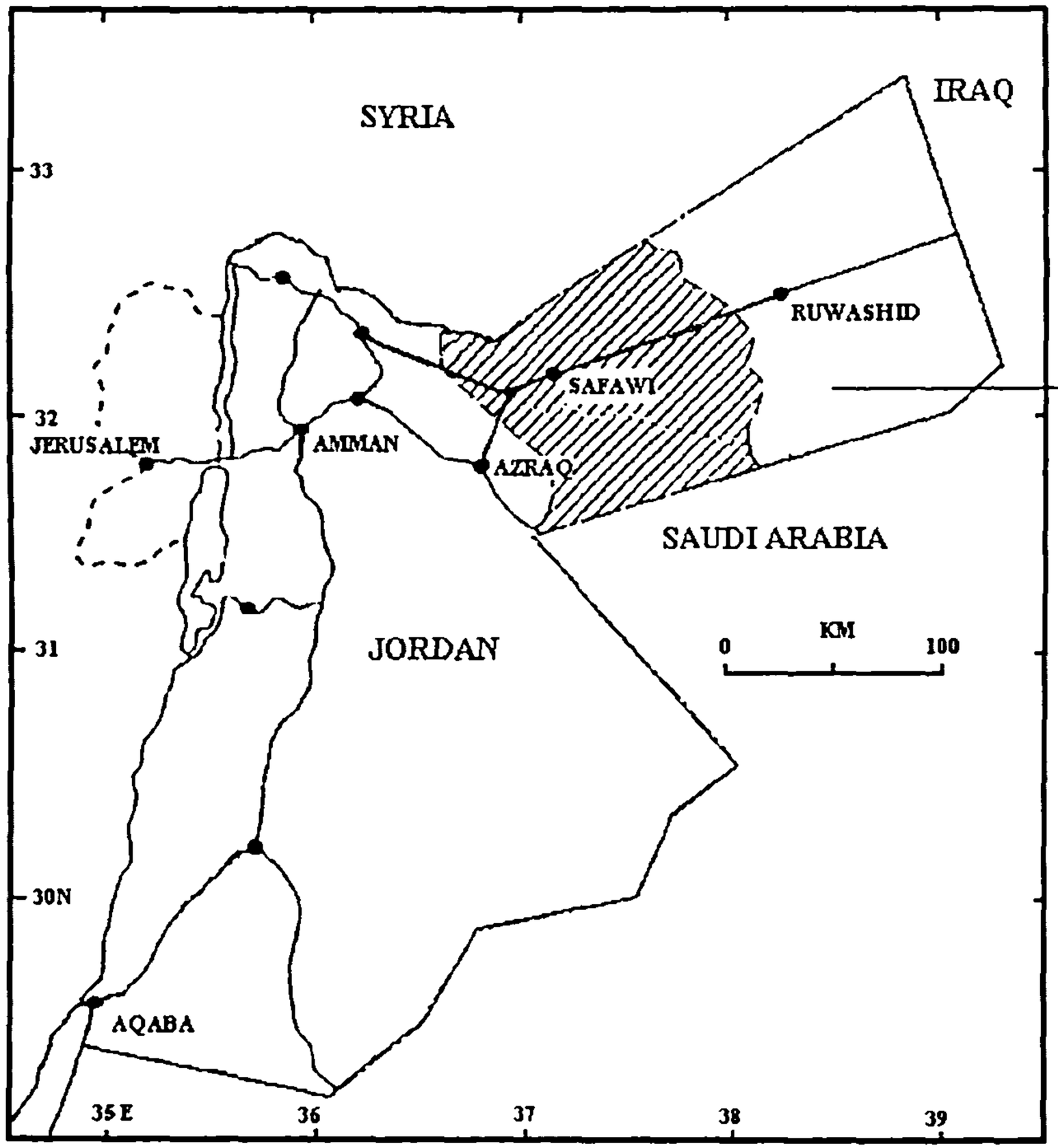
1.10.1 Terrain and geology

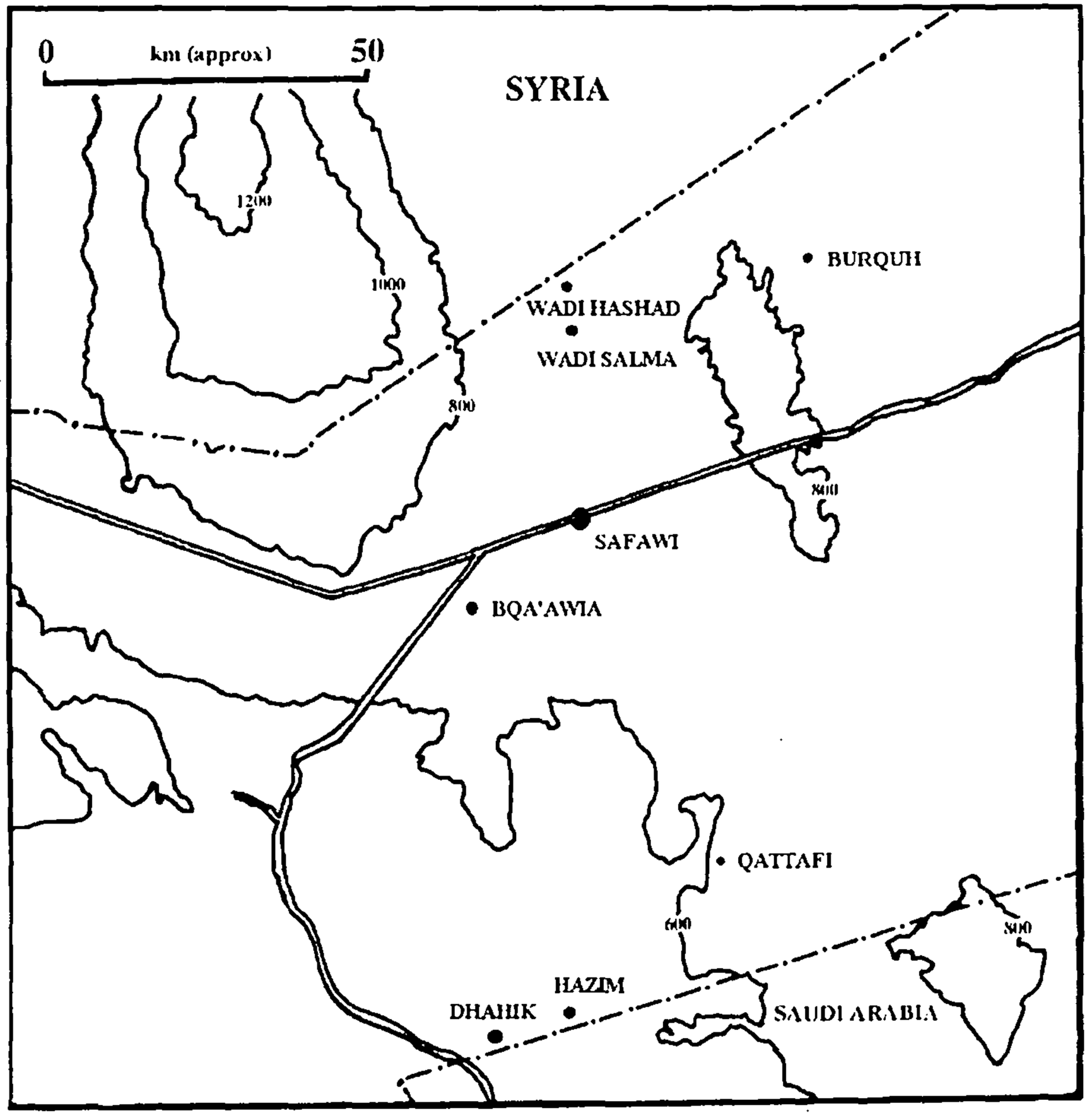
The study was conducted in an arid area of the north-east region of Jordan. Figure 1.1 shows the study area and the locations of the main study sites. The landscape of the region varied from basalt fields in the north, chert plains towards the south-east to sand dunes near the southern border with Saudi Arabia. Throughout much of the region the mean altitude is 700m, with the topography dominated by gently undulating low hills, which vary in shape depending on the age, physical and mineralogical characteristics of the basalt flows. Low areas within the region have become basins, locally known as qa'a or marab depending on the drainage (and therefore the types of deposits accumulated therein). Qa'a have fine deposits of limited permeability, whereas marabs are comprised of coarser grained deposits (Allison *et al.*, 1998).

Table 1.1 Summary of relevant literature on rodent species found in the study area. S = solitary, C = colonial, H = herbivorous, G = granivorous, O = omnivorous, Noct = nocturnal, Diur = diurnal and Crep = crepuscular.

Species	Common name	Distribution	Approx. body mass (g)	Coloration and feet	Group	Activity	Habitat	Diet	Breeding	Gestation (days)	Litter size	References
Jaculus jaculus	Lesser jerboa	North Africa & Arabia	67	Hind feet elongated and hairy, sandy grey colour	S	Noct.	Open areas	H	Winter & spring	25	2-7	Flower (1939); Happold (1967); Harrison & Bates (1991); Krasnov *et al.* (1996a)
Acomys russatus	Golden spiny mouse	Arabia	45	Melanistic sub-species. Naked soles of feet	C	Noct./ Diur.	Rocky	O	Wet season	44	1-4	Attalah (1970); Shkolnik (1971); Kingdon (1974); Searight (1987) Al-Khalili & Delany (1986); Harrison & Bates (1991)
Gerbillus cheesmani	Cheesman's gerbil	Arabia	-	Sandy colour & hind feet hairy	S	Noct.	Sandy	-	Continuous	20	1-8	Vesey-Fitzgerald (1953); Gallagher & Harrison (1988); Harrison & Bates (1991)
Gerbillus henleyi	Pygmy gerbil	North Africa & Arabia	9-10	Ash-grey to sandy colour, hind feet naked	-	Noct.	Various	G/H	Spring to early summer	-	-	Harrison & Bates (1991); Degen *et al.* (1997)
Gerbillus dasyurus	Wagner's gerbil	Arabia	21-33	Pale sandy, naked soles of hind feet	S	Noct.	Various, avoids sand	G	February to October	18-22	2-7	Harrison & Bates (1991); Krasnov *et al.* (1996a); Shenbrot *et al.* (1997)
Gerbillus nanus	Baluchistan's gerbil	North Africa & Arabia	22	Polytypic, hind feet naked	C	Noct./ Crep.	Various	G	Winter to early spring	-	-	Harrison & Bates (1991); Krasnov *et al.* (1996a); Lay (1967)
Meriones tristrami	Tristram's jird	Arabia to Asia	-	Colour fulvous, hairy soles of feet	-	Noct./ Crep.	Various	H	Continuous, max. April to Sept.	25-29	1-7	Bodenheimer (1949); Zahavi & Wahrman (1957); Harrison & Bates (1991);
Meriones libycus	Libyan jird	North Africa, Arabia & Asia	85	Reddish sandy, hind feet partially hairy	C	Noct./ Diur.	Various – near water source	H	Winter & spring	20-30	1-12	Harrison & Bates (1991); Lewis *et al.* (1965); Atallah (1967); Naumov & Lobchev (1975)
Meriones crassus	Sundevall's jird	From North Africa and Arabia to Pakistan	81	Pale sandy colour, soles of feet partially hairy	C	Noct.	Various – avoids rocky habitats	G/H	Later winter to early Autumn	18-22	3-7	Happold (1967); Koffler (1972); Harrison & Bates (1991); Krasnov *et al.* (1996b)

Figure 1.1 The study area in the Northeastern Badia region of Jordan showing the positions of study sites.





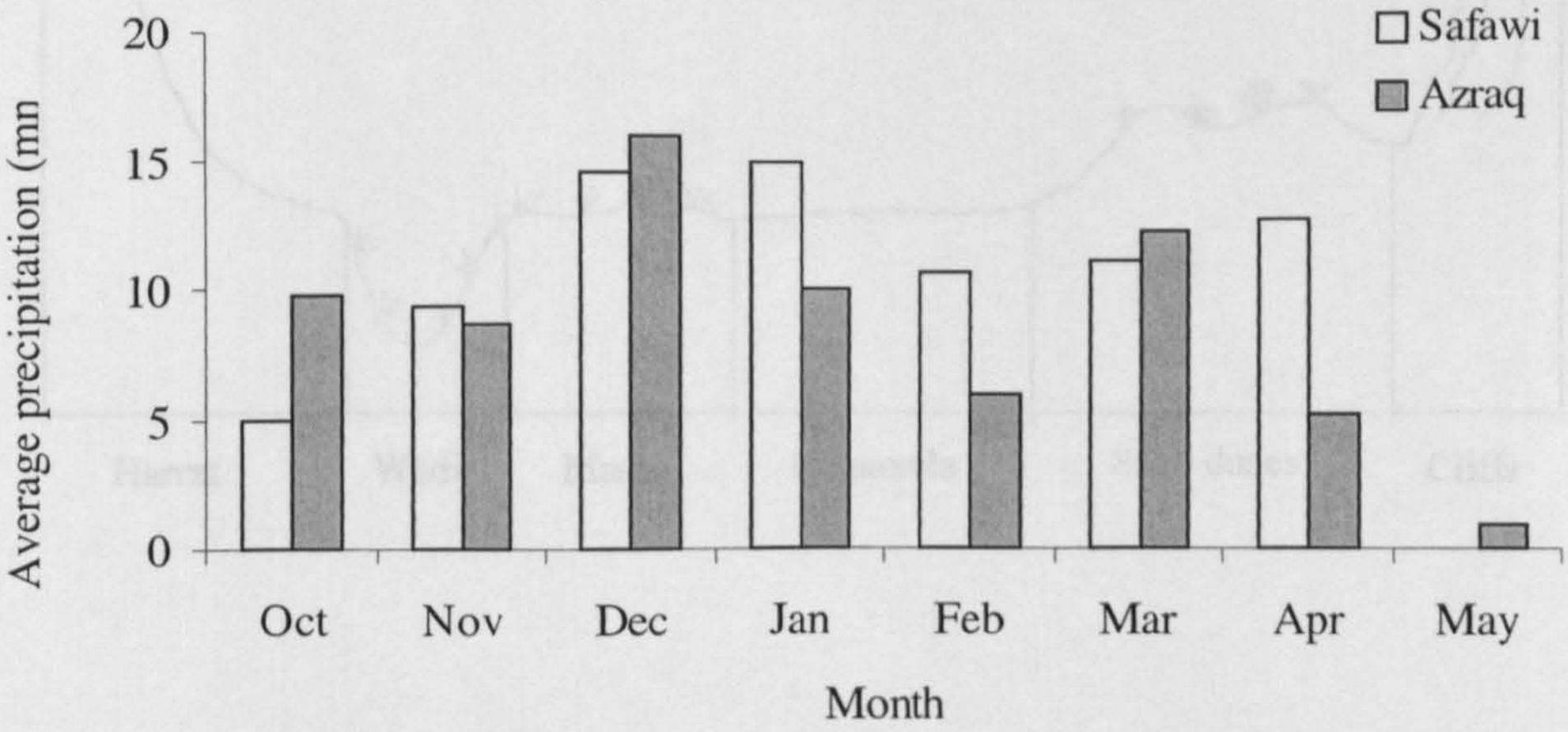
1.10.2 Soil and erosion

There are three distinct soil types in the region, the first two are associated with the northern basalt plateau and the third comprises the east limestone area (see overlay of plate A) . These differ with respect to topography and extent of weathering. The high intensity precipitation, low vegetation cover and low stability of soil aggregates contribute to water erosion of sediment, whereas wind erosion is enhanced by surface disturbance, loss of vegetative cover and high wind speeds (Allison *et al.,* 1998).

1.10.3 Climate and weather

The climate of the Badia region is described as continental. Temperatures fluctuate between summer averages of 46°C maximum to 15°C minimum and winter averages of 15°C maximum to -7°C minimum. Winter can be harsh, with snowfall and sub-zero temperatures occasionally occurring. Dust-storms occur frequently in the summer as a results of the strong winds that this region regularly experiences. Generally the annual rainfall is low, between 50mm and 200mm, mainly falling between October and April and tending to peak in December, see Fig. 1.2 (Kirk, 1998). The northern parts of the region tend to receive more precipitation than the south. The topography determines the amount of water an area receives. Catchments such as qa'a and marab effectively receive higher water input than run-off areas, and basalt boulders may increase soil moisture by inhibiting evaporation from the soil surface (Dutton *et al.* 1998).

Figure 1.2 Average monthly rainfall for two stations within the Badia region (1980-90), taken from Kirk (1998).



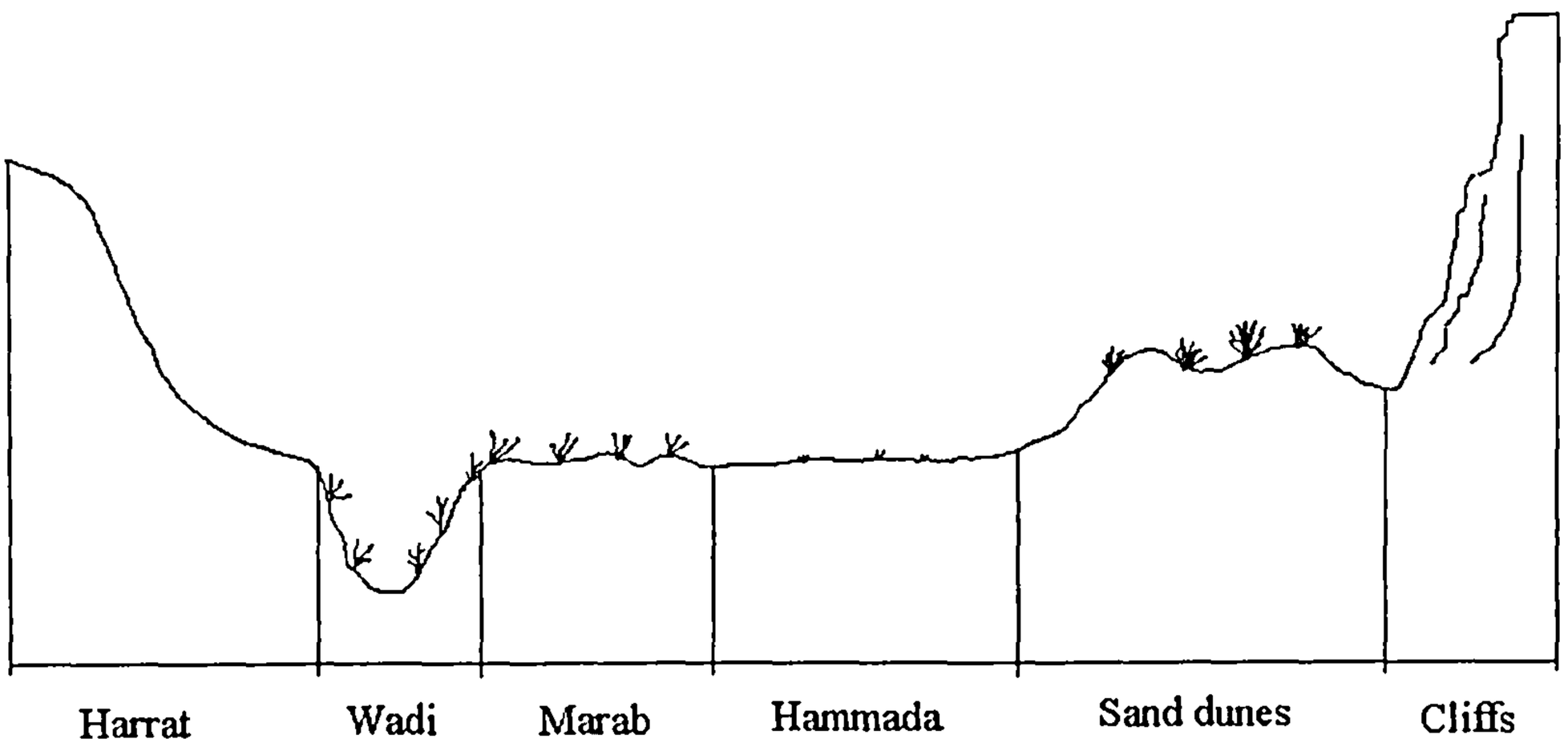
1.10.4 Land management

The largest agricultural resource in the Badia area is rangeland, which is used for growing arable crops and livestock production. Sheep, goats, cattle and camels are the main livestock, whilst the common crops are barley, vegetables, fruits and wheat. The majority of Badia land belongs to the state and although ploughing and demarcation of areas have been attempted by Bedouin to claim sites, land ownership is not recognised by law. Therefore, as no individual has the authority or responsibility for managing or protecting areas, few land management practices are employed. Hence overgrazing and agricultural malpractice have led in some cases to land deterioration (Dutton *et al.*, 1998).

1.10.5 Representative habitat types

Potentially suitable study sites, representative of different habitat types, were located by the Darwin Initiative Biodiversity team, using a false colour satellite image LANDSAT/4 Thematic Mapper, bands 4, 3 & 2, taken on the 28th August 1992 (Plate A). My study sites were finally selected following ground truthing of potential sites in spring 1996. The principal habitat types in this region shown in Fig. 1.3.

Figure 1.3 Schematic diagram of the representative habitat types found within the Badia Region.





Key to soil types
(adapted from
Allison *et al.*, 1998)

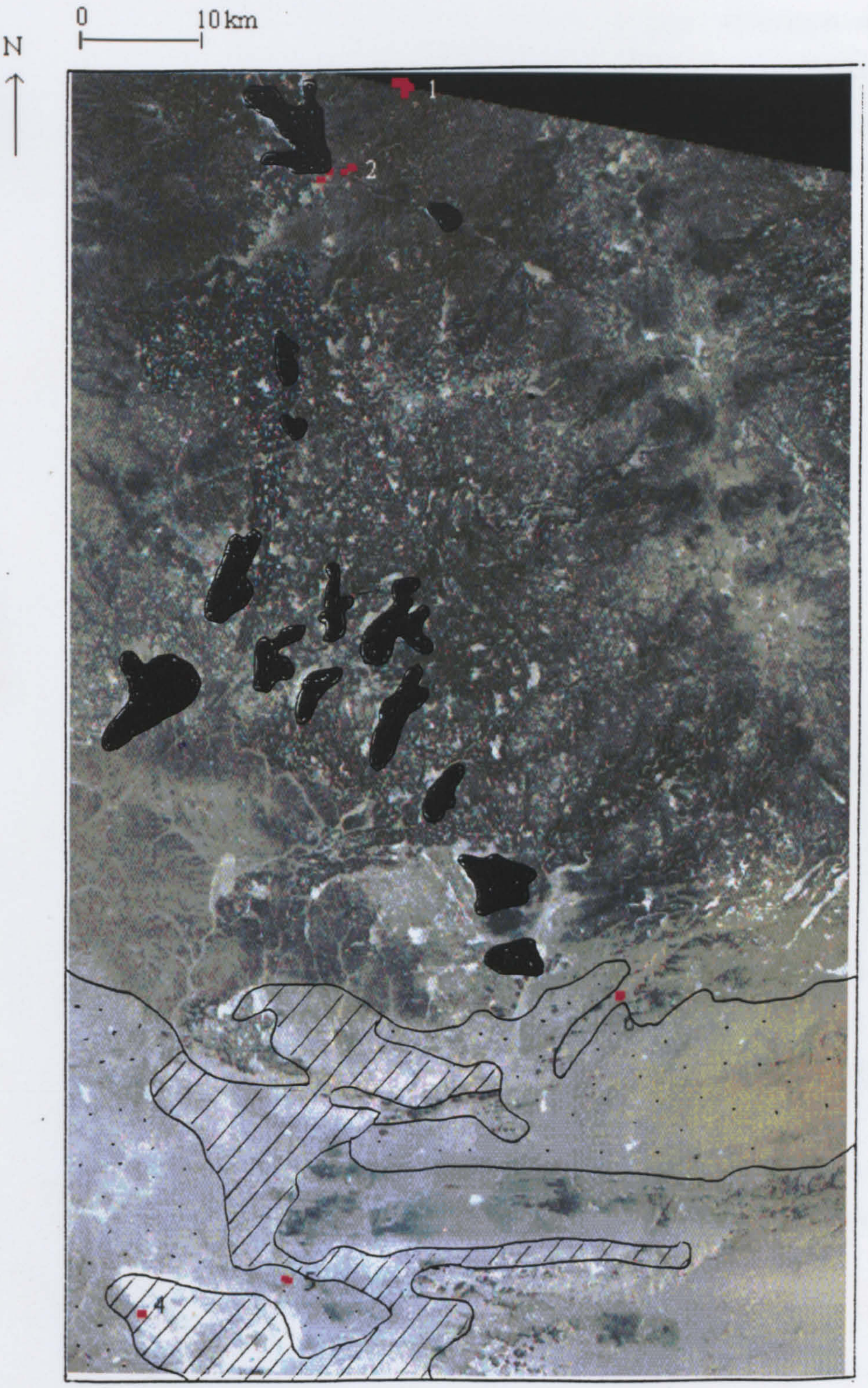
Mud flats

Basalt

Limestone

Alluvial deposits

Plate A: False colour satellite image of the study area from Landsat Thematic mapper bands 4, 3 & 2, taken on 28th August 1992.
The scene is in UTM zone 37 projection using Clark 1866 spheriod.
1 = Hashad, 2 = Salma, 3 = Bqa'awia, 4 = Dhahik,
5 = Hazim and 6 = Qattafi



Key to soil types (adapted from Allison *et al.*, 1998)

- Mud flats
- Basalt
- Limestone
- Alluvial deposits

Plate A: False colour satellite image of the study area from Landsat Thematic mapper bands 4, 3 & 2, taken on 28th August 1992.
The scene is in UTM zone 37 projection using Clark 1866 spheriod.
1 = Hashad, 2 = Salma, 3 = Bqa'awia, 4 = Dhahik,
5 = Hazim and 6 = Qattafi



Harrat: Basalt areas varying in relief from plains to undulating hills dominated by large boulders overlying basaltic soils. There are a great variety of harrat types depending on age, size, coloration, weathering and lichen cover of the basalt rocks. Vegetation occurring on the harrat is generally ephemeral, e.g. *Leysera leyseriodes* and Gramineae spp.

Wadi: A seasonal river formed by water run-off due to poor infiltration of the surrounding soils. Wadis can vary in width, length and consolidation, depending on the terrain and frequency of flooding. Vegetation within the wadi is typically comprised of *Artemisia herba-alba, Achillea fragrantissima, Astragalus spinosus, Thymus bovei* and Chenopodiaceae spp.

Marab: A low-lying site fed by a wadi, representing an area where the wadi has spread laterally. Organic material tends to be deposited in the marabs, which are commonly vegetated with *Artemisia herba-alba, Zilla spinosa* and *Achillea fragrantissima.*

Qa'a: Low-lying sandy areas which, due to poor penetrability, act as collection sites for rainwater. When the rainfall evaporates the area can form large flats, which hold accumulated saline deposits and are devoid of vegetation and rocks.

Hammada: Also known as chert plains, characterised by an absence of basalt rocks with minimal vegetation cover. Where present, vegetation is comprised of *Artemisia herba-alba* and ephemeral species, e.g. *Diplotaxis harra*, *Leysera leyseriodes* and Gramineae spp.

Sand dunes: Formed from wind-blown sediment, which is more orange-brown in colouration in the east of the region. In general, dunes tend to be vegetated with *Haloxylon salicornicum, Retama raetam, Tamarix aphylla* and Chenopodiaceae spp.

Limestone escarpment/cliffs: A limestone bedrock area covered with a chert surface. Drainage tends to be radial terminating in a large central qa'a. Limestone cliffs formed as a result of erosion from water flow.

1.11 Thesis plan

Chapter 1: The general introduction emphasises the importance of desert ecological studies. It defines the desert environment and the problems this poses for the animals which inhabit it and how they overcome these. Previous investigations into desert rodent ecology are summarised and the areas in which information is lacking are identified. The study area and rodent species that inhabit it are also introduced in this chapter.

Chapter 2: This chapter attempts to identify which environmental variables influence desert rodent community composition by determining the different habitat types present in the region and assesses the spatial and temporal rodent community composition in these.

Chapter 3: This chapter focuses on two parameters that potentially influence rodent communities, habitat structure and vegetation abundance, for which spatial differences are compared between different habitat types in two study sites. Rainfall and temporal changes in vegetation cover are also followed and the influence of the temporal and spatial differences in habitat structure and resource abundance on foraging behaviour, rodent density and community composition are discussed.

Chapter 4: This chapter addresses the spatial and temporal abundance of seed sources as a food resource for desert rodents by assessing the spatial and short-term temporal abundance of three potential 'sources' of seeds; seed production, seed rain and seed bank, in representative habitats. The results are compared with those from other deserts and also discussed in relation to their influences on foraging behaviour, rodent density and community composition.

Chapter 5: The influence of food abundance on the timing and extent of breeding activity of desert rodents is the subject of this chapter. Initially by investigating spatial, temporal, sex-related and species variations in breeding activity and by comparing breeding activity with the temporal changes in vegetation and seed abundance within the different habitat types, as assessed in Chapters 3 and 4. Supplementary feeding experiments are also presented to assess the effects of seed abundance on breeding activity in males and females and the timing of juvenile recruitment specifically in the desert rodent *Meriones crassus*.

Chapter 6: This chapter investigates the influence of vegetation availability on reproduction in *M. crassus* by reporting on laboratory experiments of dietary intake and day-length manipulations undertaken to determine the proximate triggers used for breeding, and to assess the influence of vegetation availability on several other breeding parameters. Attempts are also made to determine the energetic costs of breeding in males and females and juvenile growth.

Chapter 7: The general discussion provides a synthesis of all work undertaken and compares the findings with previous studies of desert rodent ecology. It discusses the potential applications of the findings to the conservation, management and development of arid environments and suggests ideas for future studies.

Statistical analyses: Unless otherwise stated, all statistical analyses were undertaken using SPSS version 8.0 (Norusis, 1998).

CHAPTER 2
ENVIRONMENTAL DETERMINANTS OF COMMUNITY COMPOSITION

2.1 INTRODUCTION AND OBJECTIVES

The focus of this chapter is to determine to what extent environmental variables influence desert rodent community composition. Herein, I define community composition as 'the richness and relative abundance of species present in a particular location'.

2.1.1 Determining habitat types

Remote sensing of the environment involves measuring the electromagnetic energy reflected from or emitted by the Earth's surface using sensors on board satellites. Digital information recorded over a series of grid cells (pixels) can be compiled to form an image in which each pixel has a value representing the radiation detected by the sensor over the pixel area. Wavebands can be selected to provide information on certain aspects of the Earth's surface, such as the variation in vegetation, rock, soil and water. Hence images can be interpreted in terms of habitat types, where the term 'habitat' is used to describe an area of particular relief, vegetation and soil structure. In situ *ground-truthing* of a location is also required to confirm the predictions of geographical features derived from radiation measurements. The spatial resolution or pixel size depends on the altitude of the sensor, focal length of the focusing system, wavelength of the radiation and other characteristics of the sensor (Mather, 1987; Burrough & McDonnel, 1998). A LANDSAT TM sensor allows the resolution of the pixel size of approximately $30m^2$. The spatial scale relevant to rodent ecology will differ from individuals to communities and to geographical distributions for each species, therefore a scale must be selected which is appropriate to the questions posed.

Habitats have also been considered as a patch of land or water with a particular set of environmental conditions and resources promoting the occupancy, survival and reproduction of a particular species or group of species (Morrison *et al.*, 1992). Therefore attempts have been made to classify habitats by species composition (e.g. Rogovin *et al.*, 1985). To do this they must be distinct areas and at least one species must show preference for each habitat type. However, direct associations between habitat and rodent community compositions have rarely been found.

The strength of the relationship between habitats and rodent communities varies between deserts. For example in the Negev Highlands, Israel, there was a close relationship (cluster analysis) (Krasnov *et al.*, 1996a) but in the Chihuahuan Desert, Mexico, habitats with distinct rodent assemblages could not be demonstrated (Brown & Heske, 1990). Shenbrot *et al.* (1999) collated data from the literature on world-wide desert faunal compositions in an attempt to derive a classification of geographic regions based on their rodent species composition. From this classification the Badia region falls into the North Arabian province, characterised by the dominance of gerbils and jirds. The listed desert rodents consist of one strict endemic (*Meriones sacramenti*), four sub-endemic species and other species with geographic ranges from central Saharan and Libyan to South Arabian.

2.1.2 Community composition

A community has been defined as 'a system of co-occurring interacting populations of different species that constitutes one or several contiguous trophic levels' (MacArthur, 1958). However, communities have also been viewed more simplistically as 'an assemblage of populations of living organisms in a prescribed area or habitat' (Krebs, 1994). A frequently-asked question in community ecology concerns how species respond to different environmental variables. To answer this for a particular rodent community, data must be collected on species composition alongside appropriate environmental variables recorded at several points in space and time (Ter Braak, 1988). In general the methodological approach is to record a range of parameters including soil, vegetation and topographical characteristics in sampling sites distributed across a range of habitat types occurring throughout a region. Within these sampling sites the number and species of rodents are counted over a minimum of three days using trapping or spotlighting techniques (Rogovin *et al.*, 1991; Shenbrot, 1992; Shenbrot *et al.*, 1994; Krasnov *et al.*, 1996). Identifying environmental parameters that influence community structure can also reveal resource partitioning among species and factors influencing their distribution and abundance (Shenbrot *et al.*, 1999).

2.1.3 Community analysis

2.1.3.1 Previous studies

Analysis of the relationship between rodent community composition and environmental parameters has commonly utilised cluster analysis techniques to determine species groups, and ordination to determine habitat relationships. Groups of species with

different environmental preferences have been distinguished using stepwise multiple regression for several Asian deserts (Thar, Rogovin *et al.*, 1994; Gobi, Rogovin & Shenbrot, 1995; Kyzylum, Shenbrot & Rogovin, 1995; Negev Highlands, Krasnov *et al.*, 1996a) and South African deserts (De Graaf, 1981). Krasnov *et al.* (1996a) investigated the rodent communities in the Ramon erosion cirque in Israel, using cluster analysis to separate habitat types on the basis of similarity of rodent species inhabiting them and correspondence analysis to determine what environmental factors may be influencing rodent community composition.

Ordination is a statistical method, which can provide a description of the spatial structure of plants and animal communities (e.g. Shenbrot *et al.*, 1994). Three types of ordination are commonly used in community ecology: principal component analysis (PCA), correspondence analysis (CA) and discriminant functional analysis (DFA). The techniques use different approaches, but in general attempt to place species in an ecological space derived from a composite of environmental variables and therefore attempt to identify the relationship between species and environmental parameters.

2.1.3.2 Recommended statistical analysis

Many of the previous analytical methods used to detect species-environment relationships are indirect and therefore have less strength than direct methods such as regression analysis (Ter Braak, 1988). A hierarchical analytical approach using a form of cluster analysis, correspondence analysis (DCA), and a 'stronger' ordination technique (CCA) facilitates comparisons with previous studies of similar species and/or habitats and additionally provides a statistical rather than subjective interpretation of the ordination axes.

2.1.3.3 Two Way INdicator SPecies ANalysis

TWINSPAN is a program designed to perform divisive cluster analysis on multivariate data. Typically a data set consists of a series of samples characterised by the species contained within them (Hill, 1979). The program is designed to dichotomise the principal axis of ordination giving two groups of samples, each of which is then, in turn, divided iteratively until some arbitrary endpoint is reached. This technique can be used to distinguish habitat types based on rodent community compositions and vice versa.

2.1.3.4 DEtrended CORrespondance ANAlysis (DCA)

DECORANA (Hill, 1979) is an ordination program used to undertake DCA and is similar to the reciprocal averaging technique (Hill, 1979), except that correlations between the first and higher axes have been removed. Sampling sites and species are compiled into a matrix. The program provides both sample and species scores on the first four axes of ordination, which can be subjectively interpreted in relation to environmental gradients, based on site knowledge.

2.1.3.5 Canonical Correspondence Analysis (CCA)

This is an ordination technique that uses the power of regression without the assumption of linearity and can detect unimodal relationships between species and environmental variables (Ter Braak, 1987a). It was originally designed to study plant communities and associated environmental gradients (Ter Braak, 1987b) and has previously been used in other aspects of vegetation ecology such as succession (Vanzyl & Robertson, 1991; Tsuyuzaki & Del Moral, 1994), and conservation (Taggart, 1994). More recently this type of analysis has been applied to invertebrate communities, e.g. macroinvertebrates (Ruse, 1996), waterbeetles (Behr, 1994), earthworms (Roderiguez *et al.,* 1997), Nematoda (Soetaert *et al.,* 1995), Odonata (Samways & Steytler, 1996), Polychaeta (Mackie *et al.,* 1997); to date this there has been little application to the analysis of mammalian community composition. However, canonical correspondence analysis is effective only if the appropriate set of environmental data has been collected for the samples in the analysis (Kent & Coker, 1992).

2.1.4 Habitat and species associations

Most desert rodent communities can be treated as groups within ecological space called 'guilds' or more unambiguously 'spatial species assemblages' (Simberloff & Dayan, 1991), which are defined as 'a group of species exploiting the same class of environmental resources in a similar way' (Root, 1967). Many Asian studies have revealed well-expressed spatial assemblages of rodent species which can be interpreted in terms of habitat types (e.g. Shenbrot *et al.,* 1994a; Krasnov *et al.,* 1996a). However, in the North American Chihuahua desert, rodent species did not fall into distinct spatial guilds. This difference has been partially explained by the history of arid landforms on the two continents, i.e. Asian deserts are older than those in North America (Shenbrot *et al.,* 1999). In North America, habitat partitioning in desert rodents is more readily noted on a microhabitat than macrohabitat scale (Brown & Harney, 1993).

Shenbrot *et al.* (1999) commented that the types of habitat specialisation demonstrated by rodents in several deserts showed similarities. They distinguished four main types: 1) sand dwelling, psammophily; 2) hard horizontal substrate, sclerophily; 3) alternating hard and soft horizontal substrate, open gravel plains; 4) rocks and cliffs, petrophily. As a consequence of habitat specilization, morphological features have evolved, for example the hind feet of strict psammophiles tend to be adapted to enable faster travel over sandy substrate, by the presence of hairs and the reduction of toes. In petrophiles, for example *Acomys russatus,* the claws are more curved and pointed than in non-specialised species, facilitating manoeuvrability over rock and steeper surfaces.

2.1.5 Environmental parameters

In order to identify which environmental features determine the pattern of species distribution it is necessary to measure a range of parameters that are potentially important to species existence (Shenbrot *et al.,* 1999). From knowledge of desert rodent ecology, several can be suggested as potentially important: food sources, i.e. seeds, vegetation and invertebrates, and refuges from environmental extremes and predation, i.e. vegetation, soil and rocks. Additionally, factors that influence these may also be important, for example, surface topography, soil composition, altitude and grazing pressure.

For rodent communities in general, vegetation cover and related productivity have been demonstrated repeatedly to be the main environmental determinant of community composition. In an alpine meadow (Haibei Research Station, China) Bian *et al.* (1994) showed species diversity to be significantly negatively correlated with vegetation cover and height. Other examples from grasslands include studies in Kenya (Oguge, 1995) and Taiwan (Adler, 1995).

In desert systems, soil structure and content have also been shown to be important factors in determining rodent communities. For example Shenbrot *et al.,* (1994a) suggested that in temperate Asian deserts communities were organised into spatial guilds primarily separated by environmental characteristics of soil and perennial vegetation. Rogovin *et al.,* (1991) used canonical variate and principal component analyses to show that characteristics of vegetation and substrate were primary determinants of desert rodent communities in Bolson de Mapimi, Mexico. Additionally in the Sonoran desert (Mexico) rodent distributions were correlated with plant

associations and soil substrate (Gonzalez-Romero, 1995) and in the South African semi-arid Karoo desert, small mammal composition was correlated with plant and rock cover (Kerley, 1992). In the Anxi desert, China, overall vegetation, soil moisture content and soil hardness were the main determinants of rodent community composition (Liu *et al.*, 1994). Closer to Jordan, in the Negev Highlands, Israel, rodent species were spatially separated along axes which represented the gradients from rock to sand, relief and vegetation density (Krasnov *et al.*, 1996a).

2.1.6 Spatial and temporal variations in community composition

Organisms in desert habitats have to cope with spatial heterogeneity, temporal variability and unpredictability of resources, as well as fluctuations in competition and predation (Safriel *et al.*, 1989). The dynamic aspect of desert rodent communities is well documented with annual precipitation a common factor shown to influence breeding and therefore population density (e.g. Beatley, 1969; Kenagy & Bartholomew, 1985). However, species show different responses to environmental variability (Shenbrot *et al.*, 1999) and consequentially temporal variation in community composition occurs (Brown & Heske, 1990b). As community composition changes, so will inter-specific competition (Ricklefs, 1987) and environmental fluctuations may permit high niche overlap and the co-existence of many similar species or vice versa (Hubbell & Foster, 1986). Therefore when studying desert rodent communities it is necessary to consider potential temporal variations. To begin to understand the processes determining such communities, long-term studies are required (Shenbrot *et al.*, 1999). Liu *et al.* (1994) suggested that the importance of environmental parameters determining some desert rodent communities vary seasonally. In the Anxi desert (China), detrended correspondence analysis revealed a positive correlation between the locations of the rodent communities on the ordination axes and ground water level, altitude and mean precipitation in spring, a positive correlation between locations and vegetation cover, plant height, soil moisture and soil-hard degree in summer and a significant negative correlation between locations and soil moisture content in the autumn.

2.1.7 Mechanisms of structuring a community to facilitate co-existence

Determining the mechanisms which structure a community have been the focus of many studies (e.g. Rosenzweig & Winakur, 1969) and inter-specific competition has frequently been suggested to be a main structuring force (May & Mac Arthur, 1972).

The emphasis of many of these studies has been concerned with how species partition resources thereby facilitating coexistence (Bowers & Brown, 1982; Kotler & Brown, 1988). Approaches have included investigating direct density-dependent and inter-specific competition (e.g. Heske *et al.*, 1994), differences in species morphology (e.g. Bowers & Brown, 1982), predation pressure (e.g. Kotler, 1984a; Bowers & Doley, 1993), differential foraging behaviour (e.g. Kotler, 1997), diet (Harris, 1986), and macro- and micro-habitat preferences (e.g. Price, 1978; Bowers, 1988).

A *structured* community is defined as one in which species differ more in their morphology, behaviours and environmental preferences than expected by chance (Brown, 1995). Assembly rules have been applied to the structuring process (Diamond, 1975) which state that species of 'preferable combinations' (i.e. species with little similarity therefore minimal niche overlap), will co-occur depending on the area's resources and the regional species pool from which the species can be drawn (Kelt *et al.*, 1996). Structural and functional convergence of rodent communities has been found between some geographically isolated deserts, in which the coexisting rodent species appeared to have comparable variations in morphology, foraging behaviour, and more strikingly, similar patterns of body size (Brown *et al.*, 1979). This suggests that there may be similar mechanisms of co-existence in some deserts.

2.1.7.1 Body size

Bowers & Brown (1982) investigated the regular and apparently logarithmic displacement in body size in spatial assemblages of North American desert rodents. They demonstrated that granivores of similar body size occurred together much less frequently than expected by chance and suggested that size disparity supported inter-specific competition as a major process in determining community structure. In Israeli Gerbillidae, the observed distribution of rodents with different body sizes was also thought to indicate competitive exclusion of species of similar body size within local habitats (Yom-Tov, 1991).

Seed size selection (Brown & Lieberman, 1973), seed distribution selection and diet have been suggested to be mechanisms of co-existence corresponding with differences in body size. Selection of seeds based on their spatial distributions has been shown several times in feeding trials. Larger species, (e.g. Jerboas) tend to specialise on clumped aggregations of seeds whereas smaller species (*Gerbillus*) utilise dispersed

seeds (e.g. Reichman & Oberstein, 1977; Price & Brown, 1983). However evidence that species select seeds on the basis of size alone has been disputed (Reichman, 1975; Lemen 1978; M'Closkey 1980). Dietary habits and body size tend to correlate in desert rodents. It has been suggested that small species with high energy expenditure per unit body mass must use energy rich food (seeds or invertebrates), whereas species that feed on low calorific food (foliovores) have lower energy expenditure and tend to have a greater body mass (Shenbrot *et al.*, 1999).

2.1.7.2 Foraging behaviour and locomotion

It is suggested that both predator pressure and competition for food resources may have influenced the evolution of different locomotory modes in desert rodents (Price & Brown, 1983). Bipedality may have evolved from inter-specific competition for resources, as bipeds and quadrapeds select different microhabitats based on spatial distribution of resources and differences in foraging economics (Reichman & Oberstein, 1977; Reichman, 1981). For example bipedal rodents would be expected to expend less energy specialising on clumped widely-spaced resources than quadrapeds (Shenbrot *et al.*, 1999). The importance of bipedality in desert rodent communities is demonstrated by the observation that this morphologic feature has evolved independently in at least four desert rodent taxa.

As with body size, local assemblages of bipeds and quadrapeds differ from those expected by chance. It has been demonstrated in both North American (Brown & Harney, 1993) and central Asian communities (Rogovin & Surov, 1990; Kelt *et al.*, 1996) that species with different locomotory modes co-occur more frequently than species exhibiting the same mode.

2.1.8 Objectives

The objectives of this chapter are to, i) determine the different habitat types present in the region, ii) investigate the spatial and temporal rodent community composition in the different habitats and iii) identify the environmental and non-environmental parameters associated with rodent community composition. The results are then discussed in the context of previous studies on desert living rodent communities and underlying mechanisms for community structure are suggested.

2.2 METHODOLOGY

2.2.1 Study sites and replicates

The community composition study was undertaken from February to September 1996 and from February to June 1997. Three trapping sessions were undertaken to investigate seasonal and annual variation in rodent densities and distributions during March to May (defined as spring) 1996, June to August (defined as summer) 1996 and spring 1997. Six grids of representative habitat types (harrat, marab, narrow and broad wadi, sand dunes and limestone cliffs) were trapped during each session. In 1997, a further six habitat grids were sampled. During this session four grids were trapped at monthly intervals to investigate temporal variability within a given season. A total of 12 grids of 0.8 hectares were sampled over the three sessions (Table 2.1).

In spring 1996 five sites representative of the range of habitats found within the region were selected for investigation, these were Wadi Salma (narrow wadi), Wadi Hashad (broad wadi), Bqa'awia (marab), Fai dhat al dhahikiya (limestone cliffs) and Hazim (sand dunes), see Figure 1.1 and Table 2.1. In summer 1996 replicate studies were undertaken at these sites. However at Wadi Salma trapping localities were modified to incorporate additional habitat types. In spring 1997 studies with five sites were repeated and within Hazim and Wadi Salma, two habitats types were selected to follow monthly changes in community composition and environmental parameters. Additionally in 1997, two sites, Qattafi and Burquh, were incorporated into the study. Table 2.1 shows the 31 site samples indicating site name, season and year in which of sampling and the predominant habitat type in which the grid was positioned. Samples were coded to facilitate analysis. The code indicates site name, season or month, and the year, where 'sp' denotes spring, 'sm' denotes summer.

Table 2.1 Description of sample sites.

No	Site name	Season	Year	Habitat type	Code
1	Dhahik	Spring	96	Dunes/limestone cliffs	DHsp96
2	Dhahik	Summer	96	Dunes/limestone cliffs	DHsm96
3	Dhahik	Spring	97	Dunes/limestone cliffs	DHsp97
4	Bqa awia	Spring	96	Marab	BQsp96
5	Bqa awia	Summer	96	Marab	BQsm96
6	Bqa awia	Spring	97	Marab	BQsp97
7	Wadi Hashad	Spring	96	Marab A	HSAsp96
8	Wadi Hashad	Summer	96	Marab A	HSAsm96
9	Wadi Hashad	Spring	97	Marab A	HSAsp96
10	Wadi Hashad	Spring	97	Marab B	HSBsp97
11	Hazim	Spring	96	Sand dunes	HZDsp96
12	Hazim	Summer	96	Sand dunes	HZDsm96
13	Hazim	Spring, March	97	Sand dunes	HZD3/97
14	Hazim	Spring, April	97	Sand dunes	HZD4/97
15	Hazim	Spring, May	97	Sand dunes	HZD5/97
16	Hazim	Spring, March	97	Hammada	HZH3/97
17	Hazim	Spring, April	97	Hammada	HZH4/97
18	Hazim	Spring, May	97	Hammada	HZH5/97
19	Qataffi	Spring	97	Red dunes	QDsp97
20	Burquh	Spring	97	Hammada	BHsp97
21	Burquh	Spring	97	Harrat	BUBsp97
22	Wadi Salma	Spring	96	Harrat	SBsp96
23	Wadi Salma	Spring, March	97	Harrat	SB3/97
24	Wadi Salma	Spring, April	97	Harrat	SB4/97
25	Wadi Salma	Spring, May	97	Harrat	SB5/97
26	Wadi Salma	Spring	96	Marab	SMsp96
27	Wadi Salma	Summer	96	Marab	SMsm96
28	Wadi Salma	Summer	96	Wadi	SWsm96
29	Wadi Salma	Spring, March	97	Wadi	SW3/97
30	Wadi Salma	Spring, April	97	Wadi	SW4/97
31	Wadi Salma	Spring, May	97	Wadi	SW5/97

2.2.1a Wadi Salma (Salma)

Salma is situated in the north of the Badia region within the basalt fields and incorporates several habitat types. Salma is a narrow wadi in which the gravel wadi bed meanders through an embankment of heterogeneous habitat types opening up at the wadi mouth onto a homogeneous and highly vegetated marab. Overall the wadi is surrounded and embanked by black basalt (harrat). The sampling grid on the harrat

(Table 2.1) was moved to a different location between 1996 and 1997 due to extensive disturbance from Bedouin. In summer 1996 a study grid was located in the lower wadi, but again due to extensive disturbance by Bedouin in spring 1997, an alternative grid was set up approximately 500m further up the wadi. In both cases Bedouin had set up tents directly on or in very close proximity to the study grids.

2.2.1b Wadi Hashad (Hashad)

Hashad is also situated within the basalt fields, north of Salma and also possesses a range of habitat types. It is a descending wadi with extensive areas of basalt and hammada plains surrounding a narrow gravel wadi bed embanked by areas of marab habitat. The same study location, predominately marab in habitat type, was used in all three field visits. In spring 1997 an additional grid of marab habitat was investigated.

2.2.1c Bqa'awia

This area, although referred to as a qa'a by locals was classified as a marab from the satellite imagery (Plate A). The site is relatively highly vegetated compared to other habitats and therefore frequently used by Bedouin for grazing and agriculture. Dominant vegetation includes *Artemesia herba-alba, Achillea fragrantisma, Zilla spinosa* and *Capparis ovata.* A study grid was located in the east of the site and utilised in all three field visits.

2.2.1d Fai dhat al dhahikiya (Dhahik)

Dhahik is in the south of the Badia and comprises a limestone escarpment (approximately 15km in circumference) surrounding a large plain of low dunes dominated by Tamarix trees *(Tamarix aphylla).* A trapping grid was located amongst the dunes and used during all three field visits (1996-1997).

2.2.1e Hazim

An area of sand dunes relatively highly vegetated with *Haloxylon salicornicum,* Chenopodiaceae spp. and *Raetama raetum.* This site is situated approximately 12km east of Dhahik along the Saudi Arabia border (Figure 1.1). A trapping grid was located amongst the large dunes and utilised in all three trapping sessions. East of the sand dunes is a gentle rolling black chert plain, with minimal vegetation cover, which was chosen as an additional study grid in spring 1997.

2.2.1f Qattafi

Qattafi is situated in the south east of the Badia region and is characterised by the large undulating reddish/orange sand dunes scantly covered with basalt rocks. One grid was sampled during spring 1997, which was located within a broad wadi bed, devoid of basalt rocks and containing low dunes vegetated with *Tamarix* sp.

2.2.1g Burquh

This site is situated towards the north-east of the region, and is notable due to the presence of a permanent fresh water pool, frequently used by Bedouin for watering livestock and water extraction. The surrounding area is predominantly comprised of flat plains. Two distinct habitat types were chosen for grids approximately 300m away from the water source, one hammada and one harrat plain.

2.2.2 Estimating small mammal densities

2.2.2.1 Small mammal trapping

Small mammal trapping was undertaken for three to five consecutive nights at each site using 48 Sherman traps (23cm x 9cm x 7.5cm, H.B. Sherman Traps Inc., Orlando, Florida) arranged in a six by four grid configuration with two traps per station located at intervals of 20m (adapted from previous desert studies e.g. Abramsky *et al.*, 1985) Traps were baited 1-2 hours before sunset with a mixture of cereal seeds (typically barley or wheat) and peanut butter, and checked at first light. Rodents captured were identified to species, individually marked with a unique hair clip, weighed, aged, sexed and their sexual status determined (see 5.1.1). Measurements were taken of the length of the head and body, tail, forearm, hind-foot and ear. All individuals were then released at their point of capture.

To confirm species identifications 2-3 specimens of each rodent species were collected using "Museum Special" snap-back traps. Traps were baited with peanut butter/seed mix, set opportunistically within study sites at some distance from study grids and checked for kills every two hours. Captured specimens were identified, weighed and measured, after which the skulls and skins were prepared using the methodology described by Morris & Wroot (1990) and returned to the U.K. Dr. D. Harrison, a specialist in Arabian mammal systematic taxonomy at the Harrison Zoological Museum, Kent, later verified specimen identification.

2.2.2.2 Night transects

Sherman traps were not suitable for catching jerboas (*Jaculus jaculus)*, which have previously been reported as trap-shy (Happold, 1967, Brown *et al.* 1994) possibly due to their bipedal locomotion. Cage traps as used by Hatough-Bouran & Al-Eisawi (1990) were not available or suitable for the study protocol. In this case jerboa density was estimated by means of night transects, undertaken by driving at a slow constant speed (5km/hr) along the available permanent tracks within the study sites. Tracks varied in direction and route between study sites, however using tracks enabled replication of routes and minimised habitat disturbance and degradation. Tracks that passed through representative habitat were selected. Observers spotlighted the area with a 1,000,000 candlepower searchlight commencing approximately one hour after dark. No area was scanned more than once per night. The number of individuals sighted over a set transect length (5 km) and breadth (50m) were used to estimate density, i.e. the number sighted divided by the area of habitat searched. Two to five replicates were undertaken in parallel with trapping studies, occasionally on non-consecutive nights. On each sighting, attempts were made to capture individuals with a butterfly net (Happold, 1967; Shenbrot *et al.*, 1999), if successful, the animal was processed in the same manner as described in 2.2.2.1.

2.2.3 Environmental variables

Environmental parameters (Table 2.2) were measured within the sampling grids. The majority of parameters were measured within quadrats. In general a $1m^2$-quadrat size was employed, which was thought to be appropriate for the dominant low-growing shrubs found within the majority of sites (Abu-Irmaileh, 1994). In estimating perennial vegetation cover in sites that possessed larger growing vegetation i.e. small trees or large shrubs, quadrat size was increased to $2m^2$. In 1996, 12 quadrats were used per grid, which was then increased to 20 in 1997 (see Appendix I for justification of sample size). Percentage covers of perennial vegetation, ephemeral vegetation, basalt, rocks and stones were estimated visually in each of the plots. The heights of perennial and ephemeral plants were measured to the nearest centimetre. Loose soil depth (LSD) was estimated by measuring the penetration of a graduated spike to which a fixed pressure was applied. Local topographical relief was estimated visually and scored on an arbitrary scale (where a sloping angle of 0° to 15° = 1, 16° to 30° = 2, 31° to 45° = 3 and > 45° = 4).

Human presence (1 = low to 5 = high) and grazing level (1 = low to 5 = high) were recorded for the overall site. Grazing level was based on disturbance, faeces presence and visual assessment of the effects on vegetation. There were two forms of human presence, Bedouin with associated livestock and border police at Hazim and Hashad. Therefore the presence of humans was not always indicative of grazing. Altitude measurements were taken using a Garmin GPS 45, with several fixes (3 to 5) taken per site to verify the constancy of the altitude reading, which was later compared with local topographical maps.

Table 2.2 The 16 environmental variables recorded at each plot.

Variable	Abbreviation	Unit
Altitude	Alt	m
Angle of slope of ground	Relief	Arbitrary
Level of grazing pressure	Grazing	Arbitrary
Level of human disturbance	Humans	Arbitrary
Clay content of soil	% Clay	%
Silt content of soil	% Silt	%
Sand content of soil	% Sand	%
Gravel content of soil	% Gravel	%
Loose soil depth	LSD	mm
Perennial cover	% Perenn	%
Perennial height	PerHt	cm
Ephemeral cover	% Epheme	%
Ephemeral height	EphHt	cm
Cover of basalt rocks	% Basalt	%
Cover of other rocks (> 5cm)	% Rock	%
Cover of stones (between 1-5cm)	% Stone	%

2.2.4 Soil analysis

Soil samples were collected from outside study grids by taking cores (4cm diameter x 5cm deep). In summer 1996 samples were collected from six sites and in 1997 replicate samples were taken from these sites and an additional six sites. A total of 60 samples, i.e. five random samples from the 12 sites, were selected to assess pH, electrical conductivity and particle size.

2.2.4.1 Electrical conductivity and pH

The soil samples were initially air dried in the field and passed through a 2mm sieve to remove the larger proportion of stones and organic debris. A sub-sample of 10 grams was taken from each using a sample divider. Wet samples were prepared by adding 25ml of distilled water to each sample, which were than shaken vigorously and left to stand for 2 hours. Buffers of 7.0 and 9.22 pH were used to calibrate pH, which was measured electrometrically using a glass probe (pH 192 WTW model). Conductivity was measured using a digital probe (Conductivity 192 WTW model) reading in microsiemens per mm (μS/mm) (Brady, 1990).

2.2.4.2 Particle size analysis

Dry samples were first passed through a 2mm sieve and reduced to 0.5g using a sample divider. Each sample was then treated with 2ml of 20% volume hydrogen peroxide and placed in a boiling water bath for 2 hours to remove the organic component. Distilled water was added to the tubes before centrifuging for 4 minutes at 40,000 rev/min, after which the residual organic component was decanted off and discarded. Samples were then treated with 2ml of a wetting agent (10% sodium hexametaphosphate) and stirred. Particle size was measured using a Coulter LS 230 laser granulometer, maintaining the obscuration at approximately 12% during the process. Particle size classifications for estimating the percentages of clay (<3.9μm), silt (3.9μm to 52.6μm), sand (52.6μm to 1,682μm) and gravel (>1,682μm) were according to 'The Wentworth Grain Size Classification' (Church *et al.*, 1987). Soil samples were classified into soil types, and ascribed numerical values according to a soil texture classification chart (after FAO, 1977) according to the resulting proportions of differing particle sizes.

2.2.5 Statistical analysis - multivariate methods

A matrix of sample sites and environmental parameters and a matrix of sample sites and small mammal density estimates were prepared (Appendix I). Data were then subjected to three forms of multivariate analysis using the following computer programs:

2.2.5.1 TWINSPAN

Two-way Indicator Species Analysis (TWINSPAN; Hill, 1979) was used to group samples on the basis of their rodent species composition, and to group rodent species on the basis of their spatial distribution. All parameters in the program were set at default values as standard (Hill, 1979).

2.2.5.2 DCA

Detrended correspondence analysis (DCA) was employed (DECORANA program, Hill, 1979) as an ordination technique to identify rodent and site groupings, and to determine which environmental gradients were reflected in these groupings. Species density estimates were used in the analysis and all parameters were set to the program default values. Program settings were standard options, in which no transformation was performed, rare species were not down-weighted and the re-scaling threshold was set to default (Huntley, pers. comm.). The relationship between species groups and environmental variables was assessed by comparing ecological parameters between sites within the study area.

2.2.5.3 CANOCO

Canonical correspondence analysis (CCA) was employed using the FORTRAN computer program CANOCO (Ter Braak, 1988). CCA is a method of arranging species along environmental variables (Ter Braak, 1987a). Prior to analysis environmental data were standardised to mean 0 and variance 1 by subtracting the mean of each parameter and dividing by the standard error. The subsequent addition of 2.5 to every value ensured all data were positive (Huntley, pers. comm.). Variables showing co-linearity in the initial programme output were excluded from further analysis. The data were not transformed and there was no down weighting of rare species. This ordination technique was used to detect the relationship between environmental variables and rodent species community composition. A Monte Carlo permutation test (Manly, 1990) was used to examine the significance of the correlation between the first canonical axis and rodent community composition.

2.3 RESULTS

2.3.1 Small mammal data

2.3.1.1. Trap success

During the study period from 1996 to 1997, 298 individuals of nine species of rodents were captured within the sample sites. Table 2.3 shows the number of individuals caught per species.

Table 2.3 The total number of individual rodents captured during the 1996-1997 study. Abbreviations of species names are as used in analysis.

Species	Abbreviation	No. caught
Jaculus jaculus	J. jac	15
Gerbillus dasyurus	G.dasy	101
Gerbillus nanus	G. nan	78
Gerbillus henleyi	G. hen	12
Gerbillus cheesmani	G. chees	20
Meriones crassus	M. crass	41
Meriones libycus	M. liby	18
Meriones tristrami	M. trist	2
Acomys russatus	A.russ	11
Totals		**298**

Gerbillus dasyurus was the most commonly trapped gerbil species, and *M. crassus* was the most commonly captured jird species. *Meriones tristrami* was only rarely encountered. Trap success (no. captures/no. trap nights), showed temporal variability, with values of 14.2%, 10.81.% and 7.75% calculated for spring 1996, summer 1996 and spring 1997 respectively. In spring 1997 the trap success rate for March, April and May was 7.9%, 4.7% and 10.6% respectively.

2.3.1.2 Body measurements

The mean and standard error of morphometric measurements were calculated from all adult individuals captured at every study site during the study period (Table 2.4). Only individuals for which full morphometric data are available were included in the calculations, which were undertaken to confirm species identification and to examine body mass and morphology differences between species.

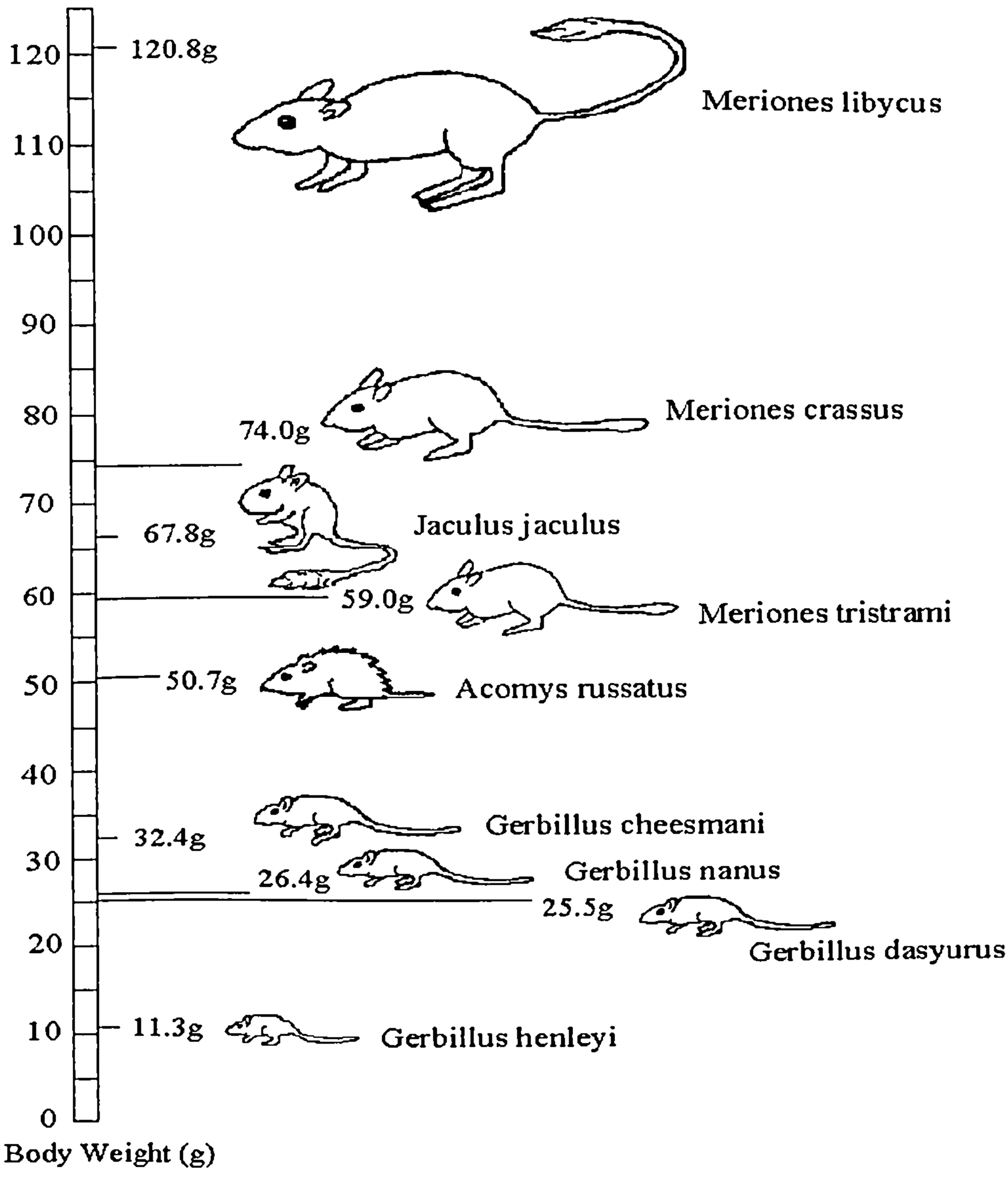
Table 2.4 Average measurements of morphology (mm) and body weight (g) for the nine different rodent species found in the Badia region. HB = head and body, HF = hind foot, FA = forearm E = ear, T = tail and Wt. = weight.

	Sex	N	HB		HF		FA		E		T		Wt.	
Species			Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
J. jaculus	M	4	**110.93**	15.66	**53.40**	1.75	**31.95**	5.31	**18.35**	1.17	**152.85**	12.59	**54.75**	7.53
	F	17	**104.54**	4.89	**54.48**	0.70	**29.33**	0.65	**19.99**	0.5	**176.50**	3.18	**67.00**	3.03
G. dasyurus	M	47	**82.93**	1.20	**24.49**	0.26	**24.30**	0.25	**11.60**	0.21	**101.68**	3.36	**26.27**	0.81
	F	35	**78.30**	1.19	**23.46**	0.65	**23.48**	0.18	**10.92**	0.21	**110.49**	1.84	**26.04**	1.02
G. nanus	M	15	**80.41**	1.24	**22.85**	0.45	**22.87**	0.29	**11.15**	0.24	**115.62**	3.16	**22.83**	0.89
	F	18	**79.86**	2.49	**23.47**	0.58	**23.04**	0.53	**11.14**	0.34	**108.71**	4.18	**23.69**	0.86
G. henleyi	M	4	**61.98**	1.19	**18.03**	0.25	**18.13**	0.39	**8.28**	0.31	**80.40**	0.59	**11.75**	1.18
	F	6	**61.90**	5.93	**17.65**	0.44	**17.23**	0.68	**7.68**	0.30	**82.66**	3.72	**10.50**	1.12
G. cheesmani	M	10	**82.56**	2.96	**27.94**	0.32	**27.22**	0.53	**11.41**	0.25	**122.25**	4.62	**31.40**	2.01
	F	4	**82.88**	1.94	**28.00**	0.73	**26.58**	0.57	**11.40**	0.57	**112.48**	9.06	**34.25**	2.17
M. crassus	M	22	**119.54**	2.03	**30.86**	0.29	**33.24**	0.65	**14.53**	0.36	**116.81**	2.16	**73.27**	2.76
	F	15	**116.23**	2.82	**30.35**	0.46	**32.30**	0.89	**13.80**	0.46	**115.33**	3.66	**73.86**	4.15
M. libycus	M	6	**137.12**	5.96	**35.02**	0.60	**35.90**	0.96	**16.30**	1.11	**124.85**	14.03	**120.50**	7.57
	F	4	**127.93**	1.28	**35.35**	0.52	**37.00**	1.65	**16.58**	1.11	**135.75**	15.81	**120.00**	6.70
M. tristrami	M	2	**100.60**	1.90	**27.98**	1.18	**31.78**	0.48	**14.05**	1.55	**131.80**	4.90	**62.00**	2.00
	F	1	**106.40**	0.00	**29.60**	0.00	**31.40**	0.00	**14.20**	0.00	**118.40**	0.00	**53.00**	0.00
A. russatus	M	1	**89.30**	0.00	**16.10**	0.00	**24.20**	0.00	**12.00**	0.00	**60.50**	0.00	**50.00**	0.00
	F	4	**85.73**	7.38	**16.85**	0.89	**24.83**	0.27	**13.18**	0.59	**60.95**	2.44	**48.75**	4.35

Body measurements for all species fell within the ranges given in the 'Mammals of Arabia' (Harrison & Bates, 1991) and identifications were confirmed by Dr. D. Harrison. Average body mass (g) ranged from the diminutive *Gerbillus henleyi* (10.5g) to *Meriones libycus* (120.5 g). Figure 2.1 depicts the morphology and body size of the different species, for which the mean body weight was calculated for 10 randomly selected individuals, five from each sex. There were no significant differences in body weight between sexes for any species (independent t-tests). Small sample sizes prevented this analysis for *A. russatus* and *M. tristrami.* It can be seen that all *Meriones* species are larger than *Gerbillus. Meriones libycus* is approximately twice the mass of the smallest jird, *M. tristrami.* The largest gerbil, *G. cheesmani* had three times the body mass of the smallest species, *G. henleyi.* Using all measurements *Gerbillus nanus* and *G. dasyurus* showed a statistically significant difference between median body weights. Variances were unequal ($F = 4.97$, $P < 0.05$), therefore a non-parametric Mann-Whitney U test was employed ($U = 942.5$, $n = 82$, $n = 33$, $P = 0.01$).

Jaculus jaculus had the largest hind foot and the smallest forearm measurements in comparison to body size (Table 2.4), suggesting bipedal locomotion in this species. *Gerbillus* and *Meriones* showed similar measurements for hind foot and fore arm, suggesting quadrapedal. *Jaculus jaculus* had the longest tail and *A. russatus* the shortest. *Gerbillus* tails tend to be longer than head and body measurements, whereas *Meriones* tails tend to be similar to head and body length.

Figure 2.1 Morphology and mean body weights (g) of rodent species found.



2.3.1.3 Density estimates

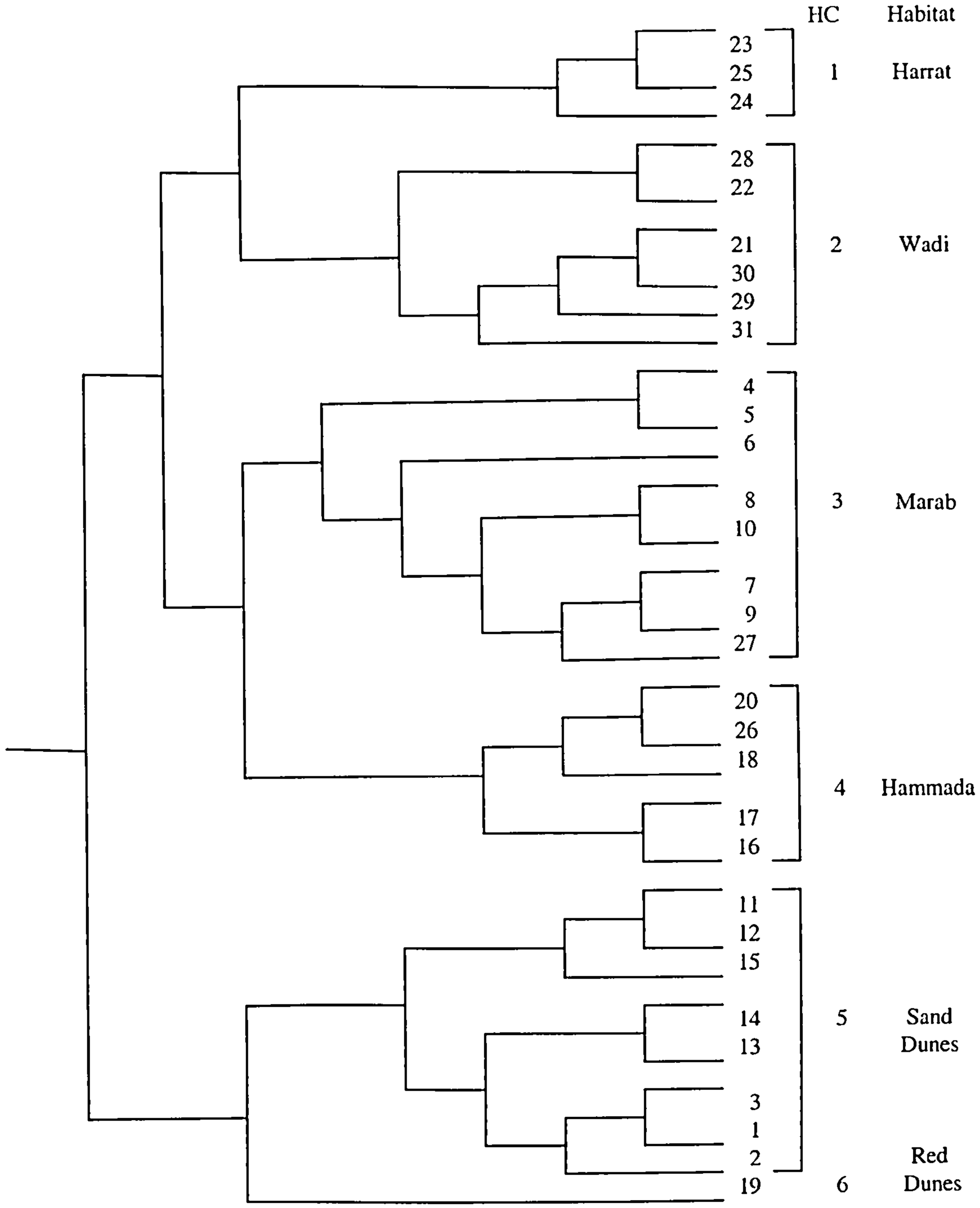
Due to the low capture and recapture rates the most suitable method of estimating density was to use the total number of individuals captured within a sample grid during one trapping period. This count was then multiplied by the grid area (120 x 80m) to give a number of animals per hectare. The overall trapping area was calculated from the grid configuration (4 x 6) plus a 10m boundary strip surrounding the grid, i.e. half the distance between trapping stations (Blair, 1940). Using animal counts per area for density estimates rather than abundance estimates, or derived density values, enabled the inclusion of *J. jaculus* density values (for which estimates calculated from trapping techniques were not valid). Therefore density values for all rodent species present could be incorporated into the multivariate analysis. Appendix I shows the density estimates for all species in the different sample sites.

2.3.2 TWINSPAN

2.3.2.1 Deriving habitat types based on rodent community composition

TWINSPAN was undertaken on rodent density estimates for each sample site to derive habitat classes (HC) based on the similarity of their rodent community composition. Figure 2.2 shows the grouping of sample sites into habitat classes from the TWINSPAN output matrix. The derived classifications were similar to the original categorisation of habitat types based on ground-truthed observations of the sites selected from the false colour satellite image (Plate A). Six main habitat classes were: (HC 1) basalt fields (harrat); (HC 2) wadi and areas with high basalt cover; (HC 3) marab; (HC 4) hammada; (HC 5) sand dunes and (HC 6) red sand dunes.

Figure 2.2 Dendrogram showing grouping of sample sites into habitat classes based on rodent community similarity (from TWINSPAN). For site numbers see Table 2.1, HC = Habitat Class.



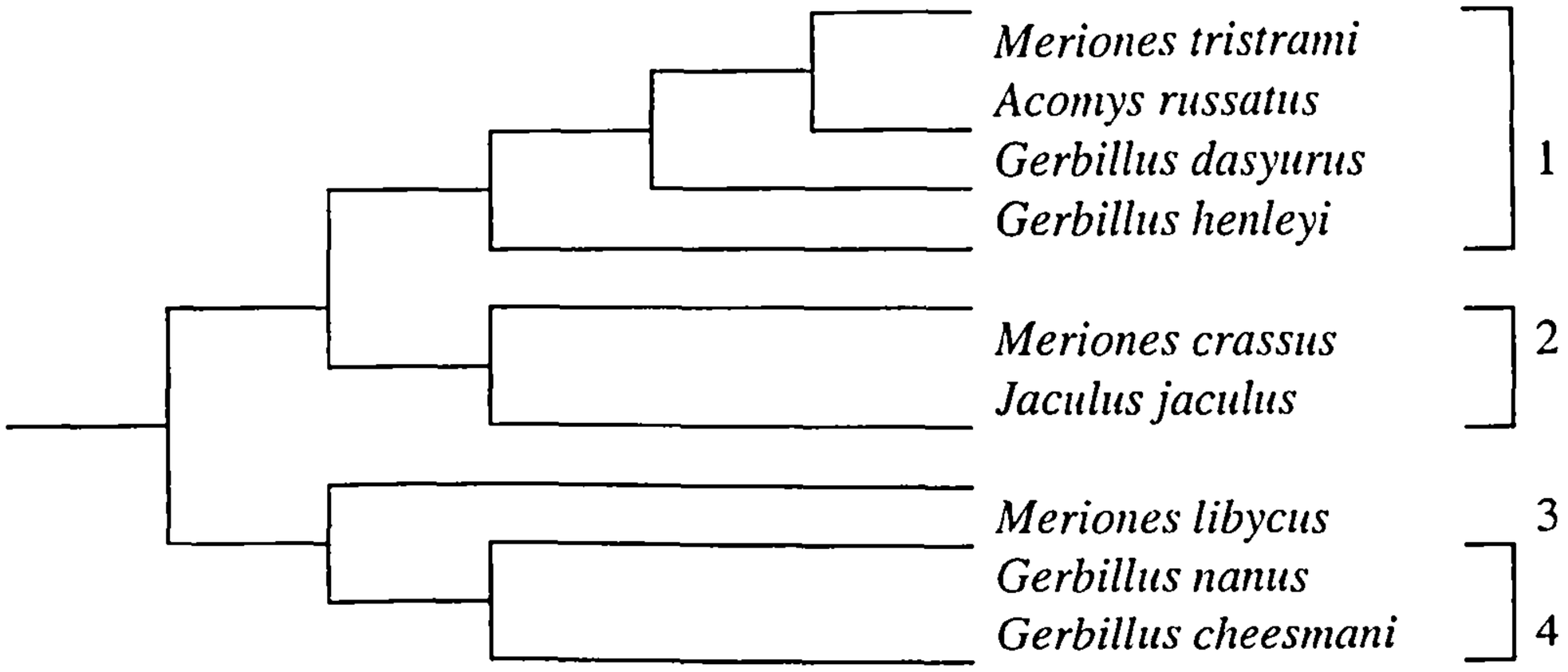
In most cases, the temporal and spatial samples grouped as expected from visual observations. For example, the monthly samples from Salma basalt (23, 24 & 25) all grouped into harrat class (HC 1). The second class, which consisted of samples from wadi habitat at Salma and from the basalt plains of Salma and Burquh, arises because the lower basalt flats are more similar in species composition to wadis than the upper basalt slopes, where *Acomys russatus* was commonly trapped. HC 3 was comprised of samples collected over different seasons from three sites (Bqawia, Hashad and Salma),

demonstrating temporal and spatial consistency within this habitat class. The hammada (HC 4) showed one anomaly; marab habitat at Salma sampled in spring 1996 was grouped in this class along with samples collected from hammada habitat at Hazim and Burquh. Variable classification of temporal samples from the same site indicates annual and seasonal variability in rodent community composition. A red sand dune class (HC 6) was identified as distinct from HC 5 (other sand dunes). This probably resulted from differences in species richness at each site, HC 5 having five species present and HC 6 only having one. Overall, these results indicate that habitat types can be defined by the distinct rodent communities they possess.

2.3.2.2 Deriving rodent groups based on habitat preferences

From the TWINSPAN analysis it was also possible to derive spatial species assemblages or 'groups' to investigate habitat preferences, where the term 'group' refers to a collection of species that occur in similar habitat types (Fig. 2.3).

Figure 2.3 Dendrogram showing grouping of rodent species based on habitat preferences (from TWINSPAN).



A summary of the species density data for the six derived habitat classes is shown in Table 2.5. Densities were calculated as the average density of the sample sites grouped into each habitat class. *Jaculus jaculus* was generally present at low densities in marab, hammada and sand dune habitats. *Gerbillus dasyurus* was trapped in all habitats except sand dunes and showed the highest density of any of the species in harrat. *Gerbillus nanus* was trapped on sand dunes exclusively, where it was present at relatively high densities compared to other species. *Gerbillus henleyi*, was trapped occasionally on the marab, but at higher densities in hammada. *Gerbillus chessmani* was associated with dunes, being present at a higher density in red dunes compared to yellow sand dunes. *Meriones crassus* was absent from harrat and red dunes and was found at greater

densities in marab and hammada habitats than sand dunes or wadi. *Acomys russatus* was captured in two habitats, marab and harrat, showing much higher densities in the latter. *Meriones tristrami* was only encountered in wadi. *Meriones crassus* and *G. dasyurus* were the most widespread species occurring in four habitat classes, whereas *G. nanus* and *M. tristrami* were the least widespread occurring in only one.

Table 2.5 Density of rodent species (no./ha) for the six habitat classes derived from TWINSPAN.

Species	HC1 Harrat	HC2 Wadi	HC3 Marab	HC4 Hammada	HC5 Sand dunes	HC6 Red dunes
J. jaculus			0.09	0.08	0.08	
G. dasyurus	11.25	6.32	7.37	0.21		
G. nanus					10.86	
G. henleyi			0.26	2.50		
G. cheesmani					2.71	8.75
M. crassus		0.21	3.46	2.46	1.04	
M. libycus			0.13	0.25	2.03	
M. tristrami		0.35				
A. russatus	4.17		0.13			

The four groups distinguished from TWINSPAN (Fig 2.3) can be described in relation to local habitat type. Species preferences relate to locally available habitat types and not to species preferences throughout their geographical distribution range. Group 1, consisting of *G. dasyurus, M. tristrami* and *A. russatus,* was considered petrophilic, i.e. rock preferring species as they tended to be present in areas of harrat or high basalt cover. *Acomys russatus* was trapped mainly on the upper basalt slopes and the range of habitats in which *G. dasyurus* was trapped had relatively high cover of basalt rocks (HC 1, 2 and 3, see 2.3.3). *Meriones tristrami* was caught on only one occasion in the sample sites, in the wadi bed of Salma. In this analysis, *Gerbillus henleyi* was also grouped with the petrophiles as it was trapped in one marab site with moderate basalt cover, however this species was more commonly trapped on hammada (HC 4). Group 2 is comprised of *Jaculus jaculus* and *M. crassus,* which were found in a range of habitat types (HC 3, 4 and 5) and therefore considered more generalist than the majority of species. However, typically these species appear to be associated with open hammada areas, where their burrows are commonly found. Group 3 has only one member, *M. libycus,* which was found at moderate densities in HC 5, but also recorded in HC 3 and 4. The fourth group is considered psammophilic as it included *G. nanus* and *G. cheesmani,* which were

trapped exclusively in sandy habitats, HC 5 for *G. nanus* and HC 5 and 6 for *G. cheesmani*.

2.3.2.3 Rodent community parameters

Several parameters descriptive of rodent communities were calculated for each habitat class (Table 2.6). Species richness was given by the number of species found in a particular habitat type. Site density was the sum of the individual species densities for each habitat class. Biomass was calculated from the density of each species (no../ha) multiplied by the mean body weight (as given in Figure 2.1). The diversity of rodents was calculated using Hill's N_2 index, ($N_2 = \Sigma\ p_i^{\ 2}$, where p_i is the proportion of individuals of a species in a sample, (Hill, 1973)), to allow comparison with previous studies, particularly those of Krasnov *et al.*, (1996a) on similar species and habitat types. Species richness was highest in marabs and lowest in red sand dunes. Species diversity was highest in yellow sand dunes and lowest in red sand dunes. Rodent biomass and density were highest in yellow sand dunes and lowest in wadi, however there was no correlation between biomass of rodents and vegetative productivity estimated by percentage cover at each site ($P > 0.05$, $n = 31$, Spearman rank correlation). Low species richness indicated areas inhabited by more specialised species, e.g. harrat (HC 1) and red sand dunes (HC 6). High species richness indicated areas inhabited by less specialised species, e.g. marab (HC 3).

Table 2.6 Species richness (no. of species), overall density, diversity (Hill's N_2 index) and biomass values (g) for the six habitat classes derived from TWINSPAN.

	Habitat Class					
	HC1 Harrat	**HC2 Wadi**	**HC3 Marab**	**HC4 Hammada**	**HC5 Sand dunes**	**HC6 Red dunes**
Spp. Richness	2.00	3.00	6.00	5.00	5.00	1.00
Site Density	15.42	6.88	11.41	5.49	16.71	8.75
Diversity	1.63	1.14	1.73	1.91	1.96	1.00
Biomass	534.71	193.91	476.33	245.26	695.45	308.00

2.3.3 Environmental parameters

Table 2.7 shows a matrix of the environmental variables recorded at each site sample. Each site was classified into habitat type based on visual observations, these were either red dunes (RD), limestone cliffs (C), sand dunes (D), hammada (H), marab (M), harrat

Table 2.7 Environmental variables recorded in the sample sites, where ALT = altitude, LSD = loose soil depth, EC = electrical conductance Per. = perennials, Ehp. = ephemeral, C = limestone cliffs, D = dunes, RD= red dunes, H = hammada, M = marab, B = harrat and W = wadi. See Table 2.1 for description of site codes.

	RD	C	C	C	D	D	D	D	D	H	H	H	H	M	M	M
Factor	QDsp97	DHsp96	DHsm96	DHsp97	HZDsp96	HZDsm96	HZD3/97	HZD4/97	HZD5/97	HZH3/97	HZH4/97	HZH5-97	BHsp97	SMsp96	SMsm96	BQsp96
Degrees North	31	31	31	31	31	31	31	31	31	31	31	31	32	32	32	32
Minutes North	49	34	34	34	35	35	35	35	35	35	35	35	37	26	26	3
Seconds North	11.3	0.6	0.6	0.6	49.3	49.3	49.3	49.3	49.3	44.5	44.5	44.5	6.8	11.7	11.7	32.6
Degrees East	37	37	37	37	37	37	37	37	37	37	37	37	37	37	37	37
Minutes East	32	7	7	7	15	15	15	15	15	15	15	15	57	16	16	9
Seconds East	58.8	53.9	53.9	53.9	25.2	25.2	25.2	25.2	25.2	38.5	38.5	38.5	21.9	12.2	12.2	25.7
ALT (m)	697	483	483	483	620	620	620	620	620	608	608	608	624	592	592	479
Relief (1-4)	1.8	1.4	1.4	1.4	1.88	1.88	1.88	1.88	1.88	1.175	1.175	1.175	1	1.1	1.1	1
Grazing (1-5)	3	1	1	4	3	3	4	4	3	3	3	3	5	3	3	4
Humans (1-5)	2	3	3	4	3	3	4	4	3	3	3	3	5	2	2	3
Soil type	12	7	7	7	12	12	12	12	12	10	10	10	10	10	10	7
Soil % Clay	0.61	38.61	38.61	38.61	3.63	3.63	3.63	3.63	3.63	4.75	4.75	4.75	11.39	13.10	13.10	32.07
Soil % Silt	0.70	29.02	29.02	29.02	2.92	2.92	2.92	2.92	2.92	8.38	8.38	8.38	17.56	18.42	18.42	30.21
Soil % Sand	98.63	32.21	32.21	32.21	93.03	93.03	93.03	93.03	93.03	84.89	84.89	84.89	64.79	68.48	68.48	36.10
Soil % Gravel	0.00	0.16	0.16	0.16	0.43	0.43	0.43	0.43	0.43	1.98	1.98	1.98	6.26	0.00	0.00	1.61
LSD (mm)	73.00	10.00	10.00	10.00	32.15	32.15	32.15	32.15	32.15	22.60	22.60	22.60	12.30			32.10
Soil pH	8.50		8.47	7.84		8.22	8.02			7.98			7.85		8.32	
Soil EC (ms)	0.16		0.21	27.37		3.41	3.13			4.16			5.96		0.26	
% Per. cover	20.00	39.00	13.30	1.25	50.00	32.50	28.10	28.25	22.25	12.50	17.20	4.45	0.00	53.00	47.50	26.30
Per. height (cm)	58.75	75.00	75.00	77.83	120.00	65.00	37.97	57.33	87.85	18.94	14.31	27.20	0.00	20.00	15.00	15.00
% Eph. cover	1.65	4.60	2.50	0.00	0.00	0.00	1.50	2.42	2.95	6.51	2.89	2.42	3.80	0.00	0.00	0.00
Eph. height (cm)	4.08	3.00	2.00	0.00	0.00	0.00	1.22	2.44	1.50	1.97	3.03	2.44	5.00	0.00	0.00	0.00
% Basalt cover	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.20	0.00	0.00	3.67
% Stone cover	0.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	13.68	13.68	13.68	8.20	0.00	0.00	0.00

Table 2.7 continued

	M	M	M	M	M	M	B	B	B	B	B	W	W	W	W
Factor	BQsm96	BQsp97	HSAsp96	HSAsm96	HSAsp97	HSBsp97	BUBsp97	SBsp96	SB3/97	SB4/97	SB5/97	SWsm96	SW3/97	SW4/97	SW5/97
Degrees North	32	32	32	32	32	32	32	32	32	32	32	32	32	32	32
Minutes North	3	3	30	30	30	30	36	26	26	26	26	26	26	26	26
Seconds North	32.6	32.6	22.5	22.5	22.5	28.7	55.2	32.6	47	47	47	45	45	45	45
Degrees East	37	37	37	37	37	37	37	37	37	37	37	37	37	37	37
Minutes East	9	9	20	20	20	20	57	17	17	17	17	17	17	17	17
Seconds East	25.7	25.7	41.6	41.6	41.6	39.7	28.6	27.6	49.1	49.1	49.1	48.3	48.3	48.3	48.3
ALT (m)	479	479	555	555	555	555	672	678	790	790	790	757	757	757	757
Relief (1-4)	1	1	1	1	1	1	1.1	1.2	2.1	2.1	2.1	1.4	1.4	1.4	1.4
Grazing (1-5)	4	5	2	2	5	5	5	1	4	3	3	3	4	5	4
Humans (1-5)	3	5	2	2	5	5	5	1	3	3	3	2	4	4	4
Soil type	7	7	10	10	10	10	9	10	10	10	10	10	10	10	10
Soil % Clay	32.07	32.07	10.94	10.94	10.94	15.10	15.73	17.52	17.52	17.52	17.52	8.51	8.51	8.51	8.51
Soil % Silt	30.21	30.21	15.85	15.85	15.85	19.34	21.45	27.78	27.78	27.78	27.78	12.76	12.76	12.76	12.76
Soil % Sand	36.10	36.10	66.61	66.61	66.61	62.98	58.09	55.12	55.12	55.12	55.12	67.35	67.35	67.35	67.35
Soil % Gravel	1.61	1.61	6.59	6.59	6.59	2.58	4.73	1.58	1.58	1.58	1.58	11.38	11.38	11.38	11.38
LSD (mm)	32.10	32.10	19.90	19.90	19.90	18.00	13.80	10.40	10.40	10.40	10.40	16.30	16.30	16.30	16.30
Soil pH	7.99	8.22		8.53	8.41	8.42	8.17		8.35				7.88		
Soil EC (ms)	0.62	0.62		0.21	0.48	0.20	5.96		4.92				0.53		
% Per. cover	21.25	6.93	3.33	5.00	8.00	8.30	0.00	0.00	0.05	0.00	0.00	23.30	11.65	23.80	24.65
Per. height (cm)	10.00	12.37	30.00	10.00	32.29	32.60	0.00	0.00	10.00	0.00	0.00	15.00	16.37	20.12	20.07
% Eph. cover	0.00	19.35	2.75	0.17	8.70	3.65	12.20	5.00	5.21	8.26	3.26	0.00	11.11	8.47	13.68
Eph. height (cm)	0.00	3.72	3.00	2.00	4.65	4.65	4.00	7.00	7.37	9.63	7.16	0.00	3.74	5.08	7.37
% Basalt cover	3.33	8.70	29.83	25.00	21.68	16.90	4.20	52.75	52.75	52.75	52.75	17.50	22.50	22.50	22.50
% Stone cover	0.00	4.90	56.75	63.17	10.20	14.05	37.20	1.80	1.80	1.80	1.80	0.00	4.10	4.10	4.10

(B) or wadi (W). Unless otherwise stated values in the table are means, see methodology for sample numbers.

2.3.3.1 Altitude and relief

Northerly and easterly positions were recorded in degrees, minutes and seconds once at every grid location. For both altitude (ALT) and local relief it was assumed that neither would vary temporally within a site, therefore these factors were not recorded on subsequent sampling. The sand dunes at Hazim and Qaffati were considered permanent over the three-year study period. The harrat slope at Salma was at the highest altitude (790m) and had the steepest relief, whilst the lowest lying area was Bqa'awia at 479m (samples BQsp96, sm96 & sp97). The latter was also one of the flattest, along with other marab and hammada sites (HZH, BH, SM, HAS and HSB).

2.3.3.2 Grazing and human disturbance

Nearly all the sites showed moderate levels of grazing and human disturbance at some time during the study period with the two values tending to correspond (Table 2.7). Throughout the study area grazing was shown to increase from 1996 to 1997. The sites with the most dramatic change in the level of grazing were Hashad (HSAsp96, HSAsp97) in which the grazing pressure increases from 2 to 5 and at Dhahik (DHsp96, Dhsp97) and Salma harrat (SBsp96, SB3/97), both showing a 1 to 4 increase. There was little visual difference in the effect of grazing between the spring and summer 1996.

2.3.3.3 Soil particle size and LSD

It was assumed that during the study period soil composition and loose soil depth (LSD) was consistent. Three different soil types were distinguished in the analysis, clay loam, sandy loam, and sandy. Examples of the soil particle size analysis are in Appendix II. It can be seen from the figures that harrat and marab have the largest proportion of smaller particle sizes compared to other habitat types. The highest proportions of clay and silt were found in samples from the low dunes at Dhahik (39% and 29% respectively), and Bqa'awia marab (32% and 30% respectively). Low proportions of clay, silt and gravel were found in sandy habitats, i.e. Hazim sand dunes (93% sand) and Qattafi (99% sand). Hammada sites had high sand content (65 to 85%), medium clay and silt content (13 to 29%) and low gravel content (2 to 6%). Generally, all sites had low proportions of gravel with the gravel content of wadi being the highest at 11%. Although Dhahik was visually classified as low dunes, it was defined as a clay loam rather than sandy soil

type based on particle size, which was more similar to soil at Bqa'awia than Hazim dunes. Due to the local topography, both Bqa'awia and Dhahik are low lying areas which act as basins for water run-off and sediment deposit, which could account for the similarity in their soil composition. Penetrability of the soil did not directly correspond to soil composition, as Dhahik and Bqa'awia which had similar particle size composition, differed in LSD by 22mm (Table 2.7). Dhahik and Salma harrat had the shallowest loose soil, approximately 10mm, whereas Qattafi had the greatest LSD at 73mm.

2.3.3.4 Soil electrical conductivity and pH

The electrical conductivity and pH of the soil were not measured for all site samples due to a lack of soil collection in spring 1996. All soils measured were mildly alkaline, with the marab at Hashad yielding the highest pH value and Dhahik the lowest. However Dhahik demonstrated the most temporal variation in soil pH, changing from 8.47 in summer 1996, down to 7.84 in spring 1997. The electrical conductivity (EC) of the soil also varied between 1996 to 1997. This was most evident at Dhahik, changing from 0.21 microsiemens per mm in summer 1996 to 27.37 in spring 1997 (Table 2.7). This was the highest EC value for the data set. The majority of other sites, e.g. Hazim dunes, Bqa'awia and Hashad showed little temporal variation in pH and electrical conductivity. However as soil samples were not taken for all site samples and both factors potentially varied over time, these parameters were not included in multivariate analysis.

2.3.3.5 Vegetation cover and height

Cover by perennials was greatest in the marab at Salma (53%) and at Hazim sand dunes (50%), where on average perennials were over 1m in height (Table 2.7). In areas other than dunes, perennials tended to be less than 30cm in height, with the lowest mean adult plant height recorded (10cm) in some grazed areas, e.g. Bqa'awia. In harrat, perennials were virtually absent or present at very low densities. In general, cover by perennials decreased from spring to summer 1996 and between spring 1996 and spring 1997. Monthly changes in perennial cover and height varied between sites, but overall there was an increase in height during spring 1997. The pattern of distribution of cover by ephemerals appeared to differ from that of perennials with highest cover recorded in marab (Bqa'awia, 19%), wadi (Salma, 14%) and harrat (Burquh, 12%), and the lowest in dunes (Hazim, 0 to 2.5% and Dhahik, 0 to 3%). Ephemerals were tallest in harrat (7 to 9.6cm) and shortest in Hazim dunes (1.2 to 2.4cm). For ephemerals temporal changes

in vegetation cover also varied between sites, particularly in monthly sampling. Overall there appeared to be a decrease in vegetation cover between spring and summer 1996 and an increase between the two years.

2.3.3.6 Basalt and stone cover

Basalt rock cover was greatest in the harrat and lowest in dunes (Table 2.7). Wadi had approximately 20% cover, whereas basalt cover of the marab varied between spatial replicates, only 9% cover was recorded at Bqa'awia, whereas approximately 30% was estimated at Hashad. Sand dunes were also virtually devoid of stone cover. The temporal variations in stone cover at Hashad are questionable (HSAsp96, HSAsm96 and HSAsp97). It is suggested that the variations may be a result of the fewer quadrats undertaken in spring 1996 than in spring 1997.

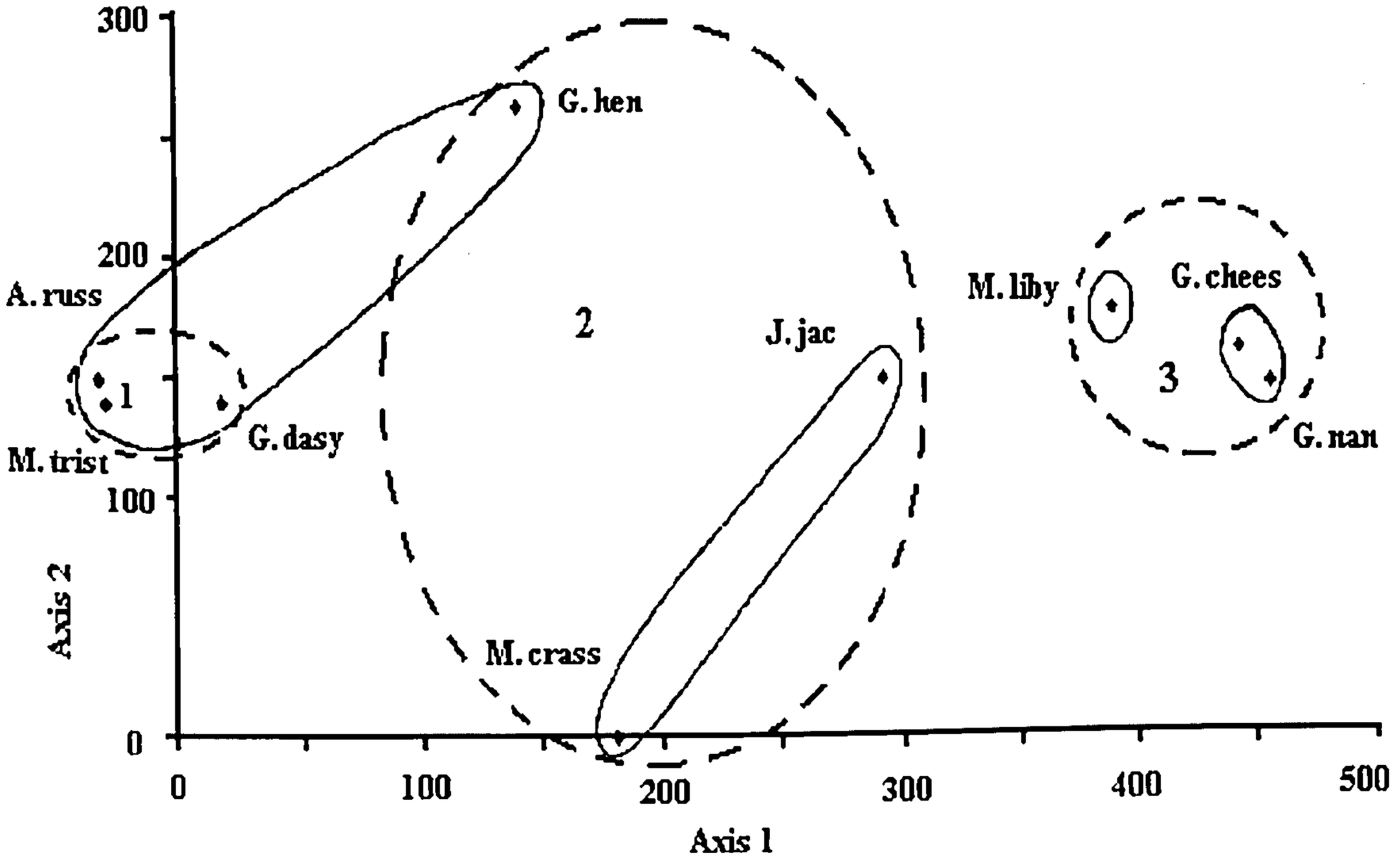
2.3.4 Detrended Correspondence Analysis (DCA)

The DCA generated species and site scores for the first four ordination axes. The eigenvalues for the first four axes for both species and sites were 0.91, 0.252, 0.199 and 0.102 respectively. In general, axes that have an eigenvalue much less than that of the first axis are unlikely to be of much significance (Malloch, 1988). Therefore in this analysis the first axis is considered to be of much higher significance than the subsequent axes.

2.3.4.1 Species ordination

The ordination positions of each rodent species were plotted from the species scores in the DCA output. Ordinations along the first two axes are shown in Figure 2.4.

Figure 2.4 Positions of rodent species along the first two ordination axes from DCA. Lines show TWINSPAN groupings and dashed lines show DCA groups which are numbered, see main text for details. See Table 2.3 for species abbreviations.

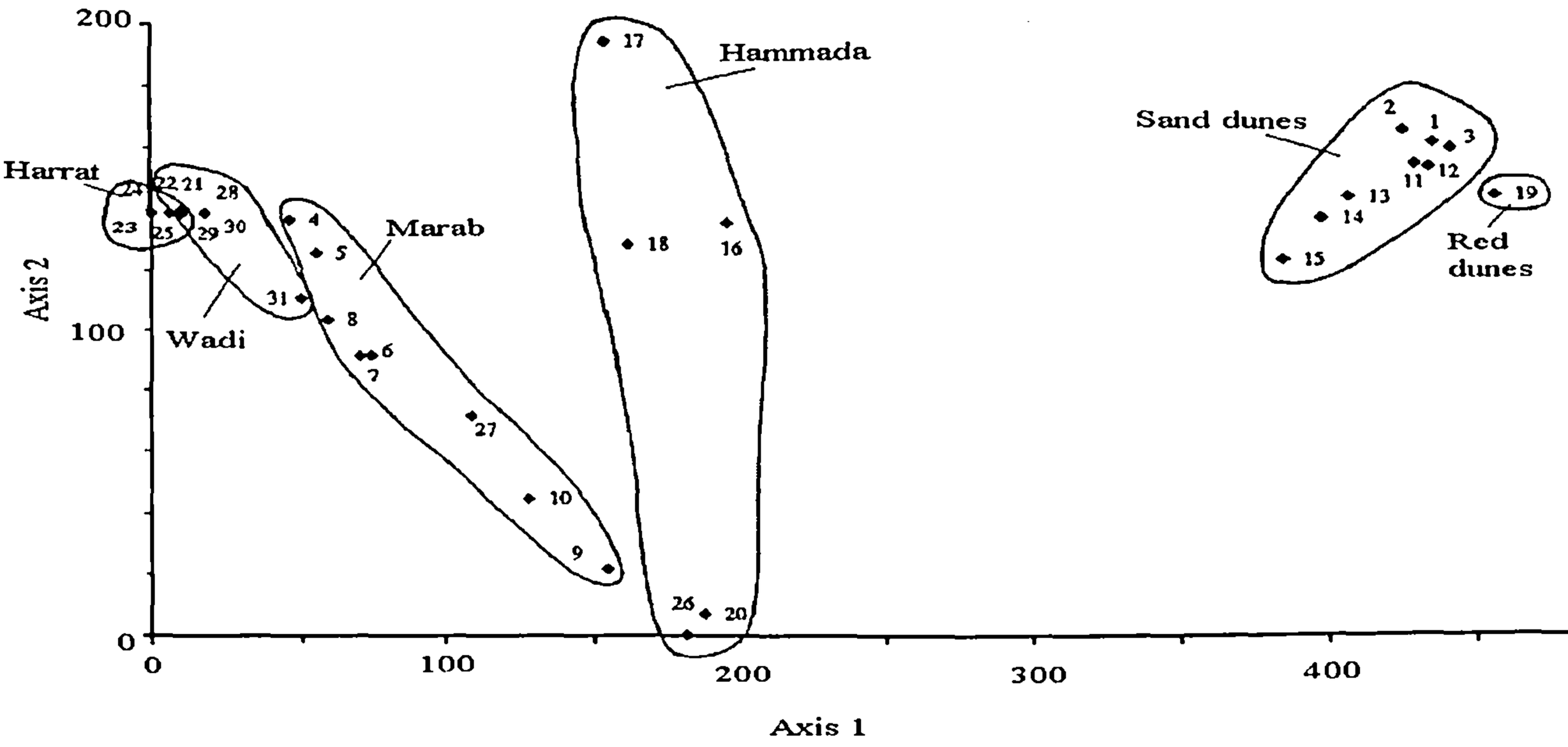


There appear to be two distinct groupings of rodent species. The first group (1) has low scores in axis one and similar scores in axis two (*A.russatus, M. tristrami.* and *G. dasyurus*) and the second group (3) has high scores in axis one and similar scores in axis two (*M. libycus, G. cheesmani* and *G. nanus*). The remaining species tend to form a central less distinct group, which vary considerable on the second axis, but fall within scores of 130 to 300 on axis 1 and have been labelled group '2'. To compare ordinations with TWINSPAN results, the TWINSPAN rodent groupings (2.3.2.2) were overlaid on the ordination. It can be seen that groupings are generally similar to TWINSPAN but with some exceptions, the first concerning the positioning of *G.henleyi,* which on the first ordination axis appears to be more similar to the central species (group 2) than group 1. The second exception is *M. libycus*, which although was separated into its own group by TWINSPAN appears to be associated with group 3 in this analysis. To enable us to speculate habitat preferences of these three groups, site ordination must also be investigated.

2.3.4.2 Sample site ordination

The ordination site scores for the first two axes from DCA are plotted in Figure 2.5. As with the rodent ordination, habitat classifications derived from TWINSPAN are overlaid on the ordination to show site groupings.

Figure 2.5 Site ordination based on rodent similarity using DCA. Sites are grouped into habitat classifications derived from TWINSPAN. Numbers represent sample sites (Table 2.1).



Site ordination is similar to rodent ordination as it shows two very distinct groups, one of low score on axis one and one of high score on axes one. The overlaying of habitat classifications from TWINSPAN clearly indicate that the low scoring group is the harrat habitat type and the high scoring group the sand dune habitat. In general the site groupings in the ordination reflect the habitat classes derived from TWINSPAN. This indicates that the majority of habitat types had distinct rodent community compositions. However, there is spatial and temporal overlap of some site groupings, indicating that these held communities that were not unique to a particular habitat class. Following the clustering of species and sites by DCA, it can be speculated that rodent groupings can be categorised on the basis of the species local habitat preferences. In the species ordination (Figure 2.4) group 1 represents the petrophiles, harrat dwelling species, group 2 the more generalist and open hammada dwelling species, and group 3, the psammophiles, sand dwelling species.

The results suggest that rodent communities are determined by habitat type and that particular environmental parameters may have a major influence on species composition. Comparing ordinations and site parameters allows speculation on which environmental variables may account for the differences in rodent communities. The first DCA axis can be suggested to represent the gradient from basalt to sand. However, it is unclear which environmental variables (Table 2.7) specifically relate to the second axis and this may therefore be a composite of several factors. From rodent community composition data (Appendix I) and species ordination it could also be suggested that the presence of *G. henleyi* might have had influence on the site ordinations in the second axis. This species was not found in the northern parts of the region, therefore species geographical distribution may also account for differences in community compositions.

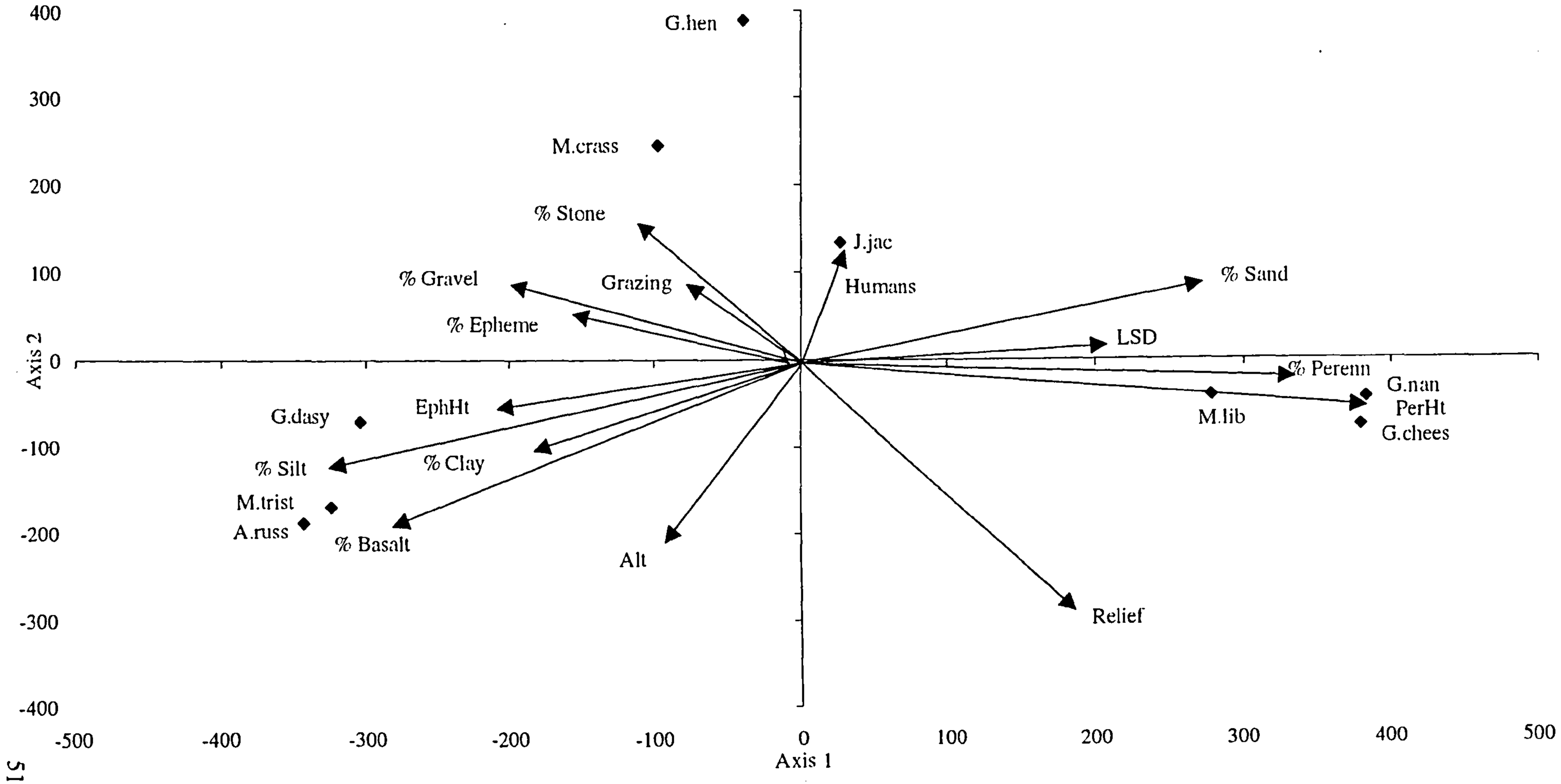
2.3.5 Canonical correspondence analysis using CANOCO

Canonical correspondence analysis (CCA) was carried out to investigate further the relationships between species distributions and environmental variables suggested by TWINSPAN and DCA. The CANOCO program was used to undertake CCA to determine which environmental factors were most highly correlated with the first ordination axis and therefore, species composition. The ordinations of environmental variables in the first two canonical axes were plotted using bi-plot scores summed with the centroids from CCA output (Fig. 2.6). Ter Braak (1987) described the ordination diagram of environmental variables as:

'The environmental variables are represented by arrows. Loosely speaking, the arrow for an environmental variable points in the direction of maximum change of that environmental variable across the diagram, and it's length is proportional to the rate of change in this direction. Environmental variables with long arrows are more strongly correlated with the ordination axes than those with short arrows, and so more closely related to the pattern of community variation shown in the ordination diagram.'

Figure 2.6 shows that the first canonical axis correlated most highly with basalt cover, soil sand content, soil silt content, perennial height and ephemeral height. This axis accounted for 42.9% of the variance in weighted average of the species with respect to each environmental variable (eigenvalue = 0.895). The second axis related to altitude and local relief, which accounted for 23.8% of the variance (eigenvalue = 0.492). The

Figure 2.6. Ordination of species and environmental variables in the first two canonical axes from CANOCO CCA.



third (eigenvalue = 0.270) and fourth axes (eigenvalue = 0.195) accounted for 12.8% and 9.6% of the total variance respectively and therefore were considered not significant enough to warrant further consideration. A Monte Carlo permutation test involving 99 permutations (Manly, 1990), showed that the first canonical axis was highly significantly correlated to species distribution patterns ($P < 0.01$).

The species scores were also plotted on the ordination diagram (Fig. 2.6). The localities of the species in ordination space are similar to those in the DCA, where the axes are not constrained to be linear combinations of environmental variables. From this it can be inferred that the environmental variables measured are associated with the patterns of species distributions. The low scoring group on the left-hand side of Figure 2.4 comprises the petrophile rodents associated with harrat (HC1) and wadi (HC2) habitats of Figure 2.5. These sites have high basalt cover, more ephemeral cover and height and tend to have a higher soil content of silt and clay. The second rodent group, found in open hammada (HC 4), is located in the cluster in the middle of Figure 2.6. This group is associated with low basalt cover and low perennial cover. The third group on the far right hand side is comprised of the psammophylous rodent species of sand dune habitats (HC 5 and HC 6) which are associated with a large percentage of sand content in the soil and increased perennial cover and height.

Statistical T-values from the analysis output are detailed in Table 2.8 in which values for the first two axes were divided by the multiplier value, in this case 100. Environmental parameters in which T-values are greater than 2.13 are considered statistically significant at the 5% level (Ter Braak, 1987). Therefore the most important variables contributing to axis 1 were soil parameters (clay, silt, sand and gravel percentages) and for axis 2 altitude, loose soil depth, ephemeral height and percentage stone cover.

Table 2.8 T-values for the first and second axes in CANOCO analysis. Values for axis 1 and 2 were divided by the multiplier 100. * shows statistical significance as the critical value at 5% significance is 2.13, d.f. = 15.

N	Name	Axis 1		Axis 2	
1	**Altitude**	0.78		-2.28	*
2	**Relief**	-0.84		-1.48	
3	**Grazing**	-0.54		1.40	
4	**Humans**	1.43		-1.83	
5	**% Clay**	2.58	*	0.56	
6	**% Silt**	2.31	*	0.49	
7	**% Sand**	2.49	*	0.59	
8	**% Gravel**	2.50	*	0.54	
9	**Loose soil depth**	0.27		-3.31	*
10	**% Perennial cover**	0.90		-0.22	
11	**Perennial height**	0.98		-0.91	
12	**% Ephemeral cover**	-1.84		-0.06	
13	**Ephemeral height**	1.42		2.83	*
14	**% Basalt cover**	-0.34		0.45	
15	**% Stone cover**	0.98		-2.24	*

2.4 DISCUSSION

2.4.1 Study sites and replicates

Ideally more temporal and spatial replicates should have been undertaken to include a range of samples along gradients of environmental variables, and autumn and winter seasons. Additional, potential study sites were surveyed for rodents using several techniques including transect walking to record spoor, night surveys and opportunistic trapping, but logistics and time limited the number of sample sites that could actually be investigated comprehensively. Whenever site localities were moved (Table 2.1) due to disturbance, as similar habitat as possible was selected as a replacement site.

2.4.2 Small mammal surveys

2.4.2.1 Trap success

The Northeast Badia is considered depauperate with respect to rodent biodiversity (Table 2.3). In comparison with the listed species composition for the North Arabian province (Shenbrot *et al.*, 1999), the Badia area possesses only eight out of the 19 desert species. This includes two sub-endemic (*G. dasyurus* & *A. russatus*), four central Saharan species and one South Arabian species (*G. cheesmani*). *Meriones libycus*, a central Saharan sub-endemic was not included in the species list for the province, but was found throughout the Badia. Additionally many of the species whose distributions from published maps (Harrison & Bates, 1991) were thought to encompass this area were not encountered during this study. For example, *Allactaga euphratica* has previously been reported to occur at low densities in Shaumari Wildlife Reserve, a protected area situated close to the Badia region (Hatough-Bouran & Al-Eisawi, 1990). Lower productivity of deserts in unprotected areas and interspecfic competition may account for the absence of this and other potential species. Species-area relationship analysis has shown a general increase in species richness with increased area due to increasing environmental diversity (Rosenzweig, 1995). The fewer species than expected in my study area may be accounted for by the relative size of the area under investigation and the predominance of basalt fields within the region. Additionally, species at the limit of their geographical range may be encountered only where conditions are favourable.

Descriptions of site localities are dependent on the spatial scale at which they are considered. Site names (Table 2.1) refer to large-scale habitat types, such as a 'wadi' in

which the wadi system can be many kilometres in length and several kilometres wide. On a smaller scale sites can be very heterogeneous and therefore the sample grids selected are also described in terms of habitat type. For the purpose of this study, the spatial scale of the sampling grid was selected as approximately 0.96/ha. It has been suggested that 'edges' will have a higher trapping success than central localities and therefore to minimise this 'edge effect' trapping grids should have the least circumference, i.e. a square (Sutherland, 1996). The grid configuration was selected to maximise area of coverage whilst maintaining the squarest shape possible, given the number of traps available.

Trapping was undertaken within homogeneous areas of chosen habitats, since border areas between habitats may contain other species and could influence community composition of the sample area. For example, only *G. cheesmani* was captured at Qattafi although *M. libycus* was observed close-by. An individual *A. russatus* was recorded in the bordering basalt area. Furthermore, grid-based live-trapping techniques may encounter individuals whilst they are utilising the area for only one particular aspect of their behaviour. Hence, spatial variation in community composition and structure can be viewed on a macro- and microhabitat scale.

Trap dimensions were selected to encompass the size range of all species likely to be encountered. Prior to the study a preliminary investigation was undertaken to assess an efficient trapping period. During this pilot study no species were found to be exclusively diurnal and the trapping period from early evening to dawn recorded as many individuals as encountered from 24-hour trapping. The restricted period chosen also avoided the death of animals due to potentially extreme day-time temperatures. As several of the species potentially encountered were colonial, e.g. *M. libycus* and *M. crassus,* two traps were set per station to prevent an underestimation in density as a result of clumping. However, on only one occasion were two animals caught at the same trap station on the same night.

Occasionally disturbance by livestock and/or adverse weather conditions invalidated the results or prevented data collection. Some traps were blown away in sandstorms, taken by carnivores and Bedu, or run over by Bedouin vehicles. Hence in some sites only three nights per trapping grid were used for density estimates. However, three nights appeared to be sufficient to capture all animals present within the grid, as subsequent

trapping usually revealed no additional individuals. Other problems encountered during trapping were removal of bait by ants and birds, which occasionally resulted in captures of birds. Birds tended to enter traps only during the early morning before traps were checked and therefore did not effect nocturnal capture rates.

Trap success appeared to be less during the colder temperatures observed in the late winter and early spring. It has been suggested that for some species activity drops during the winter and occasionally short periods of hibernation or winter dormancy have been suggested to occur, e.g. *Jaculus* spp (Harrison & Bates, 1991). Aestivation has been suggested to occur in several desert rodent species and this behavioural response to adverse conditions may account for the drop in trap success from spring to summer 1996 (2.3.1.1).

2.4.2.2 Spotlighting

Spotlighting is a technique particularly useful for assessing presence and density of nocturnal mammal species (e.g. Eltringham & Flux, 1971). This technique is also used to observe and capture *Jaculus* species (Happold, 1967), but to date has not been applied to assessing jerboa densities. Problems occurring during spotlighting result from habitat structure, for example dunes, vegetation and basalt rocks occasionally obscure the view. This may have resulted in an underestimation of rodent density in habitats where animals could potentially hide. However, jerboas tend to travel by bipedal locomotion, jumping distances up to several metres in length (or height) in one bound (Happold, 1967) and they were easily sighted when present in both marab and dune habitats. Jerboa density was measured within a distance of 50 metres from the vehicle; within this distance they could be clearly sighted without binoculars. Trapping jerboas with butterfly nets was frequently unsuccessful due to their speed and erratic escape behaviour, as well as problems with visibility at night.

Many factors may effect rodent activity during trapping periods, and may have biased density estimates derived from both spotlighting and trapping. For example the activity levels of some species, e.g. *Jaculus jaculus* are negatively correlated with lunar illumination (Happold, 1967; Kaufman & Kaufman, 1982). This is likely to be a strategy for avoiding detection by predators, many of which, for example, Blanford's fox (*Vulpes cana*) (Geffen *et al.*, 1992), have been shown to synchronise their foraging with the activity of their main prey. In Hashad during spring 1998, 44 replicate

spotlighting surveys were undertaken to estimate *J. jaculus* densities. Results showed a general decrease in activity in response to increasing lunar illumination. An approximately two-thirds decrease in density was recorded from quarter moon to full moon nights, however there was no direct relationship between the two.

2.4.2.3 Density estimates

Initially, mark-recapture data were used to estimate species densities (the Jolly-Seber method, Jolly 1965). However, at some sites, data were insufficient to generate comparative density estimates using this method. Hence, in these areas individual counts per area were used (Sutherland, 1996). This also enabled *J. jaculus* densities to be incorporated within the analysis. As species compositions were compared using standardised measurements, between rather than within sites, integration of the two methodologies to estimate densities was considered justifiable for this analysis. Furthermore, *J. jaculus* ordination position was approximately where it would be envisaged from the field observations (see Fig 2.4).

Food resources such as seeds and vegetation are highly dependent on annual rainfall (Reichman, 1984). It was reported that the winter of 1994/5 in Jordan had above average rainfall, which should have resulted in a productive spring and a large seed crop. This could have had positive effects on rodent densities (Abramsky, 1988). The winter of 1995/6, however, was drier and less productive, which could have had a negative effect on the rodent population during the following year.

2.4.2.4 Body size and morphology

For the majority of species, body weights recorded in this study differed from those recorded by Krasnov *et al.*, (1996a). Differences in sample sizes may account for these observations, since Krasnov recorded 395 *G. dasyurus* but only 82 individuals featured in my calculations (Table 2.4). Body weight differences were shown to differ between seasons, years and habitat types depending on food availability (Shenbrot *et al.*, 1994b). Significant sexual differences where shown for both *G. dasyurus* (Shenbrot *et al.*, 1997) and *M. crassus* (Krasnov *et al.*, 1996b) in which males were generally heavier than females and fluctuated more, however this was not evident in my results (Table 2.4). Some species were difficult to identify from external characteristics alone, e.g. *M. tristrami* and *M. crassus* are very similar in appearance and are distinguished primarily

on internal skull measurements. However, given the limitations of a live trapping study, I am confident that almost all species identifications are correct.

Morphology will have implications for habitat preferences of species. Bipedal locomotion will be difficult in a highly structured habitat such as marab or harrat. Evidence of this was obtained when a jerboa was chased into a marab where it frequently collided with vegetation whilst trying to traverse the habitat. Limitations in mobility will have anti-predatory consequences, which may be reflected in habitat choice (Shenbrot *et al.*, 1999).

2.4.3 Environmental parameters

Several environmental variables, such as locality, soil colour, soil type, electrical conductivity and pH were recorded that were not included in the multivariate analysis due to incompleteness, co-linearity or irrelevance to the spatial distribution of rodents (Table 2.7). The electrical conductivity and pH of the soil will have greater influences on the vegetation composition than on rodent communities directly. However it was noted that rodents appeared to avoid areas which were prone to flooding, i.e. qa'a and wadi beds.

As both soil properties and vegetation have been shown to be important in community composition, grazing may have a direct effect on rodents by reducing vegetation cover (Kerley, 1992) and contributing to soil degradation and erosion through soil disturbance. Environmental parameters which were considered constant were recorded only once, although particle size and loose soil depth may vary due to deposition of sediments and/or soil erosions. Variation was considered to be negligible for the duration of the study period. Overall, replicate samples of soil composition were similar within a site, however in Dhahik more spatial variability was evident with samples varying from predominantly sand to clay (see Appendix II). Dhahik soil characteristics were different than expected, this site grouped with dune habitats on the basis of rodent community similarity, but on average had only 30% sand content compared to over 90% in other dune habitats. *Gerbillus nanus* was found at both Hazim and Dhahik, but absent form all other habitats; hence, the presence of this species may account for the classification of Dhahik as a 'dune' (Fig 2.5).

Soil composition may influence vegetation and hence resource availability, whereas soil penetrability and particle size can determine foraging efficiency of granivores. Whereas foraging can shift to exploit different habitats and resources (Krasnov *et al.*, 1996b), burrows, which are essential refuges for survival in arid environment, can not. Habitat suitability for the construction of burrows will be determined by soil composition. In sandy habitats the problem with burrowing is that sand mobility causes the roof and walls to collapse, therefore most sand dwelling species burrow under bushes or grass clumps where plant roots provide stabilisation (Shenbrot *et al.*, 1999; Krasnov *et al.*, 1996a). Strict rock dwelling species, e.g. *Acomys russatus,* do not construct burrows but make use of rock crevices for shelter. Facultative rock dwellers such as *G. dasyurus* do not construct burrows in rocky areas but have been shown to do so in other habitat types (Hatough-Bouran, 1990).

2.4.4 Community composition

An animal's response to variations in the environment can cause spatial and temporal patterning of community composition (Yajun *et al.*, 1997). Habitat use may also fluctuate temporally depending on the variability of environmental factors (Krasnov *et al.*, 1996a). The flexibility of generalist species to exploit different habitat types is an adaptation to the highly unpredictable and variable desert ecosystems. Generalist species appear to have wider geographical distributions, e.g. *Jaculus jaculus, M. libycus* and *M. crassus* are all widely distributed throughout the south Palaearctic desert belt (Niethammer, 1985).

A year of high rainfall and consequential high productivity may allow the incursion of a new, highly competitive species, into the community. In this study *M. libycus* was grouped with the psammophiles but was trapped at low density in a variety of other habitat types (Appendix I). *Meriones libycus* is a dominant species and due to its size and the high-density colonies it forms, is possibly restricted to areas of high productivity, such as sand dunes with a high perennial cover. It is therefore envisaged that a highly productive year would allow this species to widen its habitat selection.

2.4.4.1 Evidence of mechanisms of coexistence

Desert rodent communities are complex and the mechanisms behind their composition are not discrete (Kotler & Brown, 1988). Differences in morphology, competitive ability and habitat preferences have previously been reported to aid coexistence

(Bowers & Brown, 1982; Reichman, 1984; Kotler, 1997). In the present study there is evidence to support these methods of resource partitioning as mechanisms facilitating coexistence and therefore important in determining community structure.

2.4.4.1a Habitat preferences

TWINSPAN and DCA derived rodent groups were correlated with the first environmental axis (see Fig.2.6), and this result was confirmed statistically by CCA. The grouping of rodents in relation to habitat types suggests distinct local habitat preferences. For example, both analyses suggested that *Acomys russatus* is restricted to harrat and trapping studies have demonstrated that it is only present on the upper-most basalt slopes. This preference could be due to the availability of suitable refuges affording protection from predators and against the harsh environmental conditions (Hughes *et al.*, 1994). Similarly, *Gerbillus nanus* was only found in sand dune habitats (Table 2.5), even though hammada was available nearby. *Meriones crassus* tends to burrow on hammada and therefore may show compromise in habitat selection between substrates suitable for burrowing, foraging and protection from predators. *Jaculus jaculus* may show preference for a particular habitat i.e. hammada, due to its bipedal locomotion, since this may well affect foraging economics and anti-predator behaviour (Lemen & Rosenzwieg, 1978; Thompson, 1982a). Body size and form have previously been associated with microhabitat utilisation by desert rodents (Brown *et al.* 1994).

In theory, individuals should select the best habitats to maximise fitness; however at high density competition for resources increases and consequentially fitness would be decreased. Therefore at a certain level of density it would be beneficial to some individuals to shift utilisation to less suitable habitats. At high densities species tend to become more generalist in habitat preference (Rosenzweig & Abramsky, 1985). For example *G. henleyi* prefers sand dunes at high density but prefers wadis and loess hills at low density, hence showing a density dependant habitat preference (Shenbrot *et al.*, 1999). This habitat shift in *G. henleyi* has been suggested to be a source-sink with low stable densities on open gravel plains the source and periodically high densities on sand dunes 'sinks' (Shenbrot *et al.*, 1999). Strict specialists do not tend to shift habitats with increasing density and are considered density independent (Rosenzweig & Abramsky, 1985). In the Negev, *J. jaculus* and *G. dasyurus* were found to be density independent, *M. crassus* and *A. russatus* appeared to be density dependant, whereas *G. henleyi* showed seasonal differences in density dependence (Shenbrot *et al.*, 1999). In my study

in the spring and summer *G. henleyi* was not found on sand dunes, suggesting low densities occurring during the study period. In a summer and at high densities this species may be incorporated into the sand dune community.

2.4.4.1b Size disparity

Within each derived rodent group there was considerable size disparity and degree of specialisation to habitat type, which potentially facilitates coexistence (Bowers, 1982). For example, only one *Meriones* species is represented in each group (Fig. 2.4). Where there are two or more species from the same family there tends to be either a variation in body weight or in specialisation. The first example of this is seen in group 4 from TWINSPAN (Fig. 2.3), where *G. nanus* and *G. cheesmani* have comparable body weights, but *G. cheesmani* has specialist adaptations to sandy habitats, i.e. hairy feet. The second example from TWINSPAN is seen in group 1, where *G. dasyurus* and *G. henleyi* both occur, but differ in body weight by a factor of 2 (see Table 2.4). Size disparity is also evident within habitat classes (Tables 2.4 & 2.5) with size differences following similar logarithmic patterns of spacing as described by Bowers & Brown (1982). *Gerbillus nanus* and *G. dasyurus*, which have the most similar body size, were not found to inhabit the same habitat class. As only one bipedal and one climbing species were recorded in the overall species diversity, differences in locomotory mode within spatial groups cannot be ascertained.

2.4.4.1c Competition

Competition may also account for the fact that only one *Meriones* species is represented in each group. *Meriones tristrami*, a non-desert species was only caught on a few occasions and this rarity could be due to competition with other desert *Meriones* species. This species was included in the petrophile group but may be exhibiting competitive displacement into a less productive habitat in the presence of a more successful competitor. *Acomys russatus* has previously been reported as diurnal (Shkolnik, 1971), but showed predominantly nocturnal behaviour during this study. Although activity patterns can vary seasonally, a preference for nocturnal activity possibly resulted from reduced competition with other *Acomys* species (Shkolnik, 1971); since no other *Acomys* species were captured during this study.

2.4.5 Multivariate analyses

Rodent-defined habitat types derived from TWINSPAN correspond to ground-truthed descriptions of habitat samples. The grouping of rodents generally followed what was expected from field observations. The exception was *G. henleyi* which was categorised into the petrophiles group, although trapping results indicated that it occurred more frequently and at higher density in hammada. The species has previously been recorded as hammada dwelling (Krasnov *et al.*, 1996a) and its grouping by TWINSPAN (Fig 2.3) was probably due to its occurrence in marab habitats and to associations with species occurring in rocky habitats e.g. *G. dasyurus,* which was also trapped in marab and hammada. *Gerbillus henleyi* and *M. tristrami* were not captured frequently and further evidence is required to group these species more precisely. Observations from opportunistic studies appear to support predicted community compositions from the analysis. In additional harrat sites, burrows of *Gerbillus* were regularly found whereas *Jaculus* burrows were not evident. *Gerbillus dasyurus* and occasionally *M. tristrami* were both trapped in the harrat. On hammada sites burrows of *Meriones* and *Jaculus* were encountered and *Jaculus* was regularly sighted during night surveys in this habitat. In the additional marab habitats evidence for the presence of *J. jaculus*, *G. dasyurus*, *M. crassus* and *M. libycus* were found.

The TWINSPAN grouping (Fig. 2.2 & Fig. 2.3) indicated that community structuring is not based simply on environmental factors that classify habitat types, but is complex in nature with a variety of influential factors. Anomalies in TWINSPAN results emphasise the need for temporal replicates when determining community composition. The species composition of communities and the mechanisms, which determine them, are dynamic. Temporal variations may result from the resources available at that time, which could be a consequence of environmental conditions at, or prior to the time of sampling (Ellis *et al.*, 1997). Temporal constancy of rodent communities (see Fig. 2.5) seems to be more prevalent in areas that have specialist rodent species (e.g. harrat) rather than generalist species (e.g. hammada). In habitat types which do not possess a discrete rodent fauna (e.g. marab) there tends to be greater fluctuations in community composition (Fig. 2.5). A longer-term study is required to further investigate the temporal fluctuations in rodent composition (Shenbrot *et al.*, 1999).

Environmental variables are usually highly inter-correlated and so it is difficult or impossible to separate out independent effects (Ter Braak, 1988). The CANOCO program tests for co-linearity so that these variables can be excluded from further analyses. The habitat groupings in DCA show some sites to have a variable composition of rodent species and cannot be associated exclusively with any particular defined rodent group. The CCA showed similar patterns of distribution of species and sites as the DCA.

2.4.6 Comparisons with previous studies of rodent community composition

A comparison between studies conducted in Israel (Krasnov *et al.*, 1996a) and the present work suggests differences in habitat selection by *Gerbillus nanus* and *G. dasyurus.* These differences could be accounted for by species divergence into various habitat types influenced by several factors, e.g. differential habitat availability. In Israel, *Gerbillus nanus* was recorded to be a generalist species found on hammada and in wadis, whereas in the present study it was only found in sandy habitats. This habitat shift may have been caused by potential competition with a similar sized species, *G. dasyurus,* which, in the Badia, is more adapted to basaltic habitats, such as wadis. Species showing such divergence appear to possess local adaptations to the habitats they occupy, for example, in Jordan *G. dasyurus* tended to be more petrophylic than in Israel. The Jordanian specimens appear to be a darker morph, which could be an adaptation to inhabiting a black basalt habitat. The predominant colour of the surrounding habitat has been suggested to be a potentially important factor in the formation of "substrate races" (Harrison & Seton-Browne, 1969). *Acomys russatus lewisi,* found in this study, has been previously identified as a subspecies specific to basaltic habitats (Atallah, 1967). The differences in community composition between studies reflect the adaptations of species to a different range of habitat types and competition between different species.

Some similarities and differences between the rodent communities found in these two deserts could be explained by their biogeographic histories, for example *Gerbillus gerbillus,* a strictly psammophilous species in Israel (Krasnov *et al.*, 1996a), does not occur in the north-east Badia. Here its niche appears to be filled by another psammophile of similar body size, *G. cheesmani.* Granivorous rodent communities show species convergence towards similar niches and coexisting species appear to show comparable differences in morphology, body size and foraging behaviour (Brown *et al.*,

1979). This is thought to be a mechanism facilitating coexistence by reducing interspecific competition. Stone *et al.* (1996) compared deserts across the American Southwest and identified competition as an underlying mechanism in structuring local rodent communities.

I noted considerable similarity in the partitioning of body sizes and morphology, to that found by Brown (1975) in his comparisons of North American deserts. Body sizes tend to fall into discrete categories in the range from 5 to 120g (Figure 2.1). In each category there are usually only one or two representatives. In cases with two or more representatives there appears to be variation in either morphology, locomotion (bipedal and quadrapedal) or in habitat preferences. Although foraging behaviour has not yet been investigated for rodents in the north-east Badia of Jordan, it is likely that body size and morphology will influence foraging behaviour leading to similar patterns in variation.

As predicted for an Asian rodent community in the North Arabian province, the Badia area was dominated by gerbil and jird species showing a regular displacement in body size within clearly defined groups (or guilds) that were related to specific habitat types. Asian desert-living species show a greater degree of divergence and specialisation between bipedal and quadrapedal rodents than those from North American deserts, although feeding modes were similar on both continents, Shenbrot *et al.* (1994a). Rodent diversity in Asian and American deserts was similar to that found in the present study (2-4 species per site).

CANOCO revealed soil parameters and vegetation cover to be the two most important environmental variables determining rodent community composition. For rodent communities in general, vegetation cover and related productivity appear to be the main determinants (Bian *et al.*, 1994; Adler, 1995; Oguge, 1995). In the present study and other desert systems (south Bukhara desert (Uzbekistan), Shenbrot, 1992; Asian deserts, Shenbrot *et al.*, 1994a; Anix desert (China), Liu *et al.*, 1994; Negev highlands (Israel), Krasnov *et al.*, 1996a) altitude, and soil structure and content have also been shown to be important factors. It has been suggested that plants have several roles in determining spacing in rodents. Many desert rodents utilise vegetation as a food resource when it is available (Krasnov *et al.*, 1996a; see Chapter 3), secondly as a form of cover and protection from predators (Brown *et al.*, 1992), and thirdly in providing habitat

heterogeneity and therefore additional niches to enable co-existence (Brown, 1975). Soil structure can determine the ability to construct burrow systems and foraging efficiency (Price & Heinz, 1984), additionally some species are more adapted to travel on different substrate i.e. hairy feet for locomotion over sand and therefore will have an advantage for inhabiting such areas compared to non-adapted species.

CHAPTER 3
HABITAT STRCUTURE AND VEGETATION ABUNDANCE

3.1 INTRODUCTION AND OBJECTIVES

The spatial analyses undertaken in Chapter 2 indicated that habitat structure and potential resource abundance play important roles in determining spatial and temporal differences in rodent community composition in the Badia region. Chapters 3 and 4 focus on investigating spatial and short-term temporal food abundance in two sites which possess a range of habitat types and attempt to determine which environmental and non-environmental factors may be influencing this. Both chapters attempt to derive and discuss the influences of resource dynamics on several aspects of desert rodent ecology.

3.1.1 Habitat structure

For any ecological investigation, a spatial scale must be selected that is relevant to the questions posed, as one scale may mask the effects of another (Bowers & Dooley, 1993; Jorgensen & Demarais, 1999). In studies of desert rodent ecology three spatial scales have previously been used: 'habitat patches' 'habitats' and 'microhabitat', each being a spatial sub-sample of the next (Bowers & Dooley, 1993). The scale most important in determining resource availability to an individual rodent will be defined by its home range. In general, the desert rodent species found in the Jordan Badia are ground dwelling and live in burrow systems, which vary in depth between species, but generally do not exceed 2m depth (Hatough-Bouran, 1990). *Jaculus jaculus* has been reported to travel as much as 14 km in one night (Osborn & Helmy, 1980), but generally species home ranges do not exceed 400m^2 (Harrison & Bates, 1991; Krasnov *et al.*, 1996b). Above ground, 'habitat' structure is determined by geological features such as rocks (> 5cm) and stones (> 1cm < 5cm), and vegetation, which can vary over time.

I have previously demonstrated that rodent community composition can be predicted by habitat preferences of species (Chapter 2). Additionally, smaller scale habitat structures may also determine the spatial distribution of rodents within communities, since cover provided by vegetation and rock contributes to variations in food density (seeds and vegetation), foraging capabilities and predation risk (Brown *et al.*, 1994).

Surface and soil topography of a habitat influences resource density and accessibility to rodents (Nelson & Chew, 1977; Reichman, 1984; Price & Joyner, 1997), whilst vegetation and rock cover may obstruct access to resources by larger species of rodent. For example, in North American deserts, quadrapeds of small body size (< 40g) have been shown to concentrate their activity among and under vegetation, whilst large bipeds (50-150g) forage primarily on open ground (Brown, 1975; Kotler & Brown, 1988). Therefore the structure of a habitat can provide spatial niches (Abramsky, 1988). Changes in habitat structure can cause changes in relative abundance of species as studies in North American involving manipulation of the environment have demonstrated (Rosenzwieg, 1979). An increase in vegetation cover resulted in an increase in the density of quadrupeds that favoured habitats with high vegetation density (Rosenzweig, 1973; Thompson, 1982b).

It has been commonly suggested the rodents balance the conflicting demands of foraging and safety by appropriate habitat selection (Abramsky *et al.*, 1996), as habitats vary in the levels of resource availability and predation risk (Brown *et al.*, 1988). Habitat cover is generally considered a form of protection against predation, vegetation and rocks provide refuges from predators as well as shelter from harsh environmental conditions. In an Israeli study, the addition of temporary refuges in rocky habitats resulted in an increase in rodent density, which suggested that rocky habitats may engender a greater predation risk, possibly as they potentially harbour more predators and restrict movements for escape (Abramsky *et al.*, 1990). Changes in habitat use in response to perceived risk of predation has been suggested as a mechanism of predator avoidance (Brown *et al.*, 1992; Bowers & Dooley, 1993). For example, increased levels of illumination and cues relating to the presence of predators caused a reduction in the time spent foraging by rodents in 'open', higher risk areas (Kaufman & Kaufman, 1982; Kotler, 1984b; Bowers, 1988; Kotler, 1997).

Soil characteristics, such as compaction and composition, may influence habitat choice by rodents, as penetrability will affect the costs of digging. Also, soil particle size relative to that of seeds will determine ease of food acquisition by the forager (Price, 1983; Price & Heinz, 1984; Hughes *et al.*, 1995). The soil content will also determine suitability for burrow construction (see 3.4.3).

3.1.2 Herbivory in desert rodents

Due to the limited nature of desert resources and their temporal unpredictability, many desert rodent species, particularly those in North American and Israeli deserts, are adapted to a granivorous diet (Brown *et al.*, 1979; Bar *et al.*, 1984). This is possibly a consequence of the relatively consistent availability of seeds compared to other resources (Chapter 4). Vegetation productivity is closely related to rainfall (Brown, 1973). In Jordan, the greatest abundance in vegetation occurred during the winter and spring months following annual precipitation (Gutterman, 1993; Kirk, 1998).

Many desert rodent species cannot survive solely on a diet of seeds and also need water (Khokhlova *et al.*, 1997). Hence, an ability to exploit different types of resources when they are available is crucial for survival in arid conditions. Although dietary information for rodents inhabiting the study area is lacking, studies undertaken in Israel, of the same or similar species, enable general assumptions concerning diet to be made. One study of the Gerbillinae diet (Bar *et al.*, 1984), showed seeds to be the most important food category (52% of total dry weight) compared to plants (42%) and insects (6%). In addition to the Gerbillinae, *Jaculus* and *Acomys* were also present in the study area. Both species have been reported to be partly granivorous and partly herbivorous in diet (Harrison & Bates, 1991), with *Acomys russatus* occasionally demonstrating insectivory (Degen *et al.*, 1986).

Dietary composition varies between species and over time, but generally follows patterns of resource availability. There have been several demonstrations of dietary shifts in relation to resource availability, for example, kangaroo rats (*Dipodomys* spp.) of North America (Nagy & Gruchacz, 1994) and Gerbilline rodents of Israel (Bar *et al.*, 1984). In the Israeli study seeds represented a higher proportion of the diet in the spring corresponding to the current years seed crop, whereas vegetation was more important in the winter when seedlings were most abundant, and insects during the summer when they were most numerous. Shifts in habitat use can also facilitate the exploitation of differential resource availability (Krasnov *et al.*, 1996b).

Apart from density and distribution of resources within a habitat, other determinants may affect a species diet (Randall, 1993). These include the ability to exploit potential resources determined by rodent species morphology (Kam *et al.*, 1997), individual resource characteristics, e.g. size, nutritional value and water content of potential foods

(Frank, 1988) and it has been suggested that the temporal dietary shift towards vegetation is the result of physiological requirements of breeding in desert rodents (Bradley & Mauer, 1971), see section 5.1.4.

3.1.3 Effects of primary production on rodent abundance and diversity

Population density of desert rodents has been shown to be correlated with primary productivity (e.g. Abramsky & Rosenzweig, 1984; Brown & Heske, 1990a) and may result in the invasion or withdrawal of species in an area (Abramsky, 1988). Changes in rodent density and composition will ultimately have consequences for the diversity of a community (Brown, 1973). Rogovin (1996, in Shenbrot *et al.*, 1999) investigated the diversity of rodent species in relation to vegetation and environmental parameters in the Kyzyl Kum desert (Uzbekistan) and in the Chihuahua desert (Mexico) and found a 'hill-shaped' relationship between species diversity and primary productivity, i.e. initially diversity increases with an increase in productivity, but decreases at higher levels. However, differences were reported between the two deserts, suggesting that the influence of productivity in determining rodent species diversity may vary between deserts as a result of environmental conditions and rodent fauna.

It is also evident that rodents can have direct effects on vegetation composition and abundance. Studies using experimental plots excluding rodents have demonstrated changes in plant productivity and species composition (Heske *et al.*, 1993). This could result from foraging behaviour, selective granivory of seeds (Guo *et al.*, 1995; Guo & Brown, 1996, Chapter 4), seedling herbivory, changes in soil topography (Heske *et al.*, 1993; Huntly & Reichman, 1994) or a combination of these factors.

3.1.4 Factors influencing vegetation abundance and species composition

The abundance of different plant species is potentially determined by a combination of environmental and non-environmental factors, which exert different influences on the various stages in each plant's life cycle. As individual species respond differently to environmental factors, plant communities are continually changing and observations of composition will vary depending on the timing of the investigation (Gutterman, 1997). Factors determining any aspect of the plant life cycle, such as seed germination, seedling establishment, and adult survival, could all potentially influence plant community composition at a specific locality at one particular time.

Precipitation has been shown to be of paramount importance in controlling the timing of seed germination, particularly in annual species (Bradstock & Bedward, 1992). The temperature and relative humidity, along with the timing and extent of the initial and subsequent rainfall, may all influence germination, seedling development and seedling survival (Gutterman, 1993) and therefore have an effect on plant community composition and abundance. For example, winter annuals appear after rainfall under cold temperatures whilst summer annuals appear under warm temperatures (Kemp, 1983) and the timing and extent of rainfall can cause variation in the proportions of seeds of each species germinating each year (Baskin & Baskin, 1998). Many other factors have been reported to influence germination and growth. These include day length, water stress, radiation, nutrient availability, soil type and locality. However there are great variations between species in their response to these factors and therefore, it is difficult to identify the precise determinants of community composition. (Gutterman, 1993).

Plant community ecologists have tried to distinguish which factors have the greatest influence on composition and studies of plant communities in Israeli and other deserts have repeatedly identified soil properties to be primary determinants. Tielborger (1997) suggested that the soil surface structure determines plant distribution, since this may affect the availability of moisture (Cowlishaw & Davies, 1997). It is well documented that in deserts rainfall determines productivity (Beatley, 1976; Bowers, 1987; Abu-Irmaileh, 1994; Kadmon, 1995) which may also increase the intensity of competition between plants and can therefore have an effect on plant community composition (Kadmon, 1995).

However, moisture is not uniformly distributed within an area, as rainfall intensity and soil properties will determine the proportion of rain that actually penetrates the soil. Higher intensity rainfall leads to greater run-off, which will collect in topographical depressions in the soil (Danin, 1983). Soil depressions can be created by animals such as ibex (*Capra ibex)* and porcupines (*Hystrix indica*), altering the soil structure and topography which, by acting as collection sites for seeds and rainfall, can have beneficial effects on local plant diversity and density (Shachak *et al.,* 1991; Gutterman, 1997). In soils that possess a surface crust, (e.g. chalk and clay), 70% of rainfall may be lost by surface runoff (coupled with high evaporation rates) but in sandy habitats nearly 100% of the rainfall can penetrate into the sand (Gutterman, 1993). Kutiel, (1998)

studying annual plants, showed density, biomass, species richness and diversity corresponded with the upper soil layer properties, but also demonstrated that increased organic content of the soil resulted in an increase in species richness and plant biomass. It has been suggested that altitude as well as soil substrate is important in determining plant communities and is significantly correlated with vegetation patterns found in the Negev Desert (Ward *et al.*, 1993).

In North American deserts e.g. the northern Sonoran Desert, soil texture along with the angle of slope, were strongly positively correlated with overall vegetation patterns derived by ordination and classification analysis. Nutrient gradients associated with substrate variation were also demonstrated to be an important determinant of plant community patterns (Parker, 1991).

Non-environmental factors, such as animal activity, can also have a great effect on community composition. Selective herbivory can cause a decrease in vegetation standing crop and consequently influence species diversity (Hatough *et al.*, 1986; Abu-Irmaileh, 1994; Al-Eisawi & Hatough, 1994).

3.1.5 Objectives

The objectives of the work described in this chapter are to; i) describe and compare the structure of habitats within and between sites in terms of parameters previously found to be important in determining rodent presence (Chapter 2), and to monitor temporal changes in habitat structure, i.e. vegetation cover. ii) Describe the composition, abundance, and similarity of vegetation between different habitats and sites. iii) Follow the short-term temporal changes in vegetation cover over a season. iv) Measure the timing and extent of seasonal rainfall within and between sites and relate this to the spatial and temporal abundance of vegetation. Additionally, the influences of temporal and spatial differences in habitat structure and resource abundance on foraging behaviour, rodent density and community composition will be discussed.

3.2 METHODOLOGY

3.2.1 Study sites

Two sites in the northern basaltic area of the region were chosen for a study of comparative resource availability. These were Wadi Salma (N32°, 26', 47"; E37°, 17', 49.1") and Wadi Hashad (N32°, 30', 22.5"; E37°, 20', 41.6"), hereafter referred to as Salma and Hashad. From preliminary assessment, both sites were found to possess representative areas of four habitat types, wadi, hammada, marab and harrat (see section 2.2.1). The number of study sites was limited by the availability of sites with equivalent habitat types, logistics of transportation between study areas and the duration of the investigation.

The two 'Wadis' are each over 6kms in length and run approximately parallel to one another, approximately 15km apart, in a west-south-west direction. Hence, sites were located in close enough proximity to enable investigations to be carried out concurrently. Hashad is broader with a maximal width of around 1.5km compared to approximately 700m at Salma. Hashad is located close to the northern Syrian border (approximately 5-10km away) and falls within the military 'buffer' zone. Therefore, access is restricted and this usually limits the extent of grazing and disturbance by Bedouin. However, the site experiences low to moderate grazing by police camels, which are housed at a station situated towards the mouth of 'Wadi' Hashad and the entrance to the site. Salma is not located within the border 'buffer' zone and tends to be subjected to a high level of sheep and goat grazing associated with nomadic Bedouin. As land ownership and border access is weakly defined, grazing pressures can vary considerably.

3.2.2 Sampling grids

Within the two study sites the habitat appeared to be heterogeneous, comprised of differing proportions of wadi bed, harrat slopes and plains and flat areas of hammada and marab. Habitat types that were prevalent within the sites were chosen for detailed study. Wadi habitats were excluded from the majority of temporal sampling due to its instability, i.e. prone to flooding.

Sampling grids were set up in areas of visually homogeneous habitat. At Salma (Plate B) three grids were set up in the marab (MARAB, Plate C), harrat plain (HARRAT,

Plate D) hammada (HAMMADA, Plate E). At Hashad (Plate F) six grids were marked out, comprising one marab site (MARAB, Plate G), one harrat plain (HARRAT, Plate H) and four replicate hammada sites (H1-4, Plate I), see Table 3.1. Hammada replicates were set up to facilitate supplementary feeding experiments (see Chapter 5). As aspect and altitude can influence species composition of rodents and plants (Shachak *et al.*, 1991; Ward *et al.*, 1993), flat harrat plains opposed to slopes were selected at both sites. Grids were located at least 200m apart to provide independence between trapping localities since a rodent's foraging range is generally less than 200m (Krasnov *et al.*, 1996). Replicates within sites were limited by the number of Sherman traps for concurrent small mammal trapping studies, and by logistical capabilities. The corner of each grid was chosen by throwing an object randomly into the area of homogeneous habitat. From this initial point, grids in a configuration of 4 x 5 stations at 20m intervals were measured out. Small basalt rocks painted white were used to permanently mark each of the twenty trap station positions. At these points I also marked twenty permanent $1m^2$ quadrats.

Table 3.1 Sampling grids representing three habitat types in the two study sites.

No.	Hashad		Salma	
	Grid name	Habitat type	Grid name	Habitat type
1	HARRAT	Harrat Plain	HARRAT	Harrat Plain
2	MARAB	Marab	MARAB	Marab
3	H1	Hammada	HAMMADA	Hammada
4	H2	Hammada		
5	H3	Hammada		
6	H4	Hammada		

3.2.3 Habitat descriptions

For each of the 20 grid quadrats, visual estimations of the percentage cover of rocks (>5cm diameter) and stones (< 5cm diameter) of two types (basalt and limestone), were recorded. Loose soil depth (LSD) was also measured in each quadrat using the same methodology as described in Chapter 2.2.3.

3.2.4 Temporal sampling

Resource abundance was assessed during spring 1998, from 23rd February until 31st May. Previous studies of vegetation and annual productivity, undertaken in Jordan (Abu-Irmaileh, 1994; Smettan *et al.*, 1993), define March to May as a 'vegetation period', i.e. a period of maximal vegetation cover and growth. To investigate temporal

Plate B:Wadi Salma, West facing view of wadi mouth



Plate C: Marab at Salma



Plate D: Harrat at Salma



Plate E: Hammada at Salma



Plate F:Wadi Hashad, South facing view of upper wadi



Plate G: Marab at Hashad showing trapping station



Plate H: Harrat at Hashad



Plate I: Hammada (H4) at Hashad



changes in vegetation cover, sampling was undertaken at each site, every ten days, over the 90-day study period, i.e. nine samples. Vegetation biomass was followed at monthly intervals, every 30 days for March, April and May. Intervals were selected based on logistics and envisaged rates of change for each parameter. It was not possible to investigate both sites simultaneously. Table 3.2 gives the actual date of the time periods during which investigations were undertaken at each site. Furthermore, access to Salma was prohibited for several days from 13/4/98 due to flooding hence no data could be collected in this time period.

Table 3.2 Time periods and corresponding dates used to enable site comparisons.

Time Period	Hashad	Salma
1	14/3/98	-
2	26/3/98	24/3/98
3	5/4/98	3/4/98
4	16/4/98	13/4/98
5	26/4/98	23/4/98
6	6/5/98	3/5/98
7	16/5/98	13/5/98
8	26/5/98	24/5/98

3.2.5 Weather data

Rainfall was measured using rain gauges, constructed from plastic bottles, which were positioned in each grid. The bottles, approximately 10cm in diameter were submerged to a 25cm depth with the rim 4cm above the soil surface to prevent insects and sand entering the gauge. At ten-day intervals, rainfall was measured by transferring the collected rainfall into a measuring cylinder. Mean monthly rainfall (mm) data were obtained from automated weather systems based at As-Safawi, Azraq and Ruwaished. Additionally, all observed rainfall events, which occurred during the study period, were recorded in terms of date, site, length of event (in minutes) and intensity (light, moderate or heavy). Each rainfall event was then scored on an arbitrary scale (1-10) in relation to the perceived overall amount of precipitation.

3.2.6 Vegetation surveys

Species found in the study sites were identified in the field where possible (Zohary & Feinbrun-Dothan, 1987) and representative samples were collected, dried and stored for later identification confirmation. The abundance of each species was scored using a scale of + for species present but rare (encountered 1-2% of the time during surveys),

++ for species occasionally occurring (encountered 3-60% of the time during surveys) and +++ for commonly occurring species (found >60% of the time) (Mueller-Dombois & Ellenberg, 1974). This was undertaken in each of the four different habitat types (hammada, wadi, marab and harrat) at both sites.

All vegetation was considered a potential food resource if it was within reach of a foraging rodent, i.e. annual and perennial species produced new growth at ground level, hence were susceptible to herbivory. Additionally, perennials, particularly shrubs, were considered a form of protection against predation and therefore a potentially important factor determining habitat use by rodents (Abramsky *et al*, 1996). Cover by perennials has also been shown to be an important parameter in determining rodent community composition in the Badia region (section 2.2.5).

For the purpose of this study two forms of vegetation are considered: i) annuals, available seasonally in relation to rainfall, and ii) perennial shrubs, available continuously and considered to contribute greater to the habitat 'cover'. This separation also facilitated analysis of the two predominant vegetation layers (Mueller-Dombois & Ellenberg, 1974). Two species (*Diplotaxis harra* and *Launaea nudicaulis)* are facultative perennials which have variable life spans depending on environmental factors (Gutterman, 1993). These species appeared to be more similar to annuals with regards to their contribution to cover and temporal availability in the habitat, hence they were considered within this group for the study of vegetation cover.

To follow changes in vegetation cover over time, nine temporal replicate surveys of twenty $1m^2$ quadrats per grid were undertaken. Previous studies have used $1m^2$ as an appropriate size for the investigation of vegetation composition (Abu-Irmaileh, 1994). The percentage of vegetation cover for perennials and annuals were estimated visually when viewed directly from above the quadrat. Within a site recordings were undertaken on the same day, however, due to the time consuming nature of the surveys, sites were sampled on different days.

3.2.7 Vegetation biomass

The biomass of above ground new growth of both perennials and annuals was measured every month at Salma and Hashad. Five, 50 x 50cm quadrats were chosen by throwing a marker randomly into an area of homogenous habitat. All vegetation in the quadrat area

was cropped down to soil surface and hand sorted into one of three categories; old perennial; new perennial; new ephemeral. All 'green' vegetation was classified as new growth. The fresh weight (g) was taken immediately after cutting using a 'Pesola' spring balance (0-100g, at 1g increments). Samples were then stored in envelopes and labelled with site, date and content, and air-dried to a constant weight over approximately one-week. Methodology was adapted from similar studies undertaken in Jordan to assess vegetation productivity (Abu-Irmaileh, 1994) and from Sutherland (1996). Thc water content of new vegetation was calculated as a percentage of the total fresh weight.

3.2.8 Statistical analysis

Initially data were tested for normality and equality of variance using Kolmogorov-Smirnov and F_{max} tests respectively. Data not showing a normal distribution were either normalised using an appropriate transformation to allow parametric analysis or non-parametric tests were applied. ANOVA's were undertaken on normally distributed data which had equal variances. Non parametric tests used were the Mann-Whitney U on data sets with two samples and the Kruskal Wallis on data sets with more than two samples. As temporal data were ordinal, Spearman rank correlation analysis was used.

3.3 RESULTS

3.3.1. Habitat structure

Descriptions of terrain were quantified as the percentage cover of five habitat parameters for each of the sample grids (Table 3.3.).

Table 3.3 Habitat descriptions of sampling grids showing the mean and standard error (S.E.) of the visually estimated percentage cover (n = 20 per grid) for rocks and stones (basalt and limestone) and loose soil depth (LSD). H1 to 4 are replicates of hammada habitat.

		Rock cover (%)		Stone cover (%)		Loose soil depth (cm)
		Basalt	Limestone	Basalt	Limestone	
Hashad	Marab	8.9 ± 1.6	2.4 ± 0.7	14.1 ± 1.2	11.2 ± 1.2	13.5 ± 1.0
	Harrat	42.8 ± 4.8	2.9 ± 0.6	7.7 ± 1.0	10.2 ± 1.4	19.4 ± 1.4
	H1	2.9± 0.9	0 ± 0.0	3.3 ± 1.0	0.9 ± 0.2	11.2 ± 1.3
	H2	2.6± 1.03	0 ± 0.0	4.8 ± 1.6	0.7 ± 0.1	12.9 ± 1.2
	H3	0.2± 0.1	0 ± 0.0	0.7 ± 0.1	0.5 ± 0.0	26.5 ± 1.7
	H4	2.6 ± 1.5	0 ± 0.0	1.8 ± 0.3	0.7 ± 0.1	15.0 ± 1.6
Salma	Marab	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	13.8 ± 1.8
	Harrat	40.0 ± 2.6	0.1 ± 0.1	1.3 ± 0.3	5.5 ± 1.4	29.3 ± 1.5
	Hammada	1.9 ± 1.2	0.6 ± 1.8	0.5 ± 0.0	1.0 ± 0.1	13.2 ± 1.3

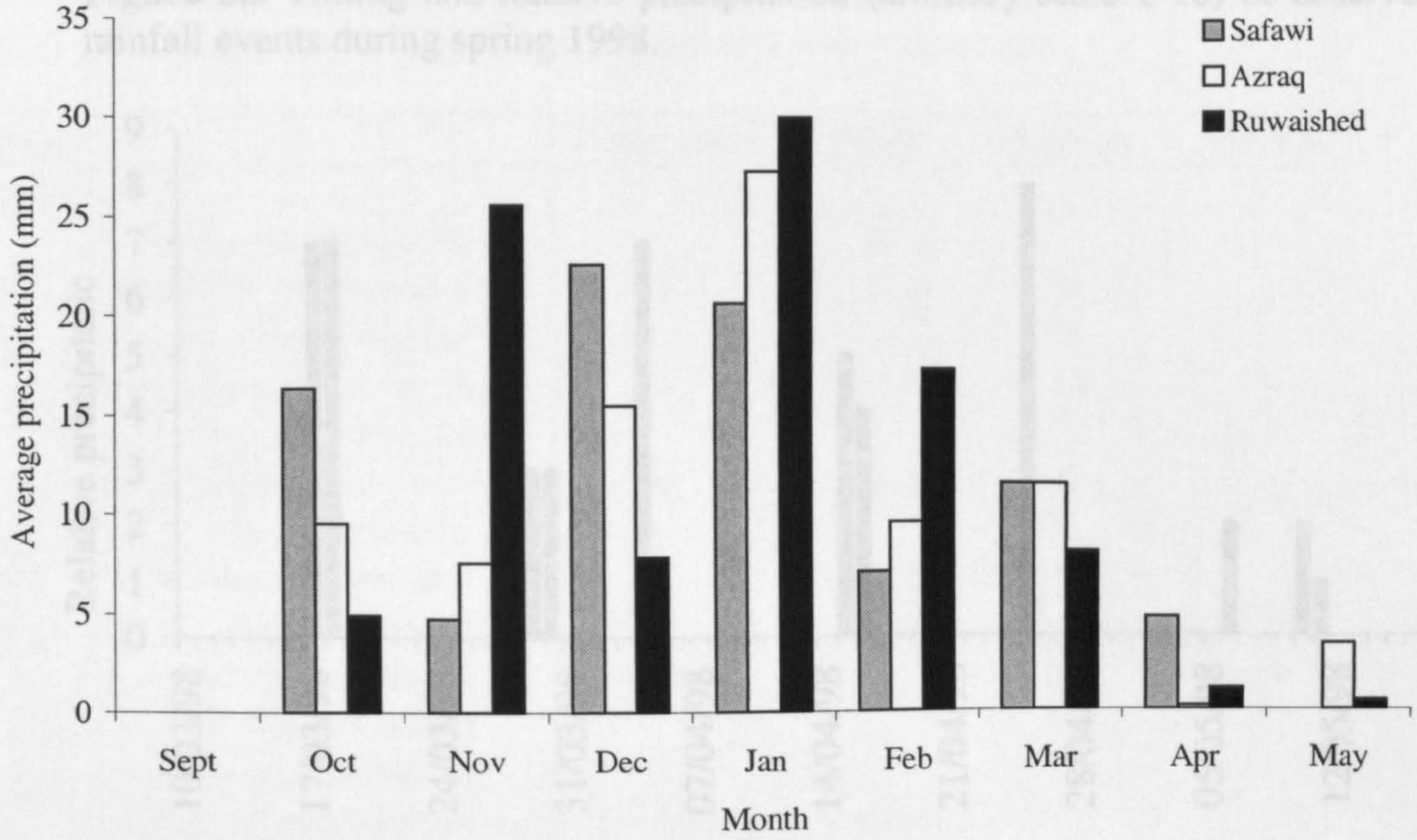
As habitats are selected on the basis of their physical characteristics, they would be expected to differ in quantitative description of rock and stone cover, but habitat types between sites and habitat replicates within sites would be similar. It can be seen from Table 3.3 that marab, hammada and harrat habitat characteristics vary at both sites. Harrat had the highest basalt rock cover, but showed inter-site variation in stone cover and loose soil depth. Marab at both sites appeared different in all aspects of rock and stone cover but showed similar loose soil depth. Hammada replicates at Hashad were similar in all aspects of rock and stone cover and of loose soil depth, with the exception of H3, which had a lower basalt stone cover and greater loose soil depth. Results show that inter-site variability in hammada was low.

As basalt rock cover and soil structure were shown to be important in determining species presence and abundance (Chapter 2.2.5), these parameters were used to check for differences between habitats and sites. Loose soil depth was normalised by log transformation (Kolmogorov- Smirnov test: $P > 0.05$, equal variances, $F_{max} = 3.034$, $P > 0.05$) before undertaking two-way ANOVA (with replication). There was a highly statistically significant difference in loose soil depth between habitats ($F = 19.191$, $P < 0.001$) but not between sites ($F = 1.037$, $P > 0.05$). There were also significant differences in the basalt cover between habitats at both sites (Hashad, $X^2 = 59.774$, $P < 0.001$; Salma, $X^2 = 49.235$, $P < 0.001$, Kruskal-Wallis), but only for the marab was there a statistical difference between sites ($U = 40.0$, $n = 20$, $P < 0.001$, Mann Whitney). In general, these results appear to confirm the validity of visually selected grids. Habitats within sites were different in terms of loose soil depth and basalt cover, whereas between sites loose soil depth and basalt cover were similar, the exception being marab habitat which showed inter-site differences in basalt cover.

3.3.2 Meteorological data

The rainfall gauges seemed successful at first, but as air temperatures increased towards the summer months it was obvious that the water collected was evaporating from the bottles between checking periods. Additionally, several bottles disappeared possibly by interference from local people. Thereafter this methodology was abandoned. Rainfall data from weather stations were used to investigate the timing and extent of rainfall during this year, to look at differences in precipitation at the sites and to attempt to relate meteorological data to changes in vegetation and seeding (see Chapter 4). The average monthly rainfall from September 1997 to May 1998, for the three sites within the Badia region is plotted in Figure 3.1. The timing of rainfall in Azraq and Safawi sites were correlated ($r = 0.911$, $P = 0.001$, Spearman rank), but at Safawi and Ruwaished rainfall was not ($r = 0.571$, $P = 0.108$). Kirk (1998), suggested that the timing and extent of rainfall in this region can vary greatly between localities. The mean annual rainfall was calculated by summing the individual monthly means. Annual rainfall at Safawi and Azraq during 1997-98 was 87.2mm and 84.2mm respectively. This was slightly greater than the average rainfall calculated for the period of 1963-1990 (76.1mm and 70.0mm respectively).

Figure 3.1 Average monthly rainfall for three stations in the Badia area (1997-98) (courtesy of B.R.D.P.).

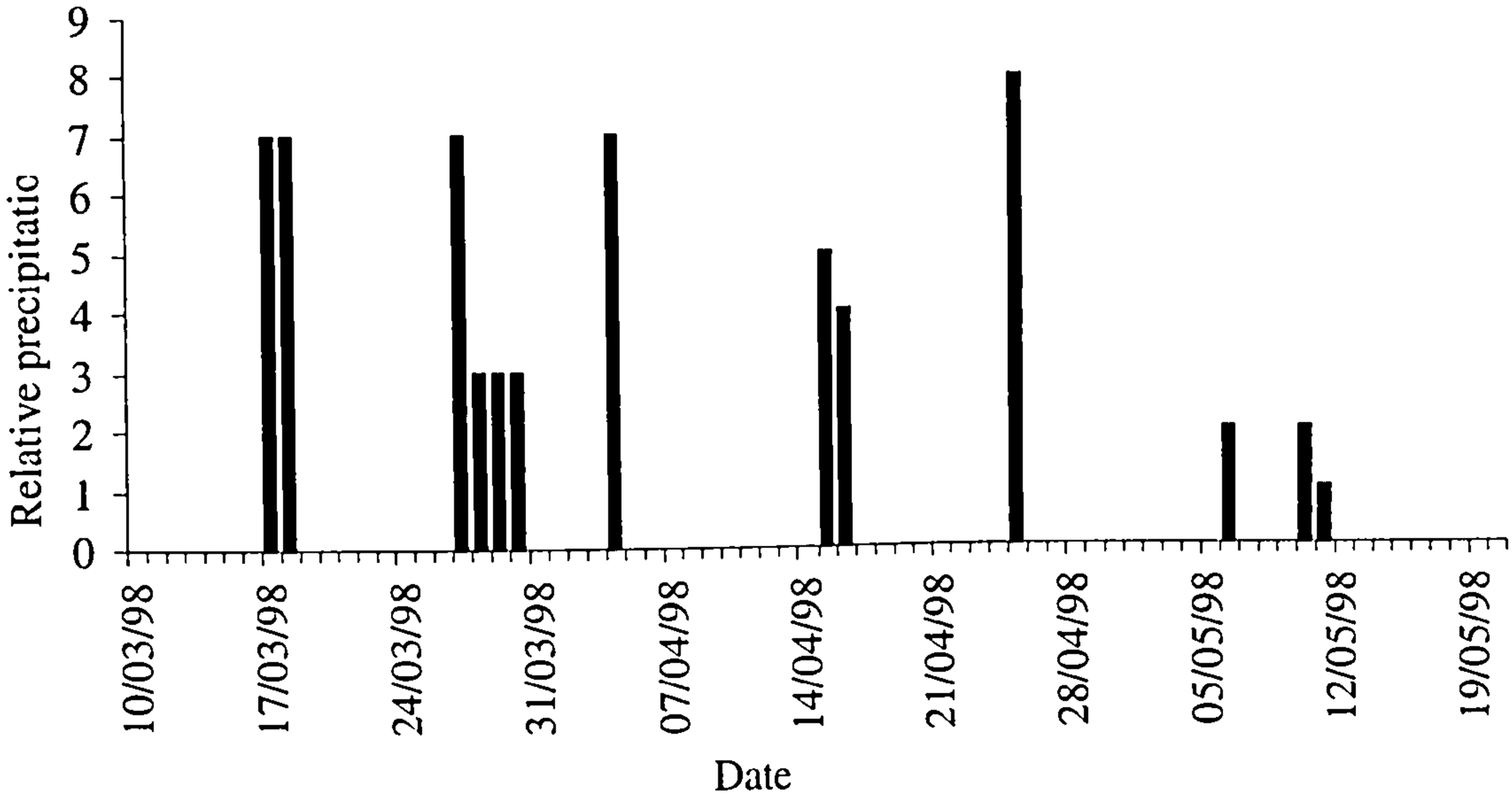


Rainfall commenced in October at all three sites and showed no corresponding single peak between sites, this agreed with observations of Kirk (1998). There was no recorded rainfall during June at Ruwaished or Azraq, however at Safawi (the closest station to the study sites), rainfall had ceased earlier and there had been no precipitation during May. Monthly rainfall patterns during 1997-8 did not correspond to average patterns for 1980-1990 (Kirk, 1998). October, November and January showed above average rainfall and November, February and April having less suggesting that in general, rainfall was greater in autumn and less in the spring than in an average year.

Figure 3.2 shows the timing and relative precipitation of rainfall events observed close to or within study sites during spring 1998. It is immediately clear that the observed rainfall does not correspond directly to the measurements from Safawi (Fig. 3.1). This further suggests that differences can occur between relatively close localities. From Fig. 3.2 it can be seen that rainfall events are sporadic, unpredictable and vary in intensity and duration. Pronounced rainfall events took place during mid-March to early April 1998, two later events in mid to late April and then two smaller events in early-middle May. Precipitation appeared to be similar for March and April with fewer lower intensity rainfall events during May, this also corresponded to the findings by Kirk

(1998) in which March and April had similar average rainfall (12-13 mm), whereas May tended to have less with many years experiencing no rainfall.

Figure 3.2 Timing and relative precipitation (arbitrary scale 1-10) of observed rainfall events during spring 1998.



From the evidence, it is suggested that during 1997-8 rainfall was above the annual mean, with earlier months experiencing above average rainfall and later months experiencing less. Rainfall during May is not uncommon but considered atypical, indicating a slightly longer rainy period than normally observed.

3.3.3 Plant species presence and abundance

Vegetation surveys were undertaken to enable comparisons between habitats and sites in terms of habitat structure, species richness, composition and abundance. Tables 3.4 and 3.5 show the presence/absence and relative abundance of plant species in four habitat types at Hashad and Salma. From initial observations it was clear that sites and habitats possessed different species compositions and abundance. Hashad had a greater species richness of perennials and a lower richness of annuals compared to Salma. The marab and wadi habitats at Hashad and the marab habitat at Salma possessed a greater abundance of annual and perennial species than other habitats. Some species, e.g. *Artemisia herba-alba* and Gramineae spp., appear to be consistently abundant in the habitats in which they were found, whereas other species were found locally abundant, i.e. abundant only in the marab at Salma (*Matricaria aurea* and *Plantago ovata).* Individual species tended to show similar habitat preferences between sites, for example

species found in all habitats at Salma (generalist) were also found in all habitats at Hashad.

Table 3.4 Plant species presence/absence in four habitats in Hashad. Abundance is scored as + = rare, ++ = occasional and +++ = common.

Species	Hammada	Wadi	Marab	Harrat
Annuals				
Anthemis pseudocotula		+	+	
Aronsolnia factorovskyi	+	+	+	+
Asteriscus hierchunticus				
Calendula tripterocarpa	+	++	++	+
Crepis spp.				
Erodium bryonifolium	+	+	+	
Erodium deserti				
Erucaria boveana		+	+	
Gramineae A		+++	+++	+++
Leysera leyseriodes	++	++	++	++
Matricaria aurea				
Medicago laciniata				
Papaver polytrichum		++		
Plantago ovata				
Reseda decursiva	+	++	++	
Trigonella stellata	+	+++	++	+
Perennials				
Achillea fragrantissima		+	+	
Artemisia herba-alba	+	+++	+++	
Astragalus spinosus		+	+	
Diplotaxis harra	++	++	++	+
Launaea nudicaulis	+	+++	++	
Linum album	+	++	+++	
Onobrychis ptolemaica		+	+	
Paracaryum rugulosum		+	+	
Scariola orientalis		+	+	
Thymus bovei		++	+	
Annual Species Richness	6	12	10	6
Perennial Species Richness	4	10	10	1
Total Species Richness	10	22	20	7

Table 3.5 Plant species presence/absence in four habitats in Salma. Abundance is scored as + = rare, ++ = occasional and +++ = common.

Species	Hammada	Wadi	Marab	Harrat
Annuals				
Anthemis pseudocotula	+		++	
Aronsohnia factorovskyi	++	+	+	++
Asteriscus hierchunticus			+	+
Calendula tripterocarpa	+		++	+
Crepis spp.		+	+++	+
Erodium bryonifolium	++	+	+	+
Erodium deserti	+	++	+	+
Erucaria boveana				
Gramineae A	++	+	+++	+++
Leysera leyseriodes	++	+	+	++
Matricaria aurea	+	+	+++	+
Medicago laciniata			++	
Papaver polytrichum				
Plantago ovata	+	+	+++	+
Reseda decursiva				
Trigonella stellata	+	+	++	++
Perennials				
Achillea fragrantissima		+	++	
Artemisia herba-alba		+++	+++	
Astragalus spinosus	++	+	++	+
Diplotaxis harra	++		+	+
Launaea nudicaulis				
Linum album				
Onobrychis ptolemaica				
Paracaryum rugulosum				
Scariola orientalis		+		
Thymus bovei		+		
Annual Species Richness	10	9	13	11
Perennial Species Richness	2	5	4	2
Species Richness	12	14	17	13

To compare species composition between habitats and sites, Jaccard's similarity coefficient (S_j, in which 0 = no species similarity and 1 = the same species composition; Krebs, 1989) was calculated for annuals, perennials and for all vegetation in each combination of habitat types (Table 3.4 and 3.5). In general, for all species, habitats between sites had approximately 0.4-0.5 similarity. Salma habitats (mean similarity = 0.67) tended to be more similar in species composition than habitats at Hashad (mean similarity = 0.54). The marab and wadi habitats at Hashad were most similar, whilst the harrat showed greatest difference when compared to these two habitats. Compared with all other habitats the hammada had approximately 0.55 species similarity. At Salma, marab, hammada and harrat sites were relatively similar in species composition with

0.7-0.8 similarity. Whilst the wadi appeared to be least similar to the other habitats with 0.55-0.60 similarity. Between and within sites, annual species composition tended to be more similar than perennial species composition. Salma tended to have a greater species similarity between habitats than Hashad for both perennial and annual species.

Table 3.6 Plant species similarity between and within habitats in the two sites using Jaccard's similarity coefficient (S_j).

			S_j		
Site	**Habitat 1**	**Habitat 2**	**Annual**	**Perennial**	**Total**
Both					
	Hammada	Hammada	0.45	0.20	0.44
	Wadi	Wadi	0.36	0.50	0.42
	Marab	Marab	0.47	0.40	0.44
	Harrat	Harrat	0.45	0.50	0.50
Hashad					
	Hammada	Wadi	0.60	0.40	0.55
	Hammada	Marab	0.67	0.40	0.57
	Hammada	Harrat	0.57	0.25	0.56
	Wadi	Marab	0.90	1.00	0.95
	Wadi	Harrat	0.50	0.10	0.30
	Marab	Harrat	0.56	0.10	0.32
Salma					
	Hammada	Wadi	0.73	0.17	0.56
	Hammada	Marab	0.77	0.50	0.71
	Hammada	Harrat	0.75	1.00	0.79
	Wadi	Marab	0.69	0.50	0.63
	Wadi	Harrat	0.82	0.17	0.59
	Marab	Harrat	0.85	0.50	0.76

3.3.4 Vegetation cover

Percentage cover estimates for Hashad marab and harrat on 13/4/98 were excluded from the analysis due to an unavoidable inconsistency in data collection, i.e. ill health, which resulted in a different researcher sampling on this date. Additionally, data collected from the harrat at Salma on 18/4/98 were mislaid. For this period values were extrapolated by taking the mean of the difference between the previous and subsequent estimates.

Visually estimating percentage cover is one method of measuring vegetation abundance within an area to enable quantitative comparisons between samples. As habitats are selected on visual observations of rock and vegetation cover, it is assumed that quantitative vegetation cover will vary between habitats within a site, but habitats between sites would be relatively similar. Vegetation cover was considered for three

aspects, total vegetation, annuals and perennials for each grid. This provides an indication of the year round vegetation cover and the contribution of annual species to the total cover in each sampling grid during the spring.

The mean percentage cover and standard deviation of annuals and perennials in all sample grids averaged throughout the study period are shown in Tables 3.7 and 3.8. Data were not normally distributed (Kolmogorov–Smirnov test, $P < 0.05$) and had unequal variances (F_{max} test, $P < 0.05$).

Table 3.7 Mean percentage cover of annuals in each of the sample grids during spring 1998.

Habitat		Hashad			Salma		
		Mean	S.D.	N	Mean	S.D.	N
Marab		3.9	5.8	180	43.2	19.8	160
Harrat		1.9	2.4	180	1.4	1.5	160
Hammada	H1	0.4	0.4	180	0.5	0.8	160
	H2	0.3	0.7	180			
	H3	0.3	0.3	180			
	H4	0.3	0.5	180			

Table 3.8 Mean percentage cover of perennials in each of the sample grids during spring 1998.

Habitat		Hashad			Salma		
		Mean	S.D.	N	Mean	S.D.	N
Marab		5.5	6.5	180	12.8	11.8	160
Harrat		0.1	0.7	180	0.0	0.0	160
Hammada	H1	0.0	0.2	180	0.0	0.0	160
	H2	0.0	0.1	180			
	H3	0.0	0.0	180			
	H4	0.0	0.0	180			

Kruskal-Wallis tests showed that the overall vegetation cover differed significantly between habitats within each site (Salma, $X^2 = 353.18$, $P < 0.001$; Hashad, $X^2 = 185.21$, $P < 0.001$) and for all habitats between sites (harrat, $U = 15052$, $n = 360$ $P < 0.001$;

hammada, U = 97663, n = 360, P < 0.001; marab, U = 8362, n = 360, P < 0.001). There were also significant differences in the cover provided by annuals between habitat types at Salma (X^2 = 318.31, P < 0.001) and Hashad (X^2 = 374.98, P < 0.001). However, only the marab habitat showed a significant difference in cover by annuals between sites (Mann-Whitney, U = 909, n = 160, n = 180, P < 0.001), despite having the most similar species composition (Table 3.6). The hammada and harrat showed no significant difference between sites (U = 64512, n = 158, n = 880, P = 0.101; U = 11618, n = 140, n = 180, P = 0.214 respectivcly). This showed that in terms of cover by annuals, habitats between sites varied less than habitats within sites. A statistical test was not performed on perennial vegetation due to multiple zero values. However, from the tables it can be seen that in contrast to annuals, which were found in all habitat types, perennials were found predominantly in the marabs and provided very little cover elsewhere.

Vegetation cover was highest in the marab at both sites. In Salma the marab habitat had 10 times as much cover by annuals and at least twice as much cover by perennials than Hashad. Hammada replicates at Hashad were similar in both annual and cover by perennials. Overall vegetation cover in marab habitats appear to be the most abundant in terms of vegetation available for herbivory, which in the form of perennials would also be the most temporally consistent. Cover of perennials in the marab would provide the protective cover from predators and a heterogeneous habitat structure to facilitate species co-existence.

3.3.5 Temporal changes in vegetation cover

Changes in percentage cover of annuals and perennials were followed during spring 1998 in each habitat in the two study sites (Figures 3.3 a-c). Data were expressed as percentages, therefore Spearman rank correlation coefficients were calculated to compare the patterns of change between habitats and sites. From Figures 3.3 a and b, cover by annuals appears to be consistently low in the hammada habitats at both sites, however, there was no correlation in temporal changes in cover provided by annuals between sites (r = 0.627, P = 0.132). There was a general decrease in cover by annuals in harrat habitats throughout the study period and the patterns of change in between the two sites was close to statistical significance (r = 0.750, P = 0.052). The temporal changes in vegetation cover by annuals in marab habitats between the two sites were correlated (r = 0.821, P = 0.023). This shows that between sites the marab and harrat were more similar in patterns of vegetation growth by annuals than the hammada,

Figure 3.3 a-c. Temporal changes in the mean percentage cover (n = 20, hammada replicates are averaged, n = 80) by annuals in three habitat types at Hashad and Salma, during spring 1998. S.E bars are shown.

Figure 3.3a Hashad annuals

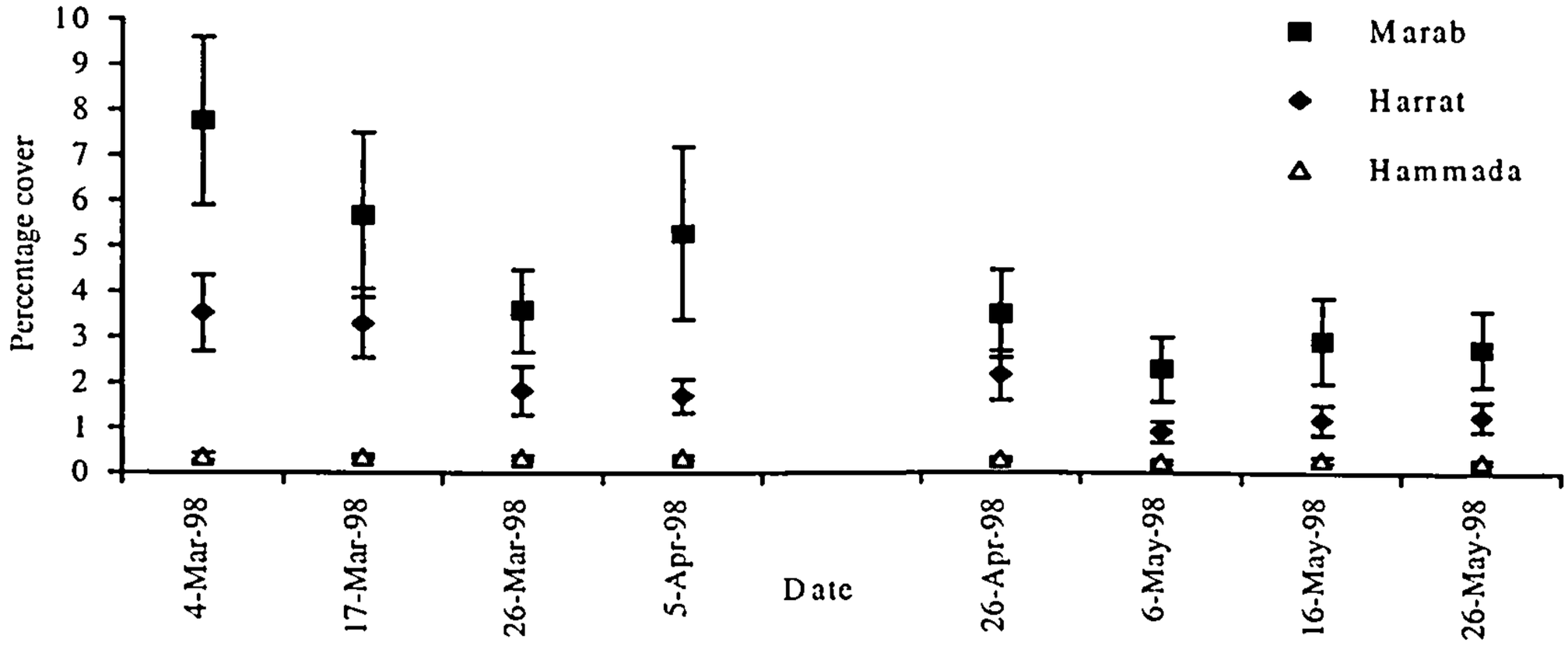


Figure 3.3b Salma annuals

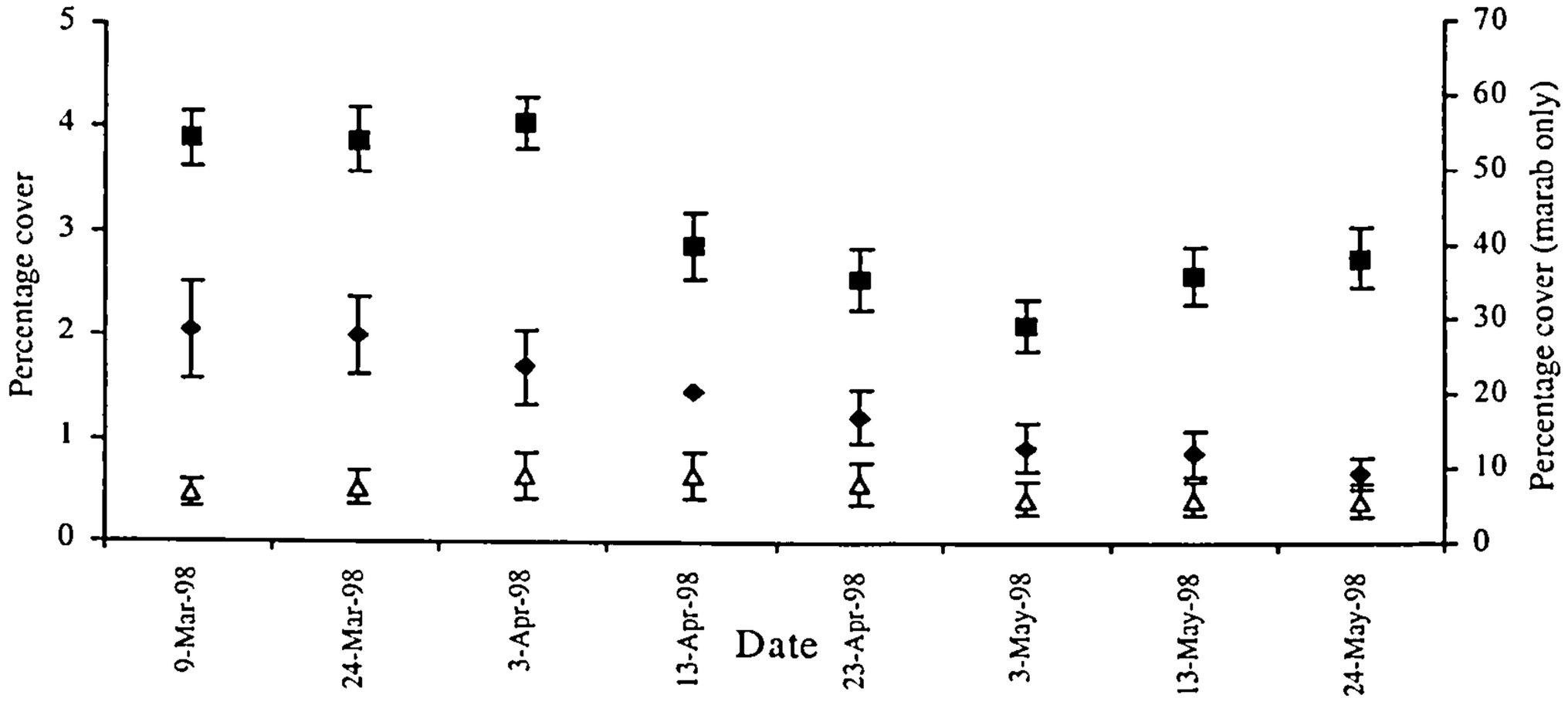
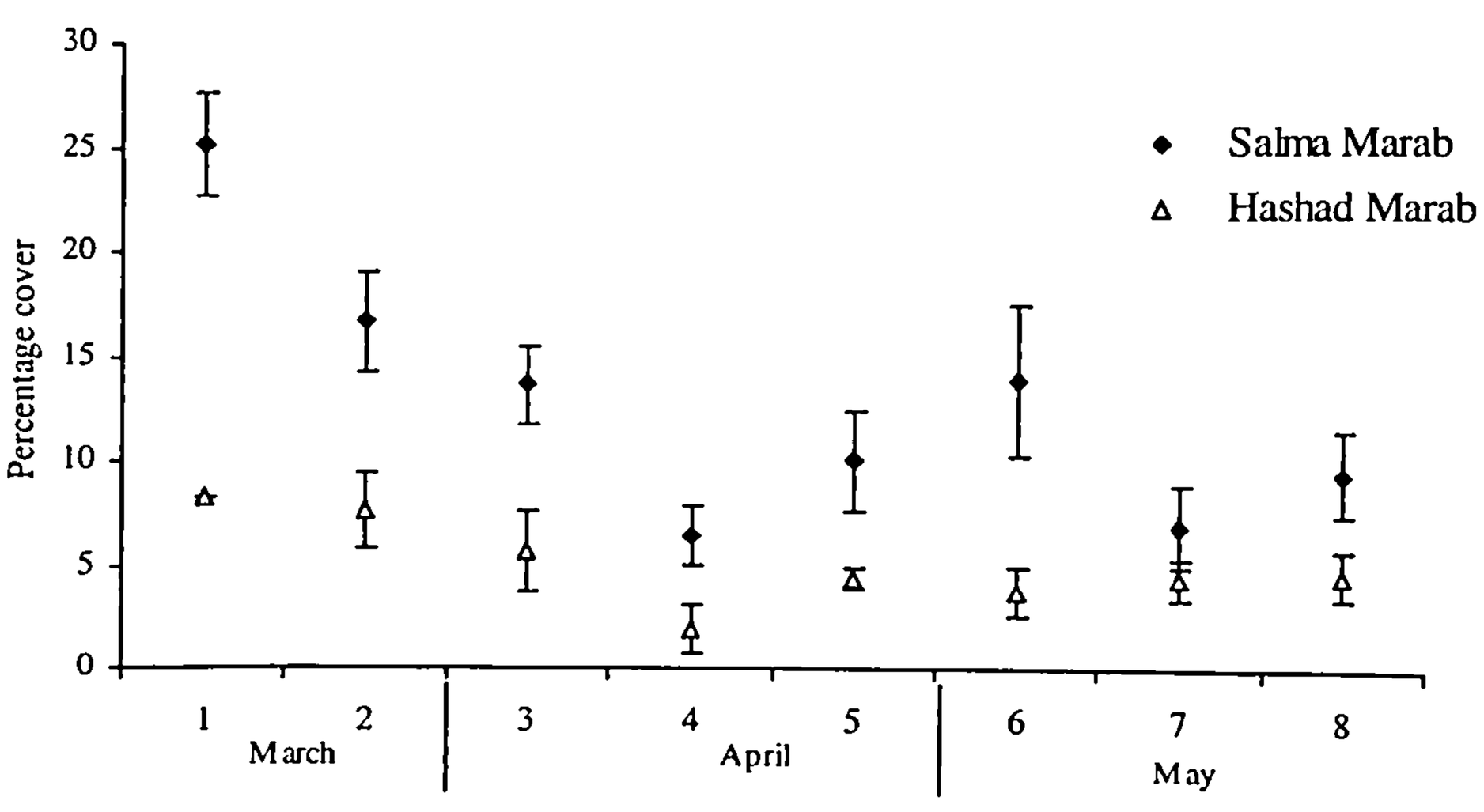


Figure 3.3c Perennial cover in marab at Salma and Hashad



despite all three habitats showing equivalent levels of similarity in species composition (Table 3.6).

If changes in vegetation cover were solely dependant on species composition within a habitat type it would be expected that habitats showing high levels of similarity in species composition would show similar patterns of vegetation change. However, the results indicated that changes in cover by annuals were positively correlated between habitats at Hashad, (marab and harrat, $r = 0.821$, $P = 0.023$; marab and hammada $r = 0.991$, $P < 0.0001$; harrat and hammada, $r = 0.757$, $P = 0.049$), whereas at Salma, which possessed higher similarity in species composition, patterns of annual change were not correlated between habitats (marab and harrat, $r = 0.571$, $P = 0.180$; marab and hammada $r = 0.432$, $P = 0.333$; harrat and hammada, $r = 0.667$, $P = 0.102$).

Figure 3.3c shows the changes in cover by perennials in the marab habitats at both sites. At Salma there was a decrease in cover by perennials, on average 0.5% per day from the beginning of the study until mid April. Subsequently there was an increase in cover from <6% to 14% in the next 20 days, this was followed by a further decrease. Corresponding patterns of decrease in cover by perennials were recorded at Hashad, but fluctuations were less marked. Changes in perennial vegetation over time at the two sites were positively correlated ($r = 0.836$, $P = 0.019$). Cover by perennials was positively correlated with cover by annuals ($r = 0.857$, $P = 0.014$) at Hashad, but not at Salma ($r = 0.357$, $P = 0.432$). The results show that changes in vegetation cover between habitat types were correlated at Hashad, however, at Salma there are differences in the patterns of change of cover by annuals and perennials, which also differ between habitat types. This suggests that factors influencing vegetation cover differ between the two sites and between habitats within Salma.

At Hashad, periods of increased cover of annuals in early-April and mid-May appear to follow rainfall events (Figure 3.2). However, rainfall events occurring during April did not correspond to any subsequent increase in cover by annuals at Salma. On the contrary, at Salma there appeared to be a decrease in cover by perennials and annuals from late March to late April during 1998. These results indicate that, overall, habitat structure and vegetation abundance as determined by changes in vegetation cover are both spatially and temporally dynamic.

3.3.6 Vegetative biomass

Biomass measurements were used to quantitatively assess vegetative resource abundance between sites and habitat types. The monthly dry weight biomass estimates of new vegetation (g/m^2), for three habitats in Hashad and Salma (marab, harrat and hammada) are shown in Figures 3.4 a, b.

Annuals comprised a larger component of the overall above ground standing crop than perennials, with some habitats (hammada and harrat) containing no perennial biomass. In both sites the marab habitat had the highest overall biomass per m^2, whereas hammada tended to have the lowest. Generally observations followed those expected from estimates of percentage cover by vegetation (Tables 3.7 & 3.8), with the exception of the marab at Hashad, which held a greater biomass of annuals than perennials, and the harrat at Salma, which had a greater biomass of annuals than Hashad harrat.

Data were not normally distributed (Kolmogorov- Smirnov test: $P < 0.001$). There was a high statistically significant difference in biomass of annuals between habitats, in both sites (Hashad, $X^2 = 19.28$, d.f. = 2, $P < 0.001$; Salma, $X^2 = 29.02$, d.f.= 2, $P < 0.001$). Using Mann-Whitney U tests, biomass of annuals was also shown to be significantly different between sites ($U = 742$, $n = 60$, $n = 45$, $P < 0.001$), and biomass of perennials was also close to significance at the 95% level ($U = 1178.5$, $n = 60$, $n = 45$, $P = 0.052$). Salma appeared to be the more productive of the two study sites, with marab habitat at Salma containing ten times as much biomass per unit area of annuals in March than Hashad. The maximum mean biomass of annuals during the study period was three times greater at Salma than Hashad. These results corresponded with the findings for vegetation cover.

Overall biomass within a site did not vary significantly between months (Hashad, $X^2 = 0.26$, d.f. = 2, $P = 0.878$; Salma, $X^2 = 0.99$, d.f. = 2, $P = 0.607$, Kruskal-Wallis). Patterns of biomass tended to correspond to percentage cover estimates for both sites (Figures 3.3 a-c) with the exception of perennial biomass changes at Hashad, with the peak in biomass in April not reflected in the percentage cover (Figure 3.3c). The two sites do not show the same pattern of changes in biomass, suggesting that the factors determining biomass were not equivalent between sites.

Figure 3.4 Monthly green vegetation dry weight biomass estimates for perennials and annuals (g/m^2) in three habitats in a) Hashad and b) Salma during spring 1998 (n = 5 per habitat, S.E. bars are shown).

Figure 3.4a Hashad

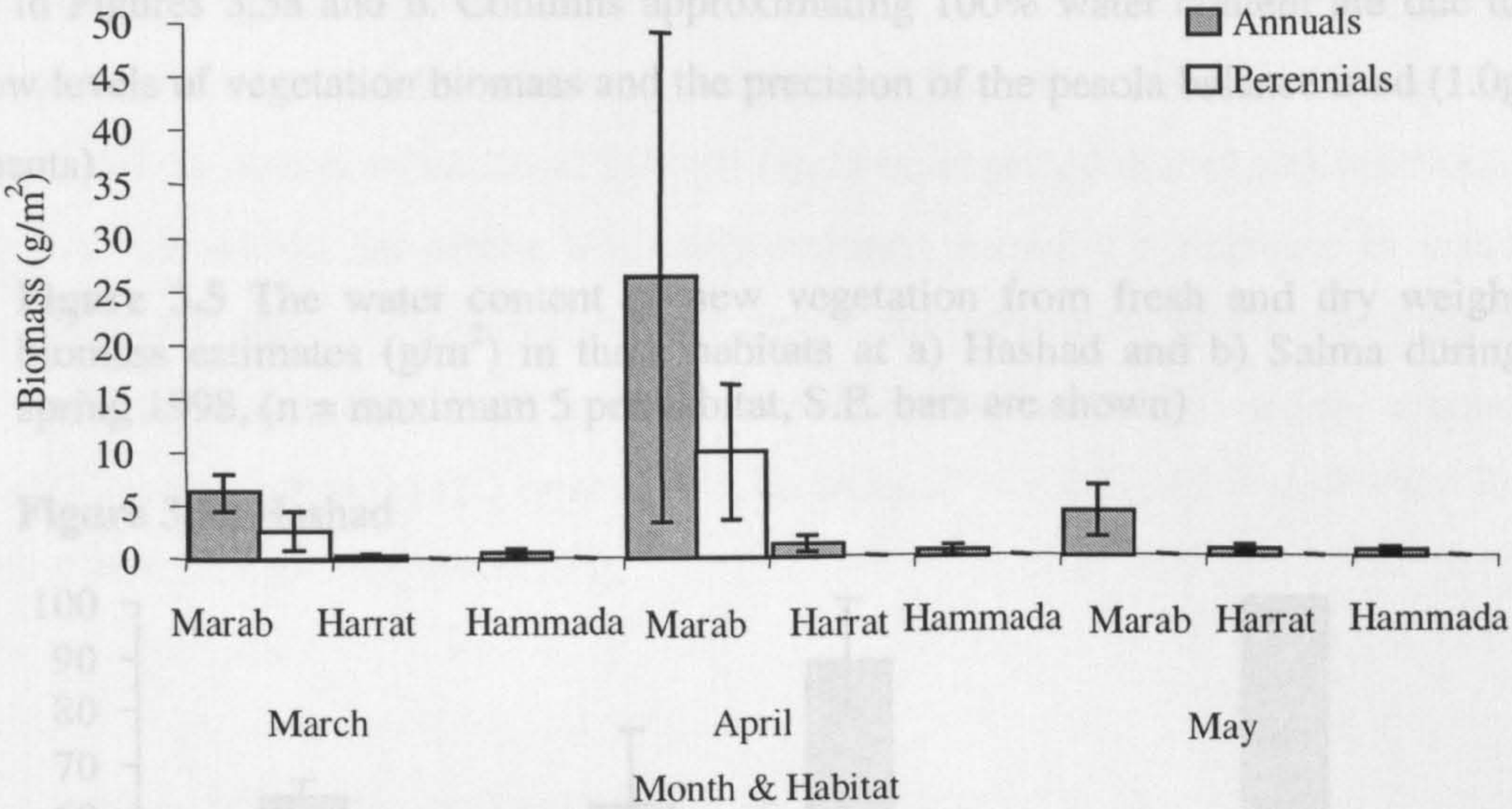
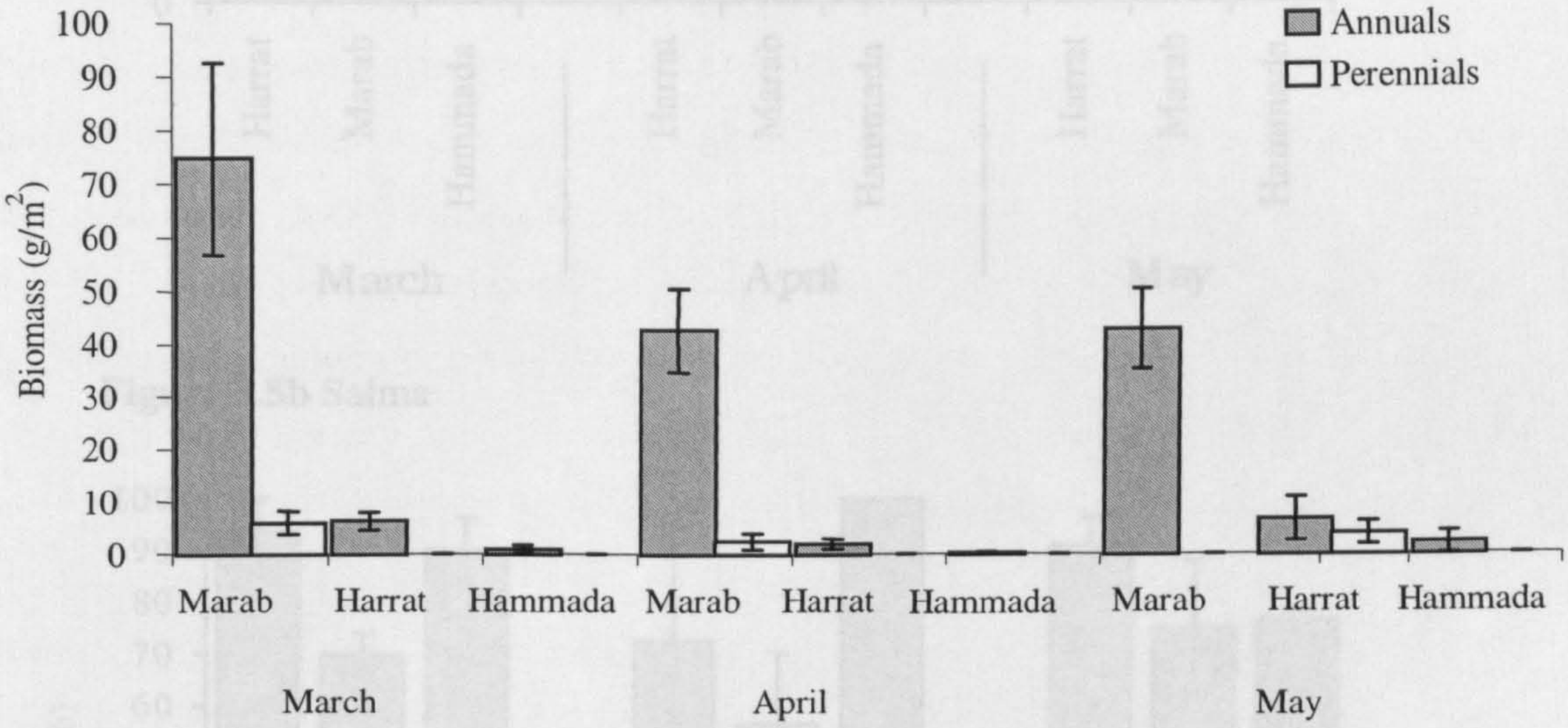


Figure 3.4b Salma



3.3.7 Water content of vegetation

The water content of new vegetation of annuals and perennials was estimated from the difference between wet and dry total biomass measured per unit area. The water content of vegetation in three habitats at Salma and Hashad for March, April and May 1998 are shown in Figures 3.5a and b. Columns approximating 100% water content are due to very low levels of vegetation biomass and the precision of the pesola balance used (1.0g increments).

Figure 3.5 The water content of new vegetation from fresh and dry weight biomass estimates (g/m^2) in three habitats at a) Hashad and b) Salma during spring 1998, (n = maximum 5 per habitat, S.E. bars are shown)

Figure 3.5a Hashad

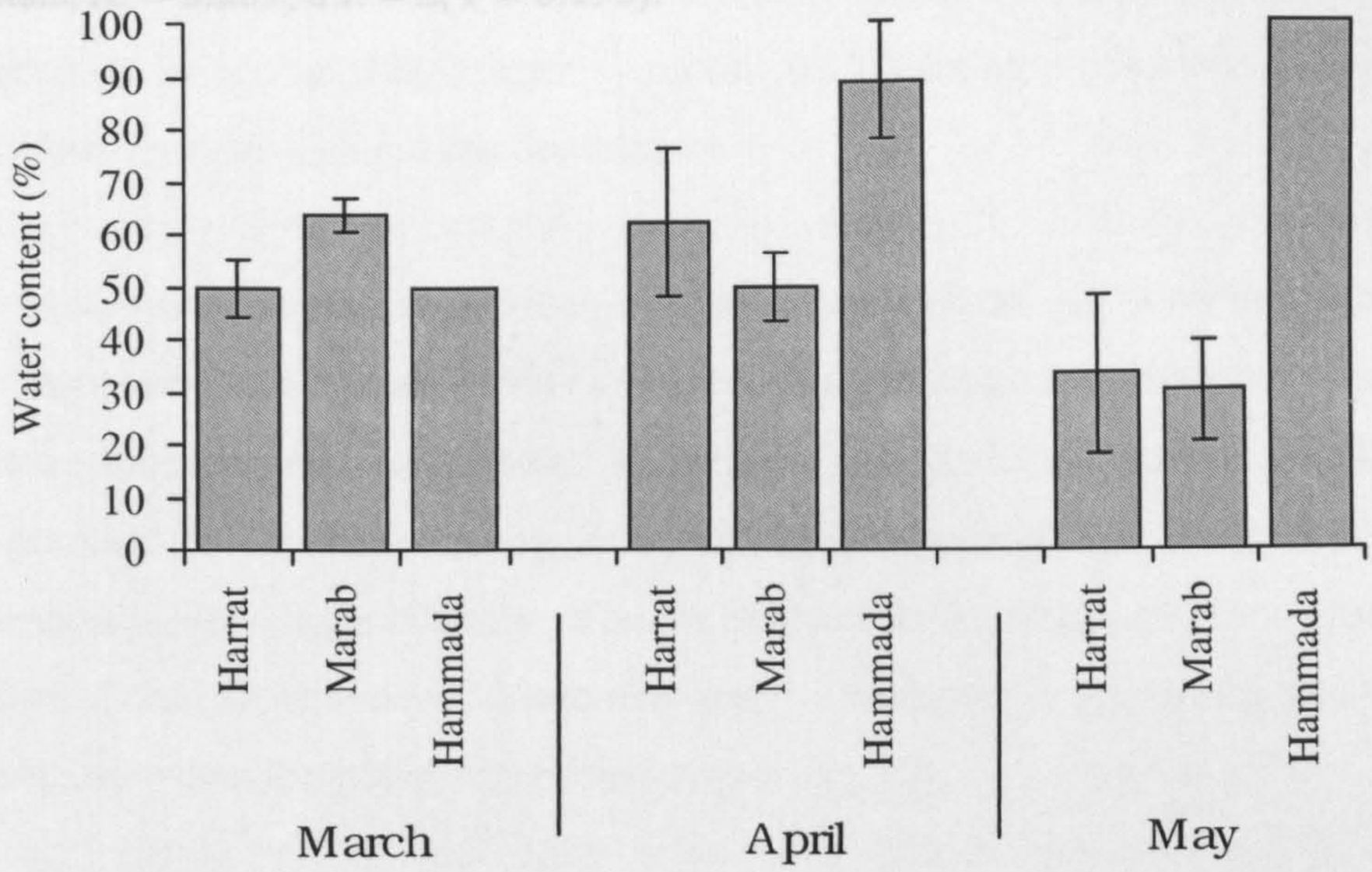
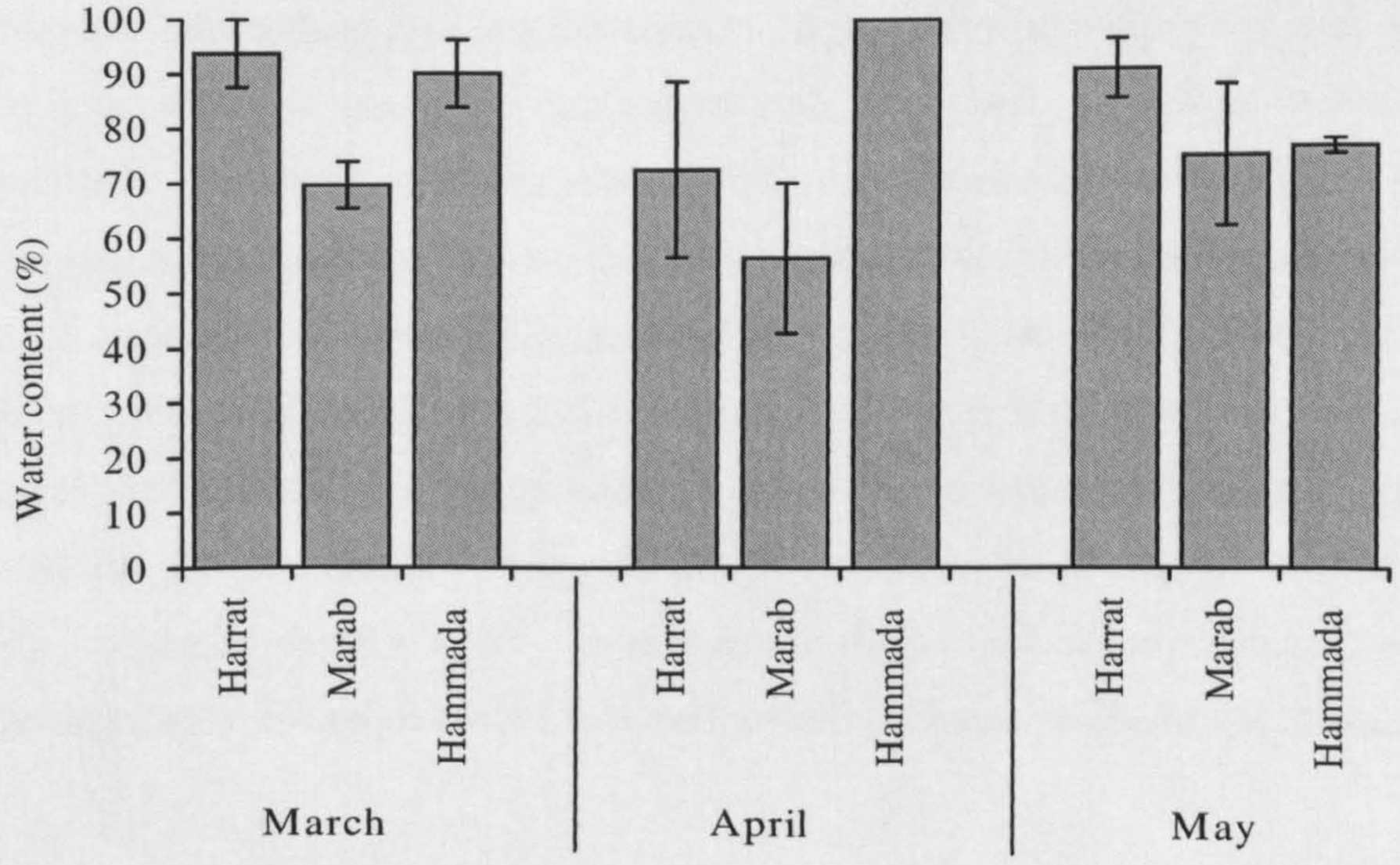


Figure 3.5b Salma



In some cases, vegetation cover was too low to obtain measurements of fresh biomass, hence results with no standard error represent single measurements, the validity of which is questionable. In general, water content appeared to be lower at Salma than Hashad (Mann-Whitney U test of median water content, $U = 15.5$, $n = 9$, $P < 0.05$). All estimated water content at Hashad were greater than 50%, whereas more than half the samples at Salma were between 30 to 50%. It might be expected that vegetation would start to dry out during the spring and early summer, showing a decrease in water content. However, there were no statistically significant differences in water content at Hashad between months ($X^2 = 0.27$, d.f. = 2, $P = 0.875$, Kruskal-Wallis) or habitat types ($X^2 = 4.356$, d.f. = 2, $P = 0.113$,) or at Salma (months, $X^2 = 0.800$, d.f. = 2, $P = 0.670$; habitats, $X^2 = 3.289$, d.f. = 2, $P = 0.193$).

3.4 DISCUSSION

3.4.1 Sampling

Cowlishaw and Davies (1997) emphasised the problems associated with spatial scale and species rarity in the study of desert plant communities. Given the limitations in patch size of homogeneous habitats and the number of available small mammal traps, the scale selected in this study was considered appropriate with respect to the habitat structure and to the cited home ranges for the species found (Harrison & Bates, 1991).

Resource sampling over two-years was initially proposed to enable year to year comparisons. However, due to an unpredicted political situation within the region, both study sites were subjected to varying levels of disturbance, which limited the possibilities of fieldwork. Therefore, a single study of resource abundance was undertaken in spring 1998, made possible by obtaining permission to work in a restricted site with minimal site disturbance.

Due to the size, structure and nature of the wadi habitat, i.e. a narrow occasionally flooding riverbed, it was excluded from investigations other than assessing plant species presence/absence and abundance. However, wadi habitats may be important in determining resource availability, as it has been suggested that they may contain a disproportionately large fraction of some resources (Kadmon, 1993). In future wadi habitats should be incorporated into investigations when it is practically feasible, i.e. in the summer when the possibility of flooding is less.

3.4.2 Habitat structure

Rock cover and soil properties influence vegetation abundance and composition, seed distribution and rodent foraging behaviour. High levels of rock cover will limit the space available for plants to germinate and may have an effect on increasing competition between species and therefore community composition. Ground temperatures are more consistent amongst rocks compared to open opens possibly because rocks act as wind shelters, reducing exposure and wind aided chilling and therefore providing some protection from harsh environmental conditions. For example, one study in Petra (Jordan) suggested that the microclimate within rocky habitats may account for the presence of species, which do not fit the present local climate (Danin, 1999). Loose soil depth was also greater in the harrat than other habitats (Table 3.3), which may be a consequence of low soil erosion. Deeper soils would favour deeper

rooting species, such as perennials (Gutterman, 1993), however this was not evident from the vegetation results (Tables 3.4 & 3.5) and it is likely that other factors, such as growing space, limit this. Both the harrat plain and the hammada are relatively flat, whereas the marab, due to its positioning in relation to surface water flow, encounters moisture more frequently and is the site of organic matter deposition (Dutton *et al.*, 1998). Both factors can influence vegetation composition and productivity (Beyer *et al.*, 1998; Kutiel, 1998).

Rock cover will have an effect on resource abundance and availability, as obstacles such as rocks, may enhance the catchment of seeds from the seed rain. Therefore, rocky habitats may have a greater seed density than predicted from seed crop estimates (see Chapter 4). The percentage of rock cover may also influence rodent community composition by restricting movement of larger bipedal species. This is possibly the reason why *Jaculus jaculus* did not occur in rocky habitats (Table 2.5). Basalt plains provide little refuge for rodents and may consequentially pose a greater predation risk (Abramsky *et al.*, 1990). However, rocky slopes, particularly upper slopes, tend to have piled rocks in which spaces could act as refuges for rodents and these areas appeared to possess a higher rodent species density and richness compared to the harrat plains (see Table 5.6).

In comparison with harrat, marab and hammada had relatively low rock cover, with the hammada being mostly devoid of rocks and vegetation (Table 3.7 & 3.8). Therefore hammada habitat would provide little protection from the environment, making it prone to soil erosion, which would influence the vegetation abundance and composition. To rodents hammada habitats provide low resource availability and minimal cover as protection from predation. However, due to the lack of obstructions, the area would be easier to transverse for bipedal rodents. From the loose soil depth measurements alone, it is difficult to conclude if a habitat is suitable for burrowing, however burrows tended to be more abundant in the hammada than in other habitat types (personal observations). Marabs generally possess high cover by perennials (Table 3.8), which would facilitate seed catchment (see Chapter 4) and act as protective cover against predation.

3.4.3 Vegetation composition and abundance

Total vegetation cover by all plant species varied between habitats, within sites and between sites. This may have been a result of large and small-scale spatial differences in

water resources and soil types. Cover provided by annuals varied less between sites than the total vegetation cover, particularly in the harrat and hammada habitats that had relatively low cover by annuals in both sites (Table 3.3).

Habitat types vary in water availability, structure, topography, organic content of the soil and nutrient availability, which have all been demonstrated to influence plant community composition and abundance. It would be expected that habitat types demonstrating similar attributes and lying within a single geographic region would possess similarities in community composition. However, it is clear from Tables 3.4 and 3.5, that this is not the case. In general, less than half the species occurring in one habitat at one site occurred in the same habitat at the other site (Table 3.6). Habitats within sites showed a greater similarity in species composition than between sites. This suggests that either, some plant species are restricted in their geographical range and distribution (Gutterman, 1993), or apparently similar habitats were not comparable between sites. Underlying factors influencing plant communities may not be immediately obvious, i.e. Salma is a steep banked wadi system, and it is suggested from vegetation abundance that this site probably experiences a greater water flow than Hashad. Larger scale parameters such as topographical features, water table or soil profiles may also cause differences in vegetation composition between sites. This illustrates the problems associated with scale when trying to define and investigate habitats.

Habitat types varied in plant species richness, with wadi and marab being the most rich (Tables 3.2 & 3.3). Both wadi and marab habitats are prone to short-term flooding, during which organic matter and seeds are carried down the wadis and deposited in the marab habitats. Therefore water flow and seed redistribution may partially account for the high species richness observed in these habitats.

Competition between plants may influence community composition, for example the marab at Salma is dominated by the perennial *Artemisia herba-alba*, which is known to compete intra- and inter-specifically for space and resources (Gutterman, 1993). Within the marab at Hashad this species was less abundant (Tables 3.7 & 3.8), which may account for the higher numbers of perennial species found.

The classification of vegetation into annuals or perennials depending on temporal availability is very broad, as some species do not fall exclusively into one category. For example, the perennial *Diplotaxis hara* is dependant on favourable weather conditions to enable it persist throughout the year (Gutterman, 1993). The timing of appearance, growth and persistence of other species also varies. For example, some annuals appear during the winter when conditions are suitable for seed germination and development, whereas others germinate during the winter, but do not fully develop into the adult form until the summer (Gutterman, 1993).

Grazing is thought to be an important determinant of the regional vegetation composition in Middle Eastern deserts (Gutterman, 1993). In a reserve within the Badia region (Shaumari), prevention of grazing resulted in an immediate increase in primary productivity and species richness of vegetation (Al-Eisawi & Hatough, 1987). Native ungulates (e.g. Ibex) show selective browsing and in good winters concentrate foraging efforts on annuals, which will consequentially reduce herbivory on perennials (Hakham & Ritte, 1993). Therefore, selective herbivory may be another factor that could potentially contribute differences in cover by perennials and annuals. Herds of Bedouin goats and sheep were recorded at Salma from early April until late April/early May 1998, which corresponded with the decrease in overall vegetation cover at Salma and therefore could be a possible explanation for this. The different grazing pressures between the two sites may account for site differences in vegetation cover. Grazing pressure between habitats may also account for the lack of correlation in vegetation cover between habitats at Salma, as grazing appeared to be concentrated more in the marab than in the other habitat types.

3.4.4 Rainfall

Results showed that rainfall measurements differed between closely located sites, therefore to enable investigation of the effects of precipitation on the timing and extent of resource abundance, it should be recorded accurately at each site. Furthermore, soil topography can determine water availability through surface and sub-surface flow, hence soil moisture within habitats and microhabitats should also be considered. In my study, the methodology for measuring rainfall within habitats was flawed due to the higher evaporation rates associated with increasing temperatures. Alternative opportunistic observations of rainfall (Figure 3.2) were inaccurate, as they were estimated on an arbitrary scale, not specific to an individual site or habitat. Rainfall may

have gone undetected if occurring during the night. Therefore, values were used only for comparing spatial differences in the measured and observed rainfall and to comment on the timing and duration of the rainy period.

In general, estimates of vegetation cover of annuals decreased during March 1998, then showed a small increase during April (Figures 3.3). These observations suggest that during winter of 1997-8 the maximum cover of annuals occurred prior to March, which would also correspond with rainfall measurements (Figure 3.1). Above average rainfall occurring during October, November and January, would hypothetically result in above average vegetation. Lower than average monthly rainfall during February and April, coupled with increasing temperatures may explain the low and generally decreasing vegetation cover, recorded for both annuals and perennials. The increase in cover in late April may be a result of the rainfall observed during late-March or be a consequence of changes in plant composition. The timing of growth varies between species and individuals (Gutterman, 1993) and therefore species contributions to the cover by annuals vary over time (personal observations).

Overall, vegetation cover by annuals and perennials varied in parallel at Salma and Hashad, suggesting that environmental conditions influencing temporal changes were similar between sites. However at Salma temporal changes in annual vegetation cover were not correlated between habitats, which suggests that other factors, such as resource availability within a site, may influence vegetation cover.

3.4.5 Biomass

There were significant differences in the vegetation biomass per m^2 between sites and between habitats (Figures 3.5a & b). Total above ground plant biomass corresponded to changes in vegetation cover (Fig 3.3), which suggests that measurements of cover can give direct indications of the relative amounts of dry weight of vegetation. Statistically, there were no significant differences in the monthly dry weight biomass in either habitats or the two sites during the study period in 1998. The difference in water content of vegetation between sites may be a result of differences in ground water influenced by site hydrogeology. Water content of new vegetation did not vary between habitats suggesting that larger scale water availability rather than differences in species composition, levels of plant competition or water availability between habitat types determines the water content of vegetation. Water content did not vary between months

suggesting that 'drying', which tends to occur towards the summer months was not significant during the study period in 1998. Again, this could be the result of the unusually long rainfall period observed (Fig 3.2).

Annuals formed the greatest proportion of biomass in all habitats. If rodent diet were related to resource abundance, annuals would form a larger component of diet at this time of year. Selection of habitat type during foraging will influence vegetative resource availability, but the water content of vegetation did not vary between habitat types. However, preferences for particular plant species during foraging may determine water acquisition, as some species will be more succulent than others (Gutterman, 1993).

From estimates of vegetation undertaken in 1998, marab habitats had the most vegetation cover, which was predicted to be at a maximum in late winter and possess the highest cover of permanent vegetation. Perennials, as a food source, may be more important during the late summer and autumn, when annuals are generally absent or scarce. Krasnov *et al.* (1996b) showed habitats with more shrub cover were utilised by rodents more in the summer, whilst habitats with high cover by annuals were utilised in the winter. Preliminary radio-tracking studies of *M. crassus* in Hashad during the summer of 1996 showed no apparent preference of animals for the marab habitat, which had the highest cover by perennials compared to other habitats (Maddox, pers. comm.). This suggests that habitat preferences during foraging may not be solely determined by vegetation availability. An additional investigation into habitat preferences was planned for spring 1998, however due to problems obtaining equipment and permission, this had to be forgone.

In summary, vegetation abundance and composition varies between and within sites. Rainfall, habitat structure, grazing pressure, soil properties and water table have been suggested to be potential causes for the spatial and temporal variability in vegetation abundance. It is suggested that during the 1998 study, there was a lower, but temporally extended, abundance of vegetation, which would have influenced rodent diet and consequentially may have led to physiological effects, if rodents require vegetation for breeding, juvenile development and/or survival.

CHAPTER 4: SEED ABUNDANCE

4.1 INTRODUCTION & OBJECTIVES

This chapter addresses the spatial and temporal abundance of seed sources as a food resource for desert rodents. Sources of seeds available to granivorous rodents will be distinguished, where a 'source' of seed denotes a particular stage in the life history of a seed in relation to its locality i.e. seeds on parent plants are considered a different 'source' from the seeds in the desert soil. Factors determining the abundance of seed sources will also be investigated.

4.1.1 Sources of seeds

Seed abundance in deserts is dynamic. To determine the temporal and spatial availability of seeds to rodent predators, 'sources' of seeds and the factors influencing them must be considered simultaneously. Simplistically, the life history of a seed can be divided into four stages: production, dispersal, dormancy and germination. Each stage is influenced by a combination of many factors, biotic and abiotic. For rodents, seed production, dispersal (seed rain) and dormancy (soil seed bank) represent potential sources of food and methodologies have been developed to quantify each (e.g. Price & Joyner, 1997). Annual seed production or seed crop, as defined by the number of seeds produced by plants in a given area during one year, is the origin of the majority of seeds found in seed rain and for the seed bank. Seed production is also important as an independent resource, as rodents have been reported to collect entire fruits and seed heads directly from the plants (Lemen, 1978). Seed rain is the proportion of seeds that reach the soil surface through dispersal and many granivores utilise this resource before excavating buried seeds (Lemen, 1978; Price & Joyner, 1997). The soil seed bank, for the purpose of this study, is defined as the total number of seeds found within the soil that are accessible to the predator (Brown *et al.*, 1979). This will be a combination of aerial and serotinous seeds from the transient and persistent seed banks.

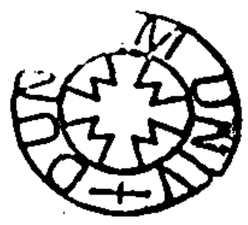
Seed production in a given area does not necessarily feed directly into the seed rain of that same area. The proportion reaching the ground will be dependent on the mechanism of seed dispersal. Some seeds are not dispersed but retained on the parent plant (serotinous). Also, not all of the seed rain is transferred to the seed bank, because some seeds either are harvested or die soon after dispersal. Independent studies of one

'source' may give a distorted view of the actual abundance of seeds to rodent consumers (Price & Joyner, 1997). For example, *Medicago laciniata* is a desert annual that retains seeds on the parent plant for some time after seed maturity (Gutterman, 1993). Hence, this species does not appear regularly in the seed rain. However, it is known to occur later in the year in the seed bank. Mass accumulations of *M. laciniata* seed cases have been found outside burrows of rodents (personal observations), suggesting that this species could be a locally important food source. Seeds would not be recorded in studies of the seed rain and would be under-represented in temporal studies of the seed bank.

Most investigations of seed resources have been limited to seed bank measurements (Nelson & Chew, 1977) and the overall abundance to granivores has occasionally been inferred from this 'source' alone (Marone & Horno, 1997). Estimates of seed production which are restricted to one plant species or family provide little information on overall seed abundance in a desert habitat (Narita, 1998). Studies that investigate different potential 'sources' of seeds are more informative and it has been suggested that annual seed production measured as seed rain, may be more important food source for rodents than the seed bank (Price & Joyner, 1997). To date there have been no published studies which have simultaneously investigated all potential forms of seed resources available to rodents in deserts. In this study I adopted a systematic approach to resource quantification to achieve a better understanding of seed resource abundance and the potential implications to desert rodent ecology.

4.1.2 Seed production in desert plants

Seed production is directly and indirectly dependent on the number of reproductive plants per unit area (Morgan, 1999); therefore factors influencing vegetation (see Chapter 3), such as rainfall, temperature and photoperiod, will be important in determining the seed crop (e.g. Ridha *et al.,* 1998). As might be expected, the monthly and yearly patterns of precipitation can cause dramatic temporal variations in the seed crop (Brown *et al.* 1979). In one Israeli study, six times as many seeds set in a year with high rainfall compared to a year with below average rainfall (Gutterman, 1989 in Gutterman, 1993). Water and nutrient availability to parent plants at the times of seed production may result in temporal and spatial differences in the seed crop. In the desert annual, *Blepharis sindica*, plant age, size and the timing of growth were influenced by rainfall, which affected the timing and output of seeds. Earlier germination as a result of rainfall also leads to higher reproductive success (Narita, 1998). Habitat topography,



such as depressions and wadis can facilitate water availability to plants and indirectly increase seed output (Kadmon, 1993). Water availability has been shown to affect seeding parameters, such as number of flowers (Milton, 1995) and seed mass (Gunster, 1994). Increased nutrient concentrations found in the soil of ant burrows were thought to have an indirect beneficial effect on seed output of plants growing in the vicinity (Wagner, 1997). Biotic factors also play an important role in determining the absolute size of the seed crop. In the South African Karoo Desert, selective herbivory during flowering resulted in a 40% decrease in the number of potentially viable seeds produced (Milton, 1995), and in the Namib Desert 25% of seeds on parent plants were lost to coleopteran and dipteran larval predation (Gunster, 1994).

4.1.3 Seed rain

The seed rain is dependent on seed production and dispersal of seeds to the soil surface. Temporal variation in seed rain tends to correspond to the timing of seed maturity (Price & Joyner, 1997), however, the timing of seed drop after maturation can vary considerably between species and individual plants (Bai & Romo, 1997). Many desert plant species have evolved anti-granivory mechanisms to aid seed survival. Mechanisms such as prolonged dispersal time, retention on the parental plant and production of large numbers of small seeds represent an attempt to prevent seed clumping and therefore reduce predation risk (Reichman, 1979). Although details of all seed dispersal mechanisms for the Badia region are not available, studies undertaken in the Negev desert, Israel (Gutterman, 1993) provide information on dispersal techniques which can be applied in part to the study area.

The majority of plant species found in the Negev, particularly annuals, produce large numbers of small seeds that mature and disperse at the beginning of the summer (May/June), depending on the timing and extent of winter rainfall. Most perennials tend to produce larger seeds later in the year (July to August) and in a few species, e.g. *Artemisia herba-alba,* seed maturation and dispersal occurs in winter, close to the timing of seed germination, hence reducing seed predation. Some species found in the Negev do not shed seeds directly after maturation but retain them on the plant as means of protection from granivory; these seeds may be dispersed later, e.g. *Trigonella stellata* (Evenari & Gutterman, 1976 in Gutterman 1993), or germinate in situ, e.g. *Emex spinosa* (Evenari *et al.,* 1977). Desert plants have several seed types and dispersal mechanisms; indeed each species may produce several forms of seed (heterocarpy) with

different morphologies and/or dispersal properties. Heterocarpy is particularly common in the families of Asteraceae, Umbelliferae and Cruciferae (Zohary, 1962). Seed dispersal may be of single or groups of seeds, e.g. *Bromus* spp. disperses a spikelet containing three seeds.

The types of mechanisms employed to disperse seeds from the parent plant will also heavily influence which seeds reach the soil surface. In semi-arid central Tanzania, wind-dispersed seeds dominate the density and diversity of the observed seed rain (Lyaruu, 1999). Negev desert plants employ many different dispersal strategies and for wind dispersal alone, 14 different mechanisms have been identified. Examples of species found in my study area using passive dispersal by wind (see Tables 3.2 & 3.3), include *Diplotaxis hara*, which produces masses of light-weight seeds designed for transportation in the air; *Calendula* spp., which possess wing-like structures (cymbiform achenes), that aid wind propulsion across the soil surface, and *Papaver* spp. from which seeds are shaken free by the wind after capsule dehiscence. Seed dispersal by rain (ombrohydrochory) is exhibited in *Anthemis pseudocotula,* where the seed capsule degenerates under mechanical pressure from the rain, and in *Trigonella stellata* which possesses hydrocastic pods that open to release seeds after wetting. Ants (Heithaus, 1981) and mammals (Izhaki & Neeman, 1997) have also been identified as dispersal agents, for example, the desert hare (*Lepus capensis*) aids dispersal of *Retama raetam* by consuming seedpods and defecating viable seeds. The diversity of dispersal mechanisms and the potential factors that influence the size and distribution of the seed rain emphasise the need to consider species composition in investigations of seed sources. After dispersal, seeds tend to accumulate in wind shadows and rain-water collection sites or under obstructions, e.g. vegetation (Nelson & Chew, 1977), or in crevices, cracks or depressions in the soil (Kemp, 1989). Following dispersal, habitat structure affects the spatial distribution of the seed rain. Variation in the species composition of the seed rain results from the differential impact of wind and rain on different types and species of seeds depending on their morphology (Marone *et al.*, 1998).

4.1.4 Seed bank

Analysis of the seed bank has been the focus of the majority of studies investigating resource abundance to granivores (e.g. Price & Reichman, 1987; Price & Joyner, 1997; Marone *et al.*, 1998). Maximum seed bank densities reported for North American hot

deserts fall within the range of 8000-30,000 seeds/m^2 (Kemp, 1989). The annual seed production of the Negev desert is reported to be similar to that of North American deserts (Gutterman *et al.*, 1982 in Gutterman, 1993). However, the density and composition of any one desert seed bank is highly variable both spatially and temporally (Kemp, 1989). This is possibly due to the array of factors which directly and indirectly govern seed bank additions (seed production and seed rain), redistribution (soil erosion and granivory) and depletion (granivory, fungi, death and germination).

The relative abundance of species in the seed bank varies spatially, but generally it tends to be dominated by the small seeds of annuals (Bertiller, 1998). Brown *et al.* (1979) estimated that annual species comprise 95% of total seed number and 80% of biomass of the desert seed bank. Hence perennials with large seeds are found in lower abundance in the seed bank (Guo *et al.*, 1998). The size-frequency distribution of the seed bank is in part the result of factors influencing the potential input. For example, larger seeds comprised a greater proportion of the seed rain than of the seed bank, suggesting that these seeds were depleted more heavily by predation than were smaller seeds before they entered the soil (Price & Joyner, 1997).

Germination has been reported to account for up to 25% of the annual seed losses from the seed bank alone (Nelson & Chew, 1977). Differential timing of germination will affect the species composition of the seed bank. Hence factors affecting germination should also be noted as minor determinants of seed bank composition. Timing of seed germination is species dependent and determined by environmental conditions experienced at the time of seed maturation and germination, i.e. temperature, rainfall and day length (Gutterman, 1994). Additionally, 'heteroblastic' responses of species to environmental conditions cause differences in seed germination timing within a species (Gutterman, 1994).

Seed bank densities in deserts possesses a high degree of variability as a result of the temporal and spatial factors which influence the seed crop and seed rain (Kemp, 1989). The phenomenon of seed aggregation in the seed rain is reflected in the spatial heterogeneity of the seed bank (Price & Reichman 1987) and the majority of seeds are found near the soil surface (Gutterman *et al.*, 1982). In the Sonoran desert of North America, 89% of seeds were found within the top 2cm of the soil (Childs & Goodall, 1973) and densities decreased with increasing soil depth (Guo *et al.*, 1998). As

expected, densities are highest after seed production, decreasing in subsequent months to be at their lowest during the growing season (Aziz & Khan, 1996; Jansen & Ison, 1996). A four-fold increase in seed density was observed between successive months at a time of seeding in New Mexico (Kemp, 1989) and a 23 –fold annual difference reported from the Mojave Desert (Nelson & Chew, 1977). However, temporal variation in the seed bank has been reported to be less than for the seed rain (Price & Joyner, 1997).

In summary, seeds are an important potential food resource for desert rodents and rodent-seed interactions are potentially important processes in desert ecosystems. There are three 'sources' of seeds available to rodents: seed production, seed rain and seed bank, each influenced by a different complement of environmental and non-environmental factors, and each in turn influencing the density and species composition of seeds present in the next stage of the seed life cycle.

4.1.5 Objectives

The objectives of the work described in this chapter are i) to quantify the spatial and short-term temporal abundance of three potential 'sources' of seeds; seed production, seed rain and seed bank, in representative habitats and ii) to investigate seed resource dynamics by comparing biomass, species composition and seed size distribution of the different seed sources, and hence to assess their potential importance as a food resource to rodents. The results are compared with those from other deserts and discussed in relation to their influences on foraging behaviour, rodent density and community composition.

4. 2 METHODOLOGY

4.2.1 Study sites and samples

Study sites and sampling grids used to assess seed resources were the same as those used in vegetation studies (see Chapter 3, Table 3.1). Temporal replicates were taken at 10-day intervals throughout the three-month study period in 1998, concurrent with the vegetation surveys.

4.2.2 Timing and output of seed production

To determine the amount of seed production in each sample grid, in terms of numbers and biomass of each species, two estimates were made i) the density of plant species present in each of the grids; ii) the mean number of seeds produced per plant Multiplication of these values was then used to estimate seed production (Mallik *et al.*, 1984).

4.2.2.1 Density estimates

The abundance of each species present in four habitat types (marab, harrat, hammada and wadi) at the two sites, Salma and Hashad, was assessed initially by visual observation and encounter rate. The three categories of abundance defined were: 'rare', 'occasional' and 'common' (see Tables 3.2 & 3.3). Species encountered were identified in the field where possible (Zohary & Feinbrun-Dothan, 1987) and voucher specimens were taken to confirm identification. At the approximate peak seeding time (early May) the densities of 'common' and 'occasional' species were estimated by counting the number of individuals of each species in five, $1m^2$ randomly selected quadrats within a homogeneous habitat type in each of the four habitat types at the two sites. Only abundant species were studied in this investigation as it was assumed that rare species contributed little to seed production in terms of biomass.

4.2.2.2 Seed reference collection

A seed reference collection was compiled to measure seed parameters and to facilitate identification of seed rain and bank samples. A minimum of 10 pre-dispersed seeds was harvested from 10 different plants of each species (sample size was considered to be adequate to incorporate potential size variation, given the scope of the investigation). Samples were stored in vials labelled with site, date and species. All seed samples collected from the field and found in subsequent seed extractions (see later) were

identified where possible (Beijerinck, 1947; Zohary & Feinbrun-Dothan, 1987). Seeds were measured under a dissection microscope and weighed (mg) (Oertling balance). As seeds of some species were too light to be measured individually, calculations of average individual seed weight were made from multiple seed measures. *Astragalus spinosus* seeds were too immature at the time of study to be sampled and so seed weight was estimated from seed size ranges found within the genus *Astragalus* (Beijerinck, 1947).

4.2.2.3 Seed output

The specific methodology used to assess seed output per plant species depended on the individual species' morphology. In general, a 'random walk' was undertaken within a site, irrespective of habitat type. Every 5th adult plant encountered during the walk was selected as a sample, with ten plants per species being sampled in total. For each sample the number of seeding structures per plant was counted, together with the number of seeds found in one randomly selected seeding structure, e.g. pod. Occasionally, the number of seeds per plant could be recorded directly. It was assumed that seed production was not influenced by habitat type. The seed production density (SPD) was calculated by multiplying the mean number of capsules per plant by the mean number of seeds per capsule. The seed production biomass (SPB) per plant was calculated by multiplying the seed production density by the mean seed weight of the relevant species obtained from the seed reference collection (4.2.2.2). The average seed production for each plant was then multiplied by species density to give estimates of seed crop in terms of density (no/m^2) and biomass (mg/m^2), for each plant species in habitat type at each site. These quantities could be summed to give overall estimates of seed crops.

4.2.2.4 Timing of seeding

The sexual status of all commonly occurring species was recorded at 10-day intervals from mid-March to late May 1998. In each study site, ten individuals were selected randomly and irrespective of habitat type, i.e. the status of every 5th individual plant encountered whilst undertaking a 'random walk' was recorded. Plant status was classified into one of the following groups: non-reproductive, flowering, seeding or dead. Categories were not mutually exclusive and habitat type of each plant examined was also noted.

4.2.3 Seed rain

Seed rain is usually measured by creating an artificial depression attached to a seed trap (e.g. Price & Joyner, 1997). The trap design depends on size and dispersal process of the plants under investigation, but, in general, it is recommended to keep seeds separated from other debris, to protect them against seed predation and to ensure dry preservation of the sample (Kollmann & Goetze, 1998).

Five sampling stations positioned at 10m intervals were set up along a transect, situated in homogenous habitat 10 m to the east of each sample grid (H1, MARAB & HARRAT at Hashad, and all three grids at Salma). Two seed rain traps were set per station placed approximately one metre apart. Where possible, one trap was set close to cover and the other in the open. Seed rain traps were a modified design of those used by Price & Joyner (1997). Traps were constructed from plastic cups (7.8cm depth, 7.5cm diameter) with plastic funnels. Funnel entrances were approx. 1cm diameter to allow seed entry but prevent granivory by insects and rodents. Rims were sealed using "Parafilm" and/or sticky tape. Holes were punctured in the bottom of the traps, large enough to allow water to drain but small enough to prevent loss of seeds (see Figure 4.1). Traps were submerged into the soil leaving a rim of 0.5cm above the ground level to prevent soil and insect entry. Seeds were collected from the traps every month, placed in a labelled envelope and air-dried for one week. Traps that were unearthed by either wind, human or animal disturbance had their samples discarded (Price and Joyner, 1997). Samples were examined in the laboratory under a dissecting microscope at x 4 magnification. All potentially viable seeds (those that did not crumble under forceps pressure) greater than 0.2mm in size were removed from the sample, counted and identified where possible using the reference collection and literature (Beijerinck, 1947: Zohary & Feinbrun-Dothan, 1987). Voucher specimens of seeds were also collected.

The seed rain density (**SRD**) and seed rain biomass (**SRB**) were calculated using formulas in equations 4.1 and 4.2 respectively.

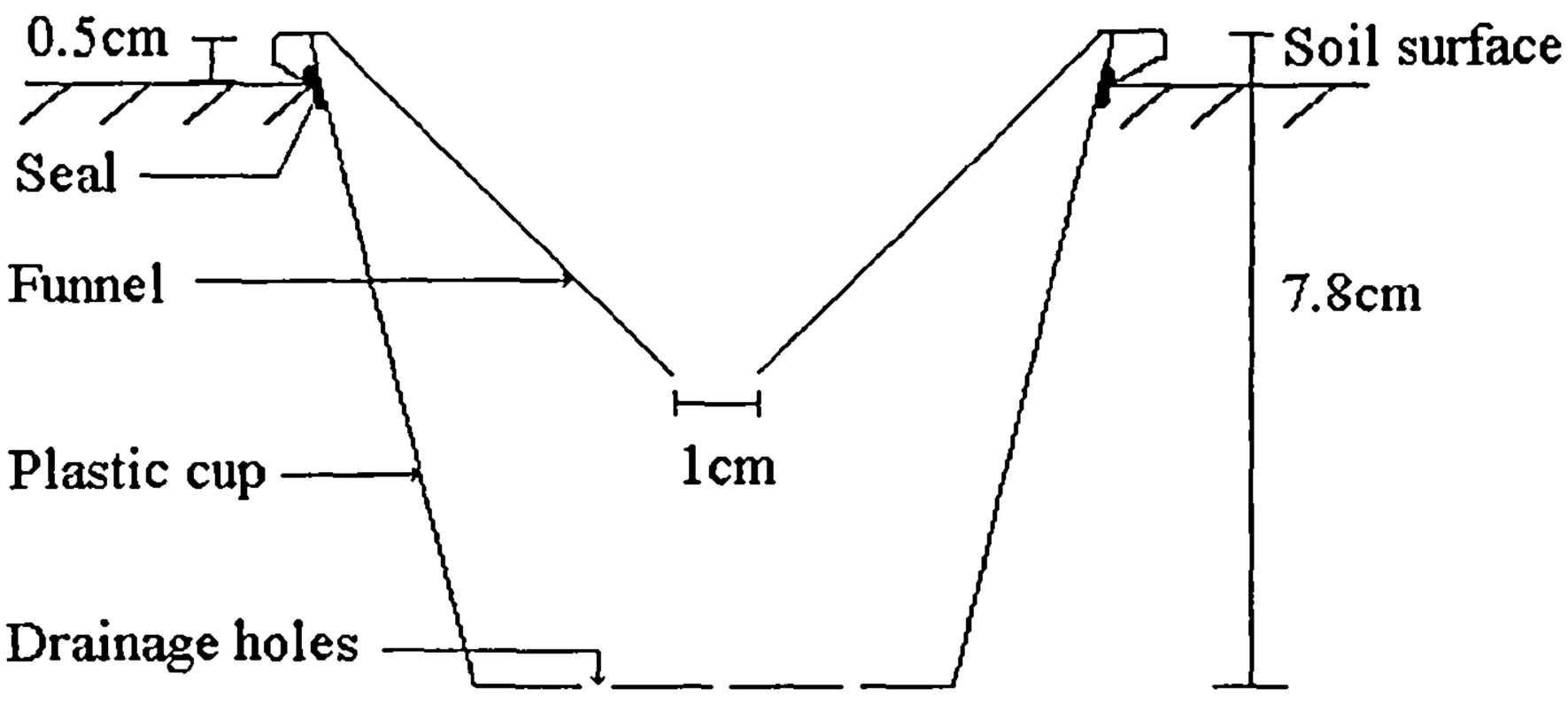
$$\mathbf{SRD} = \frac{\mathbf{(N^* K)}}{\mathbf{D}} \qquad \text{Equation 4.1}$$

where **N** is the number of seeds in the sample. **K** is a constant (226.35) derived from the diameter of the collecting vessel to convert values to numbers per m^2 and **D** is the number of days in the sampling period.

$$\mathbf{SRB} = \frac{\mathbf{(\Sigma\,(n * \overline{M}))^* K}}{\mathbf{D}} \qquad \text{Equation 4.2}$$

Where **n** is the number of seeds of a particular species in the sample. $\overline{\mathbf{M}}$ is the mean seed weight of that species obtained from the seed reference collection. **K** and **D** are as in Equation 4.1.

Figure 4.1 Diagram to show seed trap design (modified from Price and Joyner, 1997).



4.2.4 Seed bank

4.2.4.1 Collection of soil samples

Five soil samples were collected at monthly intervals from areas close to the same grids as used in the seed rain studies. Sampling sites were chosen randomly by throwing a

coloured marker within 10m of the seed rain traps to ensure sampling sites were within the designated homogenous habitat type, but outside the grid parameter (Price & Joyner, 1997). Microhabitat was standardised as far as possible within the sampling locality by visual selection, i.e. similar distances from vegetation cover and micro-topography. Samples were taken using a soil corer (8 cm diameter, 2cm depth) pressed into the ground to 2cm depth. Each sample, of approximately 50cm^2 area and 100cm^3 volume was scooped out using a trowel, stored in a labelled bag, air-dried for 24 hours and weighed using a "Pesola" spring balance to the nearest gram. To remove the larger inorganic component, the samples were passed through a 2.0mm sieve. The retained fraction was searched to check no seeds had been separated out.

4.2.4.2 Seed extraction

Other workers have used several methods to assess the seed bank. Seedling emergence has been identified as a successful technique (Terheerdt *et al.*, 1996). However, in my study, seedling emergence was not employed, because little information on the germination requirements of some of the species likely to be found, and neither adequate information nor a reference collection to identify seedlings, were available.

A standard flotation technique (Nelson and Chew, 1977; Henderson *et al.*, 1988) was used to remove organic content of the soil sample. Initially this method was attempted at the field station in Jordan. However there was a lack of suitable equipment and therefore the remaining samples were returned to Durham for analysis. Soil samples were firstly sieved through a 0.2mm sieve to remove the silt. The retained fraction was mixed with a saturated solution of $MgSO_4$ (specific gravity = 2.95, M = 246, 47g/mol) (Weast, 1968) Samples were stirred vigorously then left to stand for approximately 10 minutes allowing the heavier inorganic particles to settle. The organic component was then decanted onto a funnel lined with coarse filter paper and rinsed with tap water to remove salt. The organic residues were oven-dried at 25°C for 24 hours. Samples were then examined under the dissection microscope using the same procedure as for the seed rain. The majority of samples were investigated in their entirety. However, for samples with a large organic content, a sub-sample of approximately one-quarter of the whole sample was examined (the sub-sampling technique was verified by accumulative sub-sampling to ensure that the sub-sample proportion used was representative of the whole sample (Nelson & Chew, 1977)).

4.2.4.3 Density and biomass calculations

Seed bank densities (**SBD**) and seed bank biomasses (**SBB**) were calculated for each site habitat per month using the formula in equations 4.3 and 4.4 respectively.

$$\mathbf{SBD = N^{*}\ K} \qquad \text{Equation 4.3}$$

where **N** is the number of seeds in the sample. **K** is a constant (198.82) derived from the surface area of the soil corer to convert values to numbers per m^2.

$$\mathbf{SBB = \frac{(\Sigma\ (n * \overline{M}))^{*}\ K}{1000}} \qquad \text{Equation 4.4}$$

where **n** is the number of seeds of a particular species in the sample. $\overline{\mathbf{M}}$ is the mean seed weight of the species obtained from the seed reference collection. **K** is the same as in Equation 4.3. Biomass estimates were divided by 1000 to convert values from milligrams to grams per m^2.

4.3 RESULTS

4.3.1 Seed production

4.3.1.1 Plant density estimates

Density estimates (individuals/m^2) for commonly occurring seeding species in the four habitat types at both study sites are shown in Table 4.1 The species richness was lower than that recorded in the vegetation study (Tables 3.2 and 3.3). In all habitats at Hashad, approximately half the number of plants recorded as present were also seeding and were common enough and sufficiently widely distributed to give density values using the methodology outlined in 4.2.2.1. Habitats at Salma showed a larger variation in the number of species present and in the number of abundant species seeding. For example, only one of the 14 species recorded in wadi habitat at Salma during vegetation studies was recorded in the plant density estimates given in Table 4.1, whereas, eight of the 12 species found in hammada habitat were recorded.

For seeding species, the marab habitat in both sites had the highest total plant density. The lowest density was observed in the hammada at Hashad and in the wadi at Salma. In general, species of Gramineae possessed the highest density with numbers exceeding 477/m^2 in the marab at Salma. This location also had the highest densities of *Crepis* spp., *M. laciniata* and *Plantago ovata* relative to other habitats and the largest species density overall. Standard error values in Table 4.1 demonstrate the variation in density estimates. The Index of Dispersion (I.D. in Table 4.1), calculated from the sample variance divided by the mean, gives an indication of the distribution of vegetation in the different habitat types. In all localities, with the exception of marab and harrat habitats at Salma, the majority of species had clumped distributions (I.D. >1). Some species distribution was independent of habitat type (e.g. *E. bryonifolium*), whilst others showed differences in distribution between habitats (e.g. *L. leyseriodes*).

4.3.1.2. Seeding characteristics

The seeding characteristics for each seeding plant species are given in Table 4.2. Missing standard errors for seed weight (*) are the result of either individual seeds being too light to be measured accurately or are cases where only one seed sample was available, i.e. from the subsequent seed bank or seed rain analysis.

Table 4.1 Density estimates (m^2), mean and standard error for seeding species in four habitats in Hashad and Salma. I.D. is the Index of Dispersion (n = 5). Perennial species are in bold.

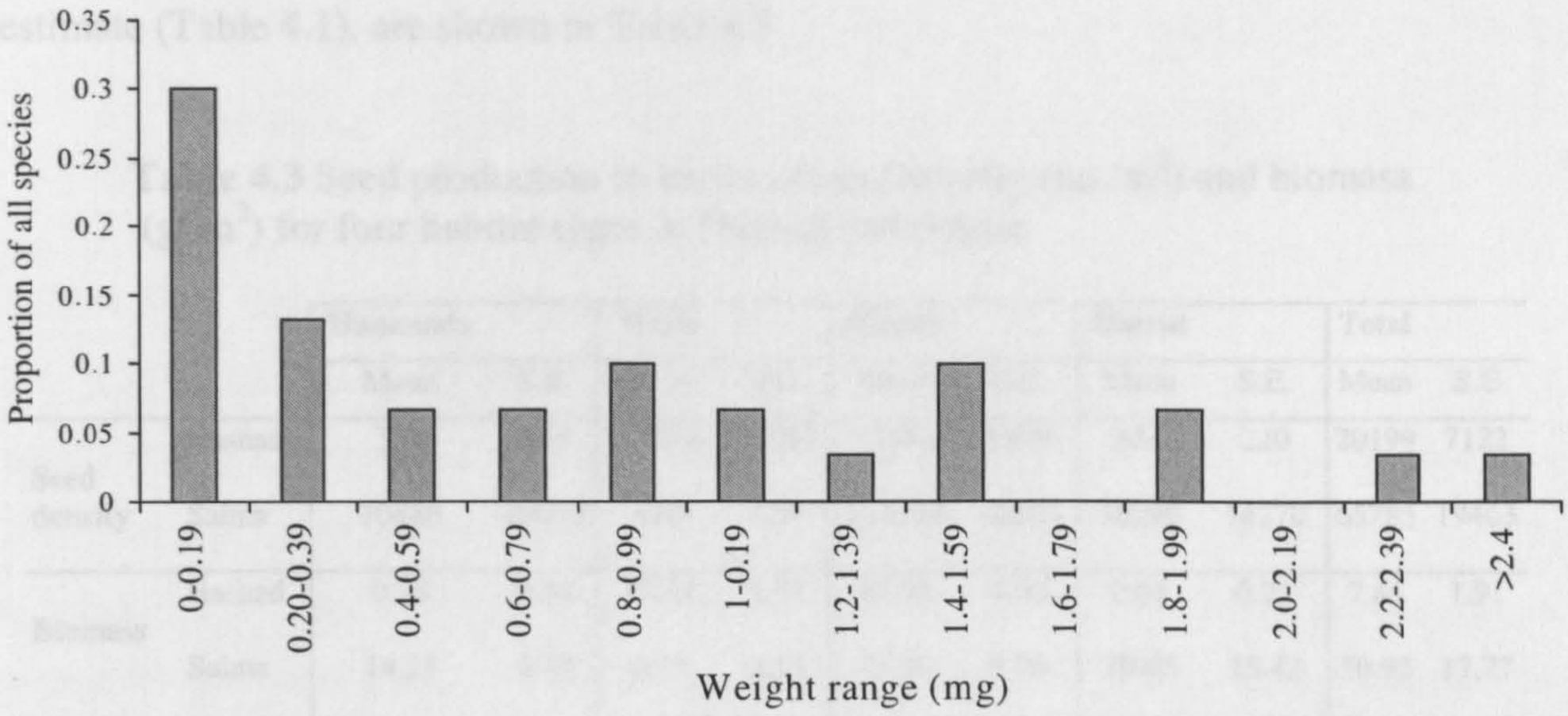
	Site/habitat																				
	Hashad												Salma								
Species	**Ham**			**Wadi**			**Marab**			**Basalt**			**Ham**			**Wadi**			**Marab**			**Basalt**		
	Mean	S.E.	I.D.	Mean	S.E.	I.D.	Mean	S.E.	I.D.	Mean	S.E.	I.D.	Mean	S.E.	I.D.	Mean	S.E.	I.D.	Mean	S.E.	I.D.	Mean	S.E.	I.D.
Astragalus spinosus													**1.6**	**1.4**	**1.3**				**0.2**	**0.2**	**4.0**			
Calendula tripterocarpa	0.2	0.2	4.0	0.4	0.4	2.8													1.6	0.5	0.8			
Crepis spp.																			85.2	16.3	0.1			
Diplotaxis harra				**1.6**	**0.7**	**0.9**	**0.4**	**0.2**	**2.2**				**0.6**	**0.6**	**2.3**									
Erodium bryonifolium	0.2	0.2	4.0	0.2	0.2	4.0	0.6	0.4	1.9				0.2	0.2	4.0									
Erodium deserti																0.8	0.8	2.0						
Erucaria boveana				0.6	0.2	1.5	1.0	0.5	1.3															
Gramineae				5.7	1.3	0.4	18.2	8.1	0.3	4.6	1.8	0.5	161.8	140.0	0.1				477.6	68.7	0.0	403.2	211.8	0.0
Launaea nudicaulis				**0.4**	**0.2**	**2.2**	**0.6**	**0.2**	**1.5**															
Leysera leyseriodes	0.8	0.6	1.7	8.2	1.8	0.3	4.8	2.6	0.6	1.2	0.6	1.1	7.8	5.6	0.5							6.4	6.4	0.7
Linum album	**0.2**	**0.2**	**4.0**	**0.8**	**0.4**	**1.4**	**3.2**	**1.7**	**0.7**															
Medicago laciniata																			45.0	8.9	0.1			
Onobrychis ptolemaica	**0.2**	**0.2**	**4.0**	**1.2**	**0.5**	**1.0**	**0.2**	**0.2**	**4.0**															
Papaver polytrichum				0.2	0.2	4.0																		
Paracaryum rugulosum				**0.2**	**0.2**	**4.0**																		
Plantago ovata													0.2	0.2	4.0				62.4	11.7	0.1	3.2	3.2	1.0
Reseda decursiva	0.4	0.4	2.8	0.4	0.2	2.2	0.4	0.4	2.8															
Trigonella stellata				8.2	1.8	0.3	1.6	0.8	1.0				0.2	0.2	4.0							3.2	3.2	1.0
Species Richness	6.0			13.0			10.0			2.0			8.0			1.0			7.0			4.0		
Total density per m^2	2.0			28.1			31.0			5.8			172.6			0.8			686.0			416.0		

Table 4.2 Plant seeding parameters; mean number of capsules per plant, mean number of seeds per capsule, mean seed weight (mg), seed production biomass, SPB (mg/plant) and seed production density, SPD (no./ plant).
N = 10.

Species	No. Capsules	S.E.	No. of seeds /capsule	S.E.	Seed wt. (mg)	S.E.	SPB (mg/ plant)	SPD (no./plant)
Gramineae A	2.60	0.60	18.80	2.96	*0.05		2.44	48.8
Leysera leyseriodes	1.00	0.00	6.60	1.24	0.05	0.00	0.33	6.6
Papaver polytrichum	2.60	0.60	17.80	3.26	*0.05		2.31	46.3
Diplotaxis harra	131.50	21.12	231.10	11.78	0.10	0.00	3038.97	30389.7
Bromus spp.	6.30	1.25	10.60	0.72	*0.10		6.68	66.8
Erucaria boveana	80.60	25.12	1.00	0.00	*0.20		16.12	80.6
Reseda decursiva	44.10	8.87	7.20	0.55	0.34	0.10	107.96	317.5
Crepis spp.	17.30	3.76	45.40	1.28	0.43	0.08	337.73	785.4
Launaea nudicaulis	60.20	8.64	18.30	0.40	0.74	0.07	815.23	1101.7
Plantago ovata	5.20	0.68	19.50	3.04	0.79	0.05	80.11	101.4
Erodium bryonifolium	33.70	10.21	5.00	0.00	0.91	0.07	153.34	168.5
Trigonella stellata	24.50	5.40	2.10	0.28	0.98	0.09	50.42	51.5
Erodium deserti	30.10	5.62	5.00	0.00	1.09	0.06	164.05	150.5
Astragalus spinosus	42.30	2.43	9.60	1.99	*1.50		609.12	406.1
Paracaryum rugulosum	188.80	29.92	4.00	0.00	1.52	0.17	1147.90	755.2
Linum album	10.00	0.00	175.00	39.85	1.52	0.14	2660.00	1750
Medicago laciniata	10.60	1.57	6.50	0.27	1.80	0.18	124.02	68.9
Calendula tripterocarpa	6.80	1.54	7.80	0.44	1.91	0.22	101.31	53.0
Gramineae B	8.50	1.92	11.30	1.08	*2.20		211.31	96.1
Onobrychis ptolemaica	59.80	14.92	1.90	0.10	7.79	0.43	885.10	113.6
Mean	40.29		30.23		1.20		525.72	1827.9
Median	24.50		8.70		0.85		138.68	107.5
Range	2.6 - 188.8		1 - 231.1		0.05 -7.79		0.33- 3039	7-30390

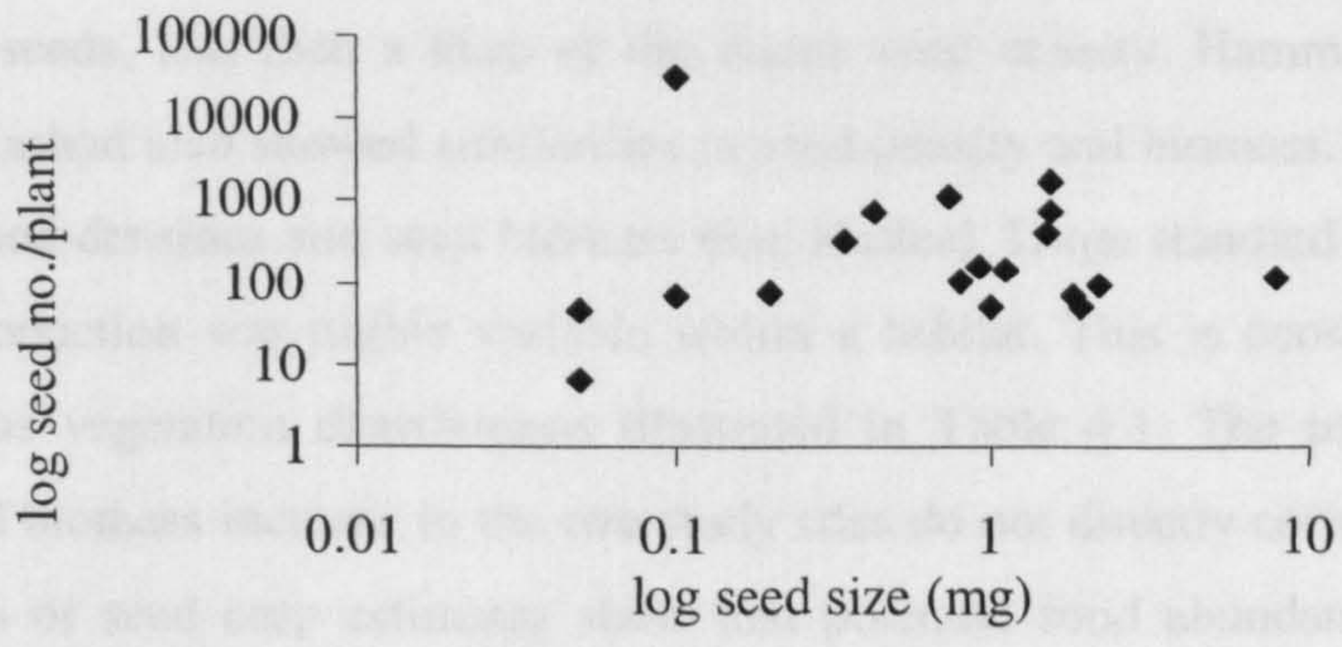
The variability in seeding characteristics amongst plant species can be seen in the mean, median and range. Individual seed weights ranged from 0.05mg (Gramineae) to 7.79mg (*O. ptolemaica*), the total number of seeds produced by an individual plant ranged from seven (*L. leyseriodes*) to 30390 (*D. hara*) and the total seed biomass produced by a plant ranged from 0.33mg to 5.2grams, for *L. leyseriodes* and *D. hara* respectivcly. Comparisons of the mean and median values of seed size indicate that the data are skewed towards smaller values. To investigate this, the proportions of species (n = 30) with particular seed size ranges were plotted against seed size (mg) for all seeds found in the study (Figure 4.2). The figure shows the skew towards smaller sizes with more species producing smaller seeds (< 0.2mg) and fewer species producing larger seeds (> 1.0mg).

Figure 4.2 Distribution of mean seed weights of 30 different plant species.



It would be expected that smaller seeding species (e.g. annuals) would produce higher densities of seeds. However, the spring seeding species showed no correlation between seed size and the number of seeds produced by a plant (Figure 4.3, r = 0.252, P = 0.283, n = 20 Spearman rank correlation) even when the apparent 'outlier' was excluded from the analysis (r = 0.354, P = 0.137, n = 19) In general, species producing smaller sized seeds did not produce more seeds than a larger seed species.

Figure 4.3 Scatter diagram to show relationship between seed size and the number of seeds produced for seeding species during spring 1998.



4.3.1.3. Spatial differences in seed crop

It can be seen from Table 4.1 that sites and habitats vary in plant species density and composition. It would be expected that seed density and biomass would differ between sites and habitats, however this is not clear from Table 4.1 alone. Seed productions for

each locality in terms of seed number (no./m^2) and biomass (g/ m^2), calculated from the mean seed density and biomass per plant (Table 4.2) multiplied by the plant density estimate (Table 4.1), are shown in Table 4.3.

Table 4.3 Seed production in terms of seed density (no./m^2) and biomass (g/ m^2) for four habitat types at Hashad and Salma.

		Hammada		Wadi		Marab		Harrat		Total	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E
Seed density	Hashad	539	463	52378	20784	17683	6670	684	220	20199	7122
	Salma	30888	19093	120	120	111594	16566	30295	14270	65785	19463
Biomass	Hashad	0.78	0.55	10.02	2.78	13.34	4.90	0.65	0.21	7.45	1.91
	Salma	14.23	9.49	0.13	0.13	73.26	9.76	30.05	15.42	50.92	17.77

A two-way ANOVA with replication undertaken on biomass values (F_{max} test: $F > 0.05$, variances homogenous) showed that there were significant differences in the seed production biomass (g/m^2) between sites ($F = 18.97$, $P < 0.01$), between habitats ($F = 10.82$, $P < 0.01$) and the biomass produced in a specific habitat type also varied between sites ($F = 7.55$, $P < 0.01$). At Hashad the wadi habitat produced the highest number of seeds per m^2, almost 100 times as many as were recorded in the harrat habitat and three times as many as in the marab habitat at this site. At Salma, the marab produced the most seeds, almost 1000 times as many as in the wadi and the greatest density recorded in any habitat at either site. Within a site some habitats were more similar in seed production than others. The harrat and hammada habitats at Salma produced similar numbers of seeds, less than a third of the marab seed density. Hammada and harrat habitats at Hashad also showed similarities in seed density and biomass. Overall Salma had larger seed densities and seed biomass than Hashad. Large standard errors indicate that seed production was highly variable within a habitat. This is consistent with the heterogeneous vegetation distributions illustrated in Table 4.1. The patterns of seed numbers and biomass increase in the two study sites do not directly correspond (Figure 4.4). Results of seed crop estimates show that potential food abundance is different between sites and, in general, between habitat types.

Figure 4.4 Comparisons of seed production between habitats.

Density	Hashad:	hammada < harrat < marab < wadi
	Salma:	wadi < harrat < hammada < marab
Biomass	Hashad:	harrat < hammada < wadi < marab
	Salma:	wadi < hammada < harrat < marab

4.3.1.4 Seed size distribution within seed crop

The relative abundance of seeds of particular size classes is an important component of rodent foraging behaviour. The total seed production (see Table 4.3) was divided into five seed size categories, defined following Price and Joyner (1997), (< 0.2mg, 0.2-0.5, 0.5-1.0, 1.0-2.0 & > 2mg). (Seed weights were used to standardise measurements irrespective of seed shape). The percentages of the total seed abundance represented by each of the size categories in all four habitat types in both study sites are given in Table 4.4.

Table 4.4 The percentage of the total seed numbers represented in the five seed size categories for the four habitats in Hashad and Salma.

Seed Size	Site: Hashad				Site: Salma			
(mg)	Ham.	Wadi	Marab	Harrat	Ham.	Wadi	Marab	Harrat
<0.2	0.96	94.63	66.87	100.00	97.65	0.00	30.58	98.31
0.2-0.5	23.12	0.34	1.03	0.00	0.00	0.00	60.72	0.00
0.5-1	6.13	1.73	4.19	0.00	0.21	0.00	5.74	1.69
1-2	65.64	3.03	27.79	0.00	2.14	100.00	2.96	0.00
>2	4.13	0.26	0.11	0.00	0.00	0.00	0.00	0.00

Due to the limitations of the data, statistical analysis could not be undertaken to test differences between habitats or sites. However, from Table 4.4 it appears that there were differences between the two study sites when habitat types are compared within a site and between sites. At Hashad the wadi and harrat habitats have the highest proportions of small seeds (95-100%), whereas the hammada habitat had the greatest proportion of seeds > 1mg. Within Salma the harrat and hammada habitats held the highest proportions of small seeds (< 0.2mg) and approximately 90% of all seeds found in the marab were less than 0.5mg. All seeds found in the wadi site fell within the 1-2mg category, as expected from the plant species composition of this habitat (see Table 4.1). Between sites, the harrat appeared most similar in terms of size frequency distribution of seeds.

4.3.1.5 Timing of seeding

The timing of seeding in different species was followed to investigate the differences in the onset, duration and extent of seeding between species. It was expected that annuals would be more predominant in the spring (March-May). Most of the commonly occurring plant species (87% at Salma, n = 15 species, and 75% at Hashad, n = 16) showed seeding at some time during the spring study period and of all species recorded, annuals were observed seeding on more occasions (100% of occasions, n = 18 species) than perennials (60%, n = 10). Figures 4.5a-l and 4.6a-l show for each seeding species the proportion of plants (n = 10) seeding at Hashad and Salma respectively, during spring 1998. The observed timing and duration of seeding within the study period varied greatly between species, i.e. *C. tripterocarpa* (Fig. 4.5b) seeded continually from March to May, whilst *A. fragrantissima* did not seed during the study. Examples of the variation of timing are shown in (i) Gramineae spp. (Fig 4.6g), seeding before the start of the study period, (ii) *Matricaria aurea* (Fig 4.6j) seeding in April and (iii) *Aronsohnia factorovskyi* (Fig 4.6i) seeding in May. The majority of species (70%, n = 24) set seed towards the later part of the study period, mid-April to May, with all seeding perennials being reproductively active after early April. Variation in duration can be seen in the example of *R. decursiva* (Fig. 4.5l), which showed a single, relatively short (50 days) seeding period compared to *C. tripterocarpa* (Fig. 4.5b) which seeded throughout the study period (>90 days) and displayed more than one peak in seeding. Secondary peaks in seeding were observed for *A. hierchunticus* (Fig.4.6a) and *C. tripterocapa* (Fig. 4.5b).

To investigate if the overall timing of seeding was similar between sites, the proportion of seeding species showing seed set at a particular time was calculated and plotted for each study site (Figure 4.7). Following the methodology used in the vegetation analysis (Chapter 3) to enable between-site comparisons, sampling dates were classified into time periods rather than absolute dates (see Table 3.2).

Figure 4.5 The proportion of plants seeding during spring 1998 at Hashad a) *A. factorovskyi* b)*C. tripterocarpa* c) *D. hara, d) E. boveana, e) E. bryonifolium f) Gramineae, g) L. nudicaulis, h) L. leyseriodes, i) O. ptolemaica,* j) *P. rugulosum*, k) *P. polytrichum,* l) *R. decursiva*, m) *L. album* and n) *T. stellata*

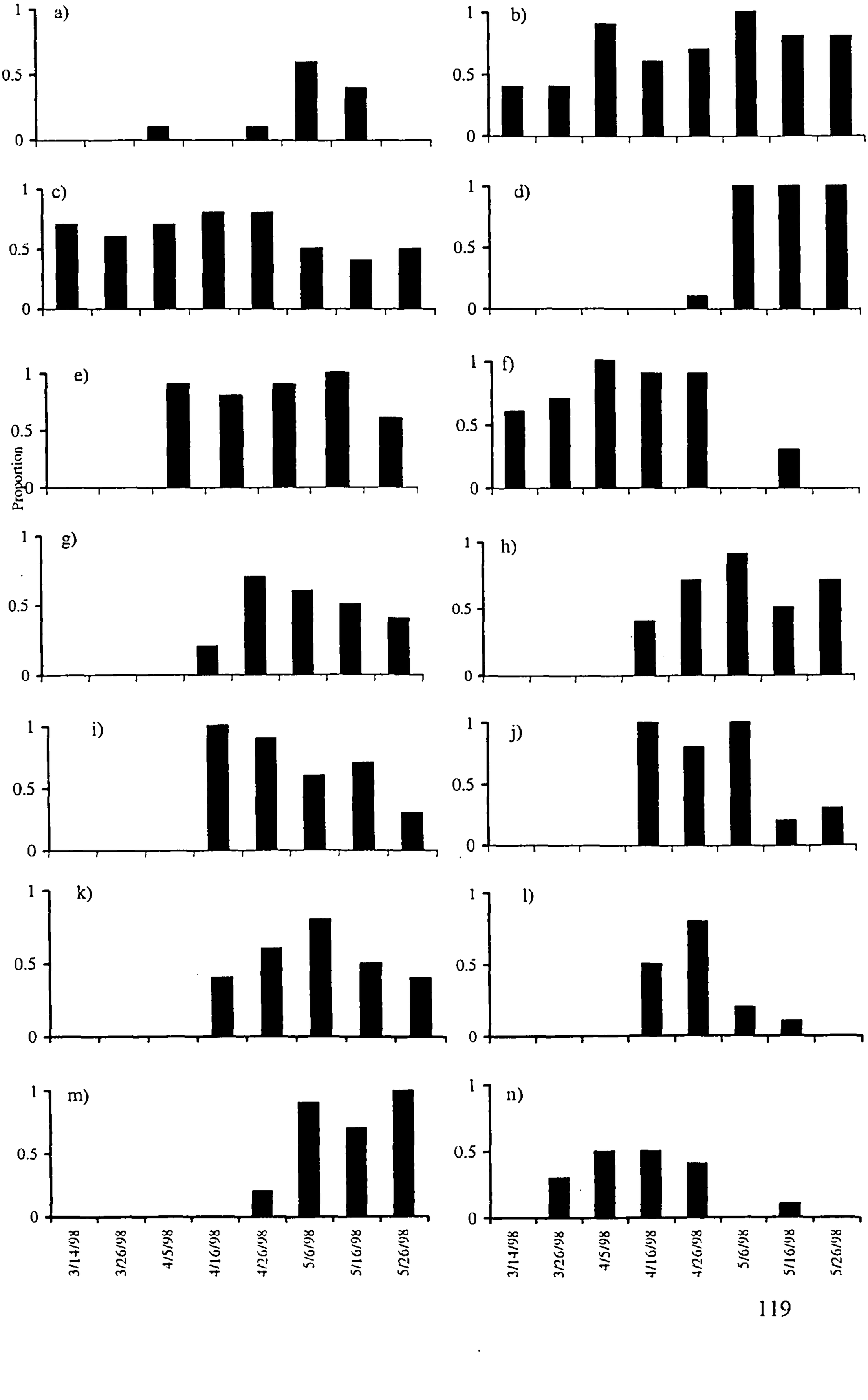


Figure 4.6 The proportion of plants seeding during spring 1998 at Salma a) *A. hierchunticus* b) *A.spinosus* c) *C. tripterocarpa, d) Crepis* spp., *e) D. hara, f) E. bryonifolium,* g) *E. boveana,* h) Gramineae, i) *L. leyseriodes* J) *L. nudicaulis* k) *A. factorovskyi* l) *M. aurea*, m) *T. stellata* and n) *P. ovata*

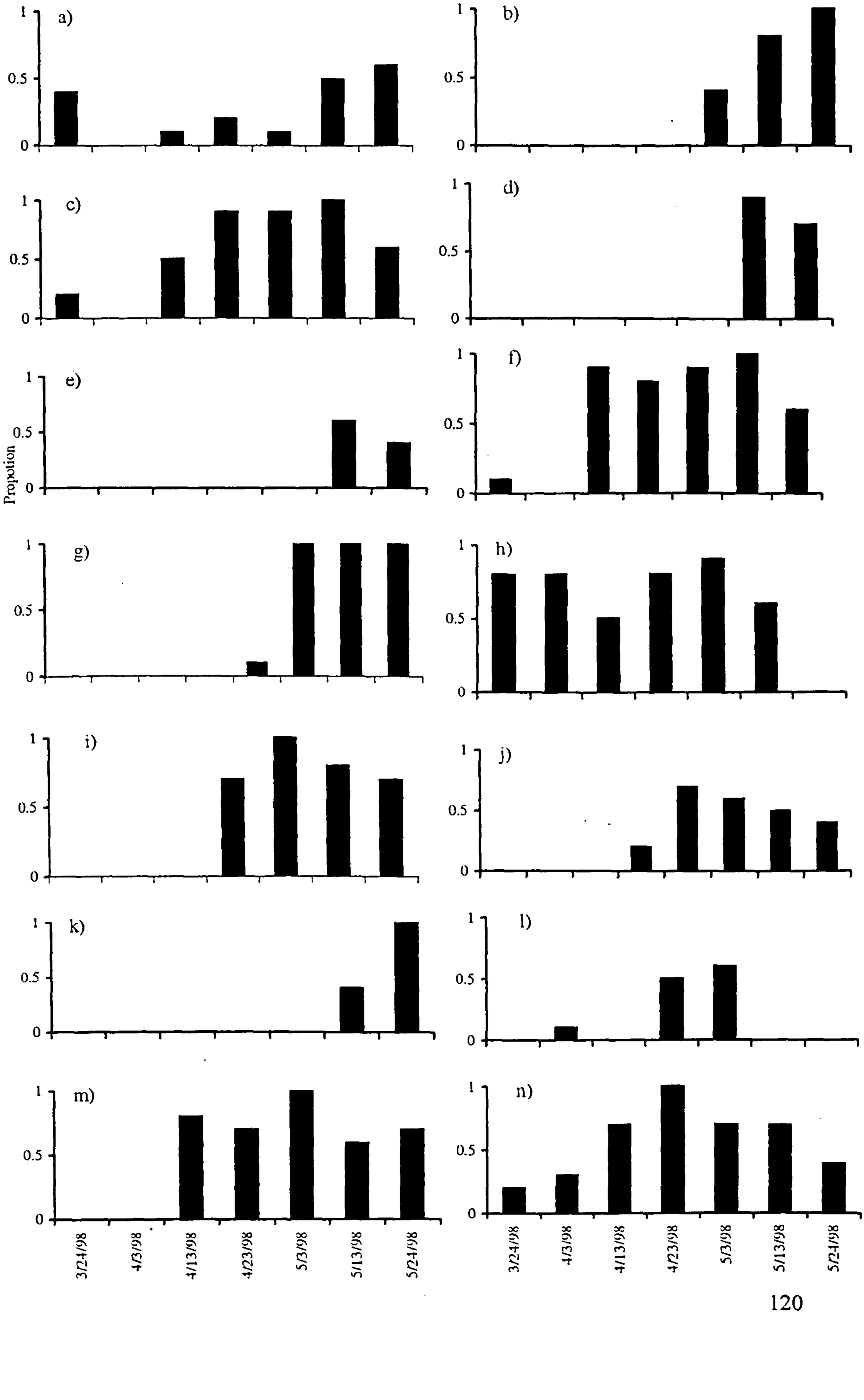
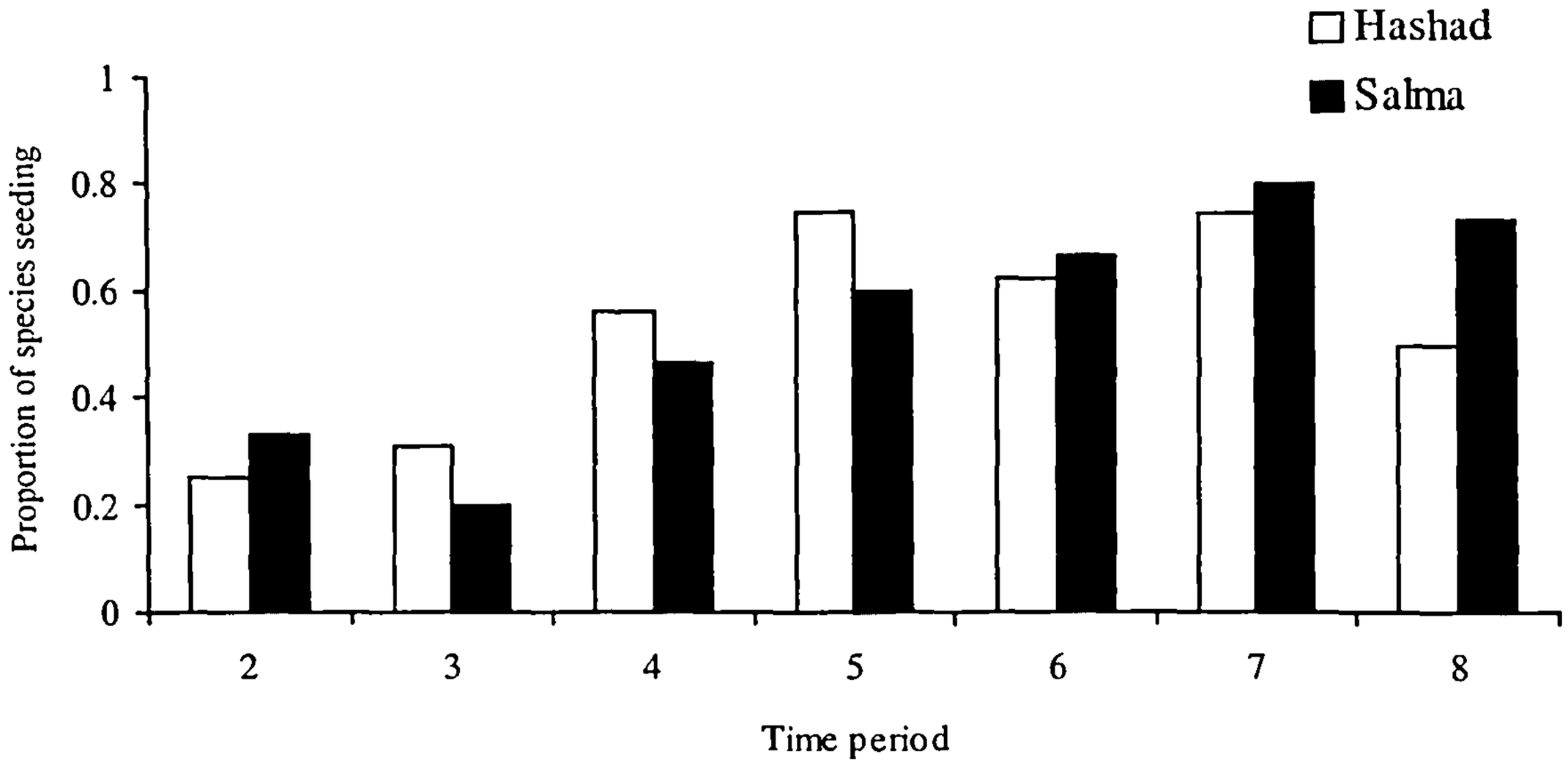


Figure 4.7 The proportion of species showing seeding at the different time periods during the 1998 study period at Salma and Hashad.

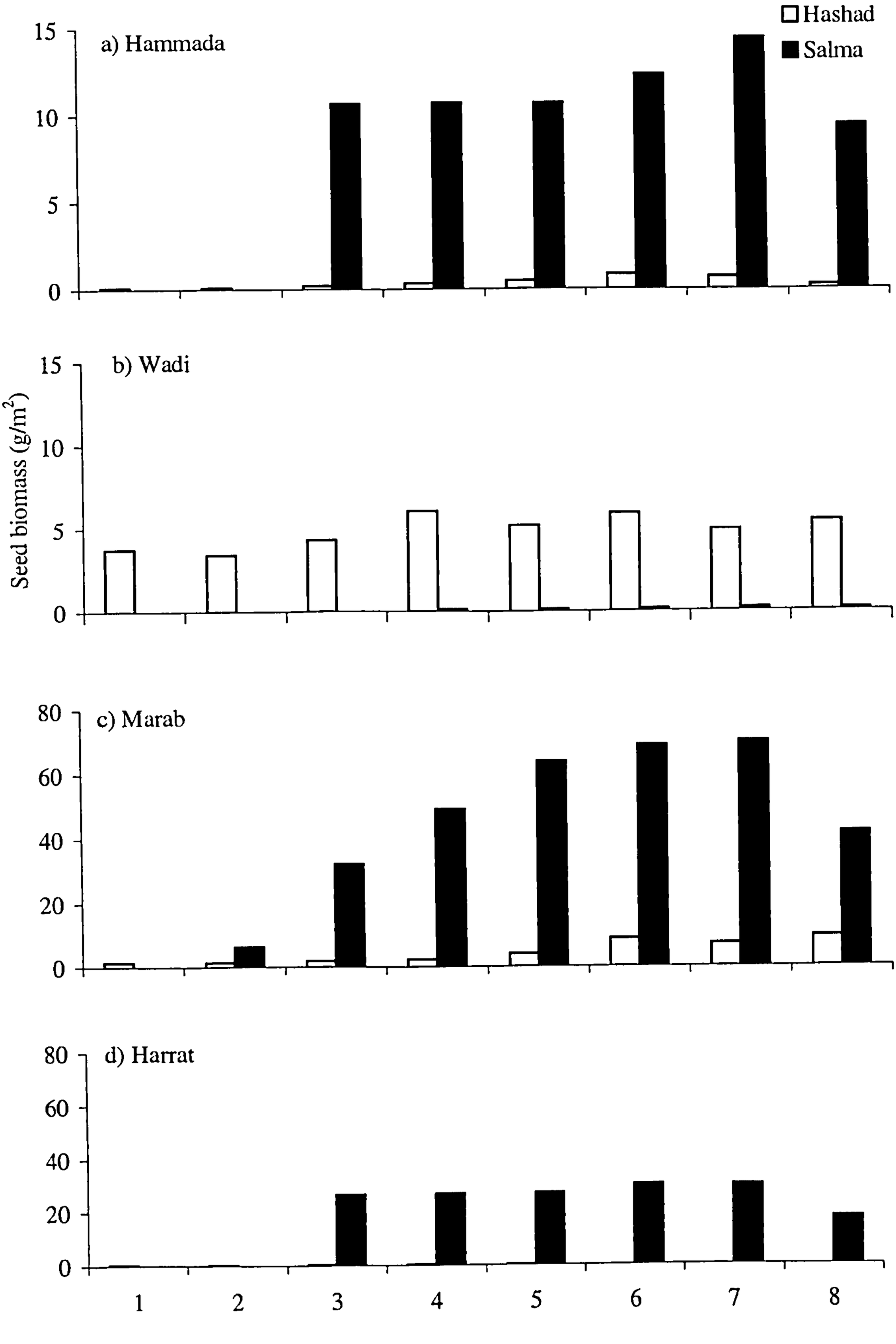


As data were in proportions, a Spearman rank correlation was undertaken showing that the timing of seeding between sites was not significantly correlated ($r = 0.667$, $P > 0.1$). Seeding at Hashad tended to occur earlier than at Salma, with peaks in seeding occurring during the 5th and 7th time periods (late April and early May). During the study, the proportion of species seeding was greatest at Salma during time period 7 (early May), when 80% of species seeded. The proportion of species seeding decreased at both sites in late May. Differences were also observed between sites in the timing of seeding of individual species, e.g. *Trigonella stellata* (Figs. 4.5l and 4.6k) in which the seeding peak occurred approximately 20 days earlier at Hashad than at Salma. These observations may be the result of the differences in the timing of rainfall events between sites. Unfortunately rainfall data for the individual sites were not available to investigate this further.

4.3.1.6 Timing of seed production between habitat types

To compare the changes in seed abundance over time between habitats, the seed biomass output for each habitat in both sites was calculated for each time period. For each plant species, seed biomass estimates (g/m^2) were multiplied by the proportion of plants recorded seeding at 10-day time intervals throughout spring 1998 and then summed for all species in the habitat. Temporal patterns in seed production in terms of biomass for four habitats in the two study sites are shown in Figures 4.8 a-d for the spring 1998. Values for Salma during time period 1 are not available. In general there

Figure 4.8 Biomass of seed production over the study period at Hashad and Salma.
a) hammada, b) wadi, c) marab and d) harrat habitats. Note differences in scale.



was greater seed biomass production at Salma than Hashad, except in the wadi habitat. At Hashad, both harrat and hammada habitats had consistently low levels of production compared to the wadi and marab habitats, which appeared to have highest levels of seed biomass during early to mid May. The timing of seed biomass production at Salma differed from that at Hashad with hammada, marab and harrat habitats showing higher levels of seed production earlier (early March) and slightly lower levels in mid-late May. Data were normally distributed (Kolmogorov-Smirnov test, $P > 0.05$) hence to investigate the correlation in timing between habitats the Pearson product moment correlation co-efficient was calculated for each habitat permutation (see Table 4.5).

Table 4.5 Correlations in the timing of seed biomass production between habitat types at Salma and Hashad (Spearman rank correlation, * Statistically significant results, *** highly statistically significant result).

Site	Habitat 1	Habitat 2	Correlation Coefficient (r_s)	Probability
Hashad	Hammada	Wadi	0.664	0.073
	Hammada	Marab	0.666	0.071
	Hammada	Harrat	-0.480	0.229
	Wadi	Marab	0.601	0.115
	Wadi	Harrat	-0.349	0.397
	Marab	Harrat	-0.890	0.003*
Salma	Hammada	Wadi	0.674	0.097
	Hammada	Marab	0.890	0.007*
	Hammada	Harrat	0.969	<0.0001***
	Wadi	Marab	0.870	0.011*
	Wadi	Harrat	0.623	0.135
	Marab	Harrat	0.865	0.012*

The results showed that in general there was statistically significant correlation in the timing of seeding at Salma but not at Hashad. As timing of seeding is dependent on the individual species responses it would also be expected that habitats showing similar species composition (Table 3.3), would be more similar in seeding than habitats with different compositions and correspondingly Salma showed overall, higher similarities in species composition than Hashad. However, two sites with very similar species compositions, the wadi and marab at Hashad (Jaccard's similarity co-efficient = 0.95), did not show a significant correlation in the timing of seed production, and conversely, habitats with low species similarity (e.g. marab and harrat at Hashad) were significantly correlated (Table 4.5).

4.3.2. Seed rain

4.3.2.1. Seed rain density and biomass

Seed rain densities were measured at monthly intervals, in three habitat types, in both study sites (Figures 4.9a & b). Corresponding seed biomass estimates are plotted in Figures 4.10 a & b. Data from marab habitat at Salma are not included in the analysis due to extensive trap loss and damage. For these reasons sample sizes also vary. For the two sites, neither biomass or density data sets were normally distributed (Kolmogorov–Smirnov test: $P < 0.05$); nor had they equal variances (F_{max} test: d.f. = 9, $P < 0.05$ for all cases). Therefore, non-parametric tests were used to investigate site and habitat differences in seed rain.

Figure 4.9 Seed rain density (no/m^2) in three months at a) Hashad and b) Salma (n = 5 and S.E. bars are shown).

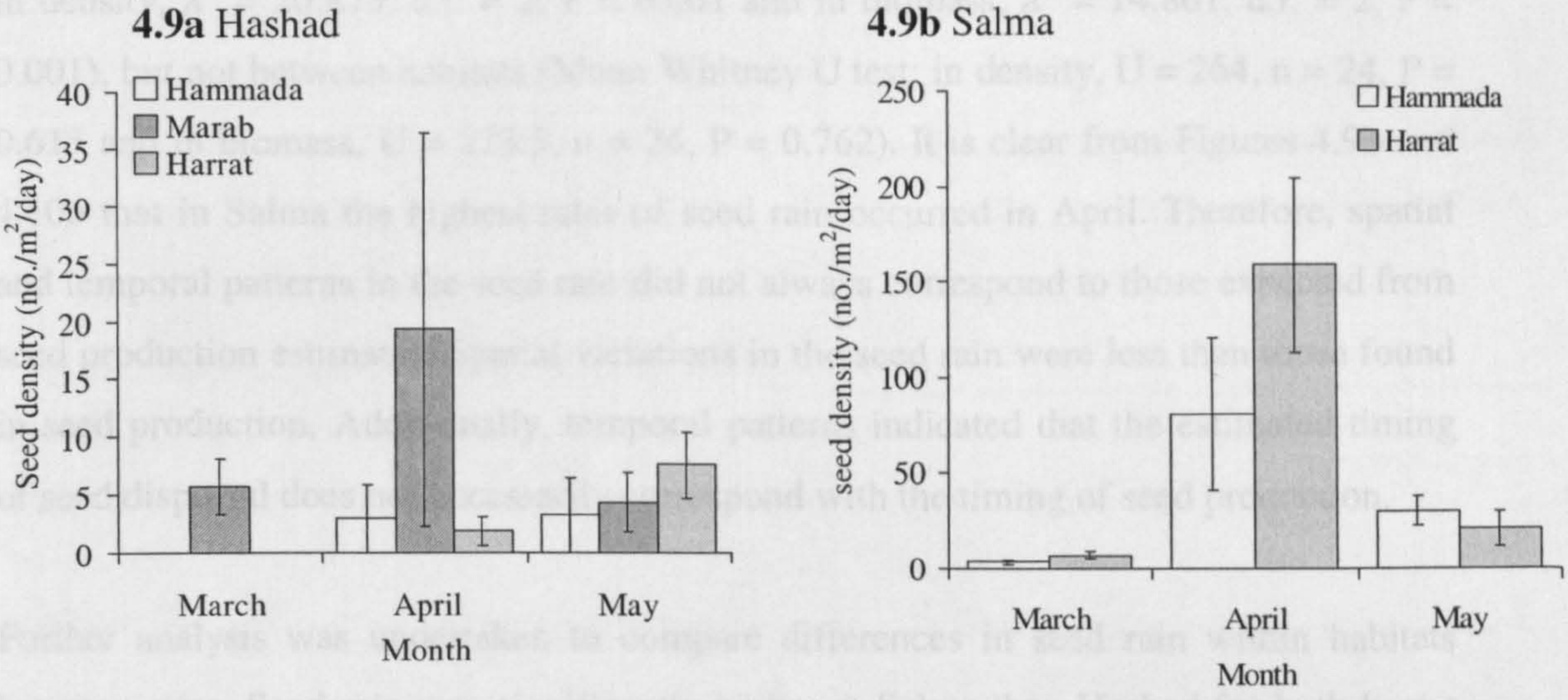
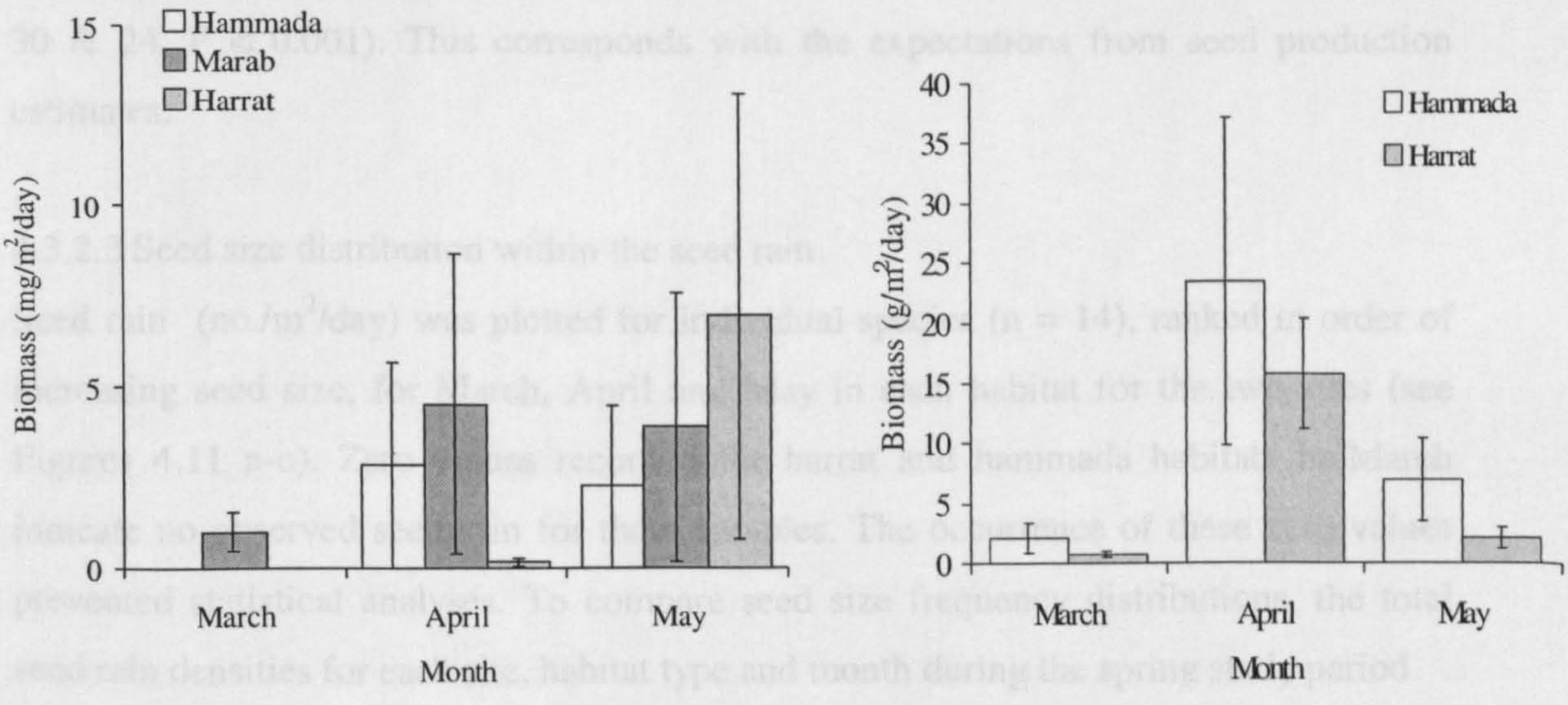


Figure 4.10 Seed rain biomass for three months in a) Hashad (mg/m^2/day) and b) Salma (g/m^2/day), (n = 5 and S.E. bars are shown).



If the seed rain were composed from seeds that were produced in close proximity to seed traps, i.e. in the same habitat, spatial variation in seed production should lead to spatial variation in seed rain. Additionally, if seed dispersal occurred immediately after seed maturity, temporal patterns in the seed rain should be similar to those in seed production. An increase in seed rain density in late April to early May, when seed production is at a maximum, would be expected.

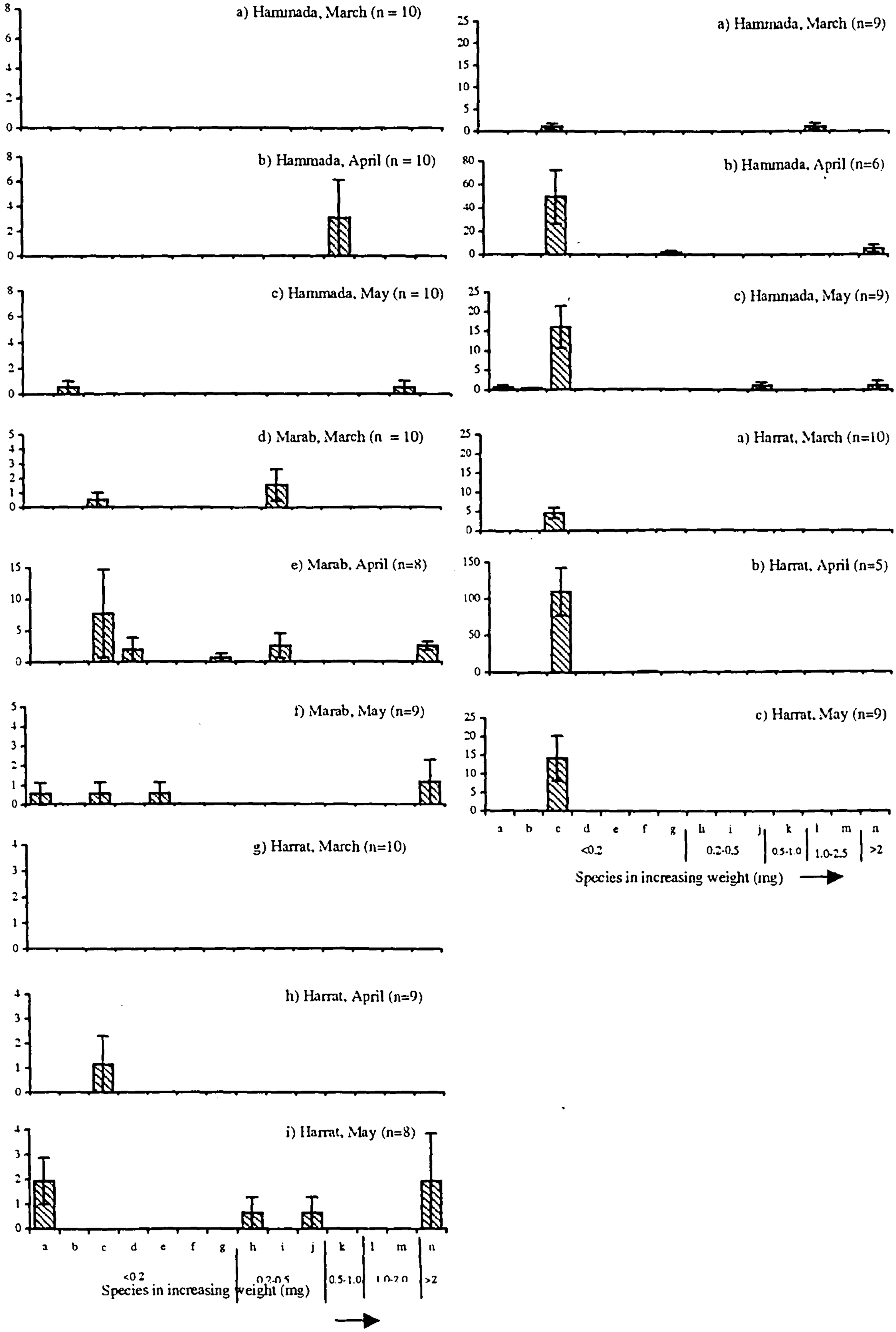
A Friedman test using median values showed that at Hashad there were no statistically significant differences between habitat types or months for either seed rain density (habitat: $X^2 = 1.0$, d.f. = 2, P = 0.607, month: $X^2 = 1.0$, d.f. = 2, P = 0.607) or biomass (habitat: $X^2 = 1.0$, d.f. = 2, P = 0.607, month: $X^2 = 1.0$, d.f. = 2, P = 0.607). However, at Salma there were statistically significant differences between months (Kruskal-Wallis: in density, $X^2 = 20.875$, d.f. = 2, $P < 0.001$ and in biomass, $X^2 = 14.861$, d.f. = 2, P = 0.001), but not between habitats (Mann Whitney U test: in density, U = 264, n = 24, P = 0.615 and in biomass, U = 273.5, n = 24, P = 0.762). It is clear from Figures 4.9b and 4.10b that in Salma the highest rates of seed rain occurred in April. Therefore, spatial and temporal patterns in the seed rain did not always correspond to those expected from seed production estimates. Spatial variations in the seed rain were less than those found in seed production. Additionally, temporal patterns indicated that the estimated timing of seed dispersal does not necessarily correspond with the timing of seed production.

Further analysis was undertaken to compare differences in seed rain within habitats between sites. Seed rain was significantly higher at Salma than Hashad for both harrat (density, U = 120, n = 27 & 24, $P < 0.001$; biomass, U = 132, n = 27 & 24, $P < 0.001$) and hammada habitats (density, U = 132, n = 30 & 24, $P < 0.001$; biomass, U = 140, n = 30 & 24, $P < 0.001$). This corresponds with the expectations from seed production estimates.

4.3.2.2 Seed size distribution within the seed rain

Seed rain (no./m^2/day) was plotted for individual species (n = 14), ranked in order of increasing seed size, for March, April and May in each habitat for the two sites (see Figures 4.11 a-o). Zero values recorded for harrat and hammada habitats in March indicate no observed seed rain for these samples. The occurrence of these zero values prevented statistical analyses. To compare seed size frequency distributions, the total seed rain densities for each site, habitat type and month during the spring study period

Figure 4.11 Seed rain density (no./m^2) for Hashad (a-i) and Salma (j-p) in hammada, marab and harrat over three months (n = 5, S.E. bars are shown). a = Grass C, b = *L. leyseriodes*, c = Grass A, d = Spp. G, e = Spp. H, f = Spp. K, g = *A. factorovskyi*, h = *E. bovei*, i = Spp. S, j = *Crepis* spp., k = *T. stellata*, l = *E. descursiva*, m = *P. rigulosum* and n = *Bromus* spp.



were separated into five categories by seed size and expressed as percentages following 4.3.1.4. (Tables 4.6 & 4.7).

At Hashad there was a statistically significant difference amongst months in seed size distribution (X^2 = 157.98, d.f. = 3, P < 0.01) and, in general, an increase in the proportion of larger seeds within the seed rain samples from April to May. However, at Salma (with the exception of the hammada sample taken in March) there were similar patterns of seed distribution between and within months. Samples had a consistently high proportion of small size seeds (< 0.2mg) and in the hammada habitat there was a slight decrease in the proportion of larger seeds from March to April.

Table 4.6 Percentage frequencies of seed sizes within the seed rain over three months (M = March, A = April & My = May) in three habitats in Hashad.

	Hammada				Marab				Harrat			
Range (mg)	**M**	**A**	**My**	**Mean**	**M**	**A**	**My**	**Mean**	**M**	**A**	**My**	**Mean**
<0.2	0.00	0.00	50.00	25.00	25.00	76.19	60.01	53.73	0.00	100.00	37.50	68.75
0.2-0.5	0.00	0.00	0.00	0.00	75.00	19.05	0.00	31.35	0.00	0.00	25.00	12.50
0.5-1.0	0.00	100.00	0.00	50.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1.0-2	0.00	0.00	50.00	25.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
>2	0.00	0.00	0.00	0.00	0.00	4.76	39.99	14.92	0.00	0.00	37.50	18.75

Table 4.7 Percentage frequencies of seed sizes within the seed rain over three months (M = March, A = April & My = May) in two habitats at Salma.

	Hammada				Harrat			
Range (mg)	**M**	**A**	**My**	**Mean**	**M**	**A**	**My**	**Mean**
<0.2	49.98	90.91	88.93	76.60	100.00	100.00	100.00	100.00
0.2-0.5	0.00	0.00	5.53	1.84	0.00	0.00	0.00	0.00
0.5-1.0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1.0-2	49.98	0.00	0.00	16.66	0.00	0.00	0.00	0.00
>2	0.00	9.09	5.53	4.87	0.00	0.00	0.00	0.00

As expected from the differences in plant species compositions between sites and amongst habitats there were significant differences in seed size distributions amongst habitats within Salma (X^2 = 30.87, d.f. = 3, P < 0.01, Chi-squared test) and Hashad (X^2 = 45.229, d.f. = 4, P < 0.01) and between sites for hammada (X^2 = 1195.88, d.f. = 3, P < 0.01) and harrat habitats (X^2 = 45.92, d.f. = 2, P < 0.01). The greatest proportion of large seeds occurred in the marab habitat at Hashad and overall, Hashad appear to have a greater proportion of larger seeds than Salma (excluding the marab habitat at Salma). These results are reflected in the presence and abundance of perennial species in various habitats and sites (Tables 3.3 and 3.4).

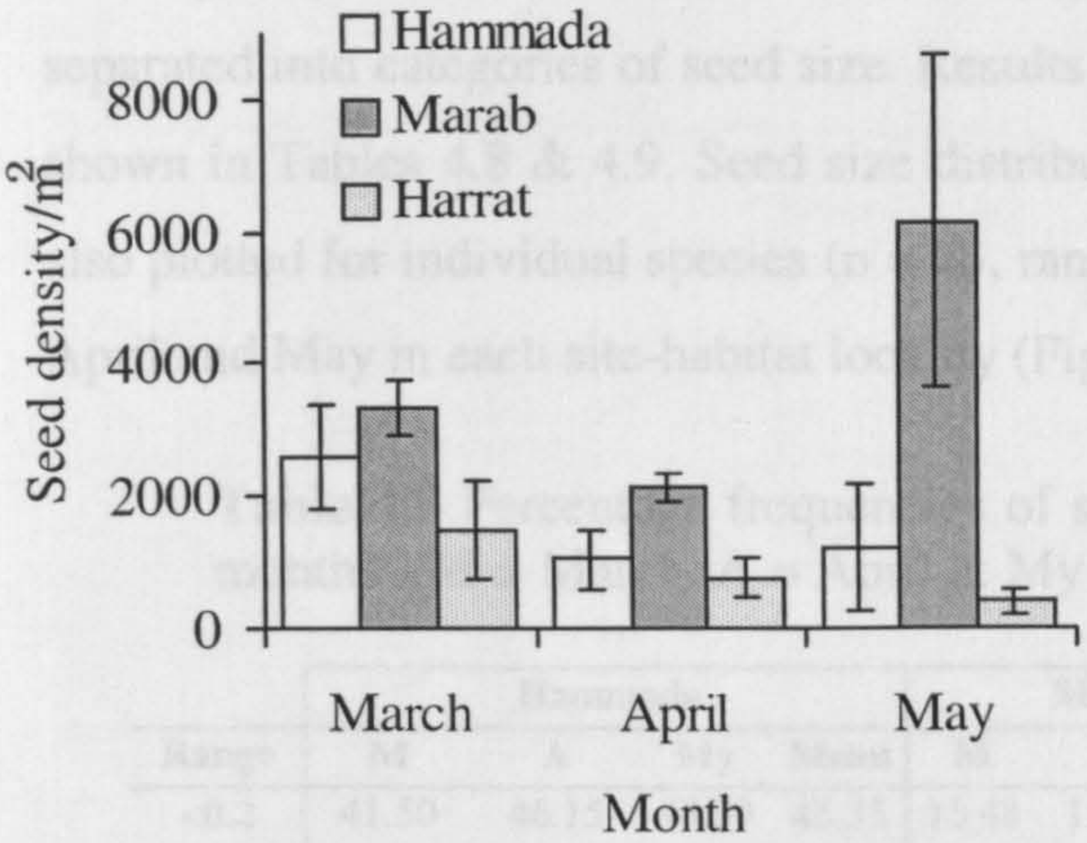
4.3.3. Seed bank

4.3.3.1. Density and biomass

Monthly seed density and biomass estimates for three habitats in Hashad and Salma are shown in Figures 4.12 a & b and 4.13 a & b respectively.

Figure 4.12 Soil seed bank density (no./m^2) measured over three months for a) Hashad and b) Salma, (n = 5 and S.E. bars are shown).

4.12 a Hashad



4.12b Salma

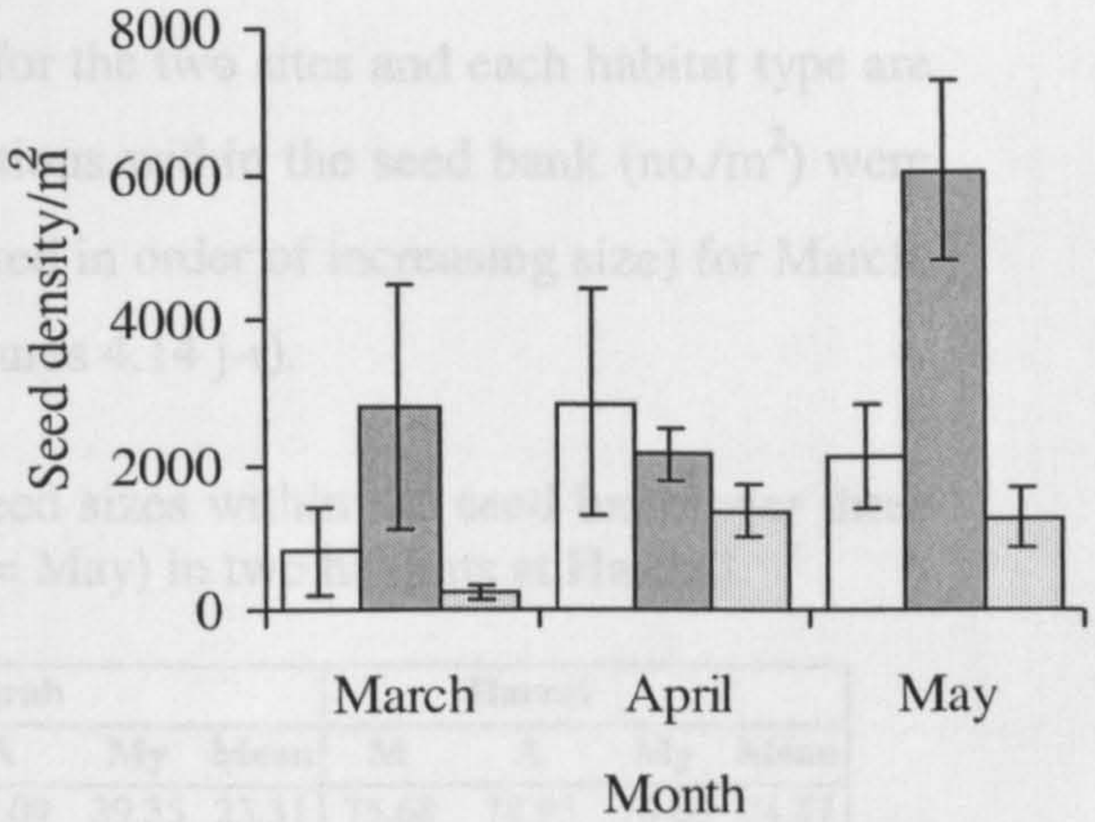
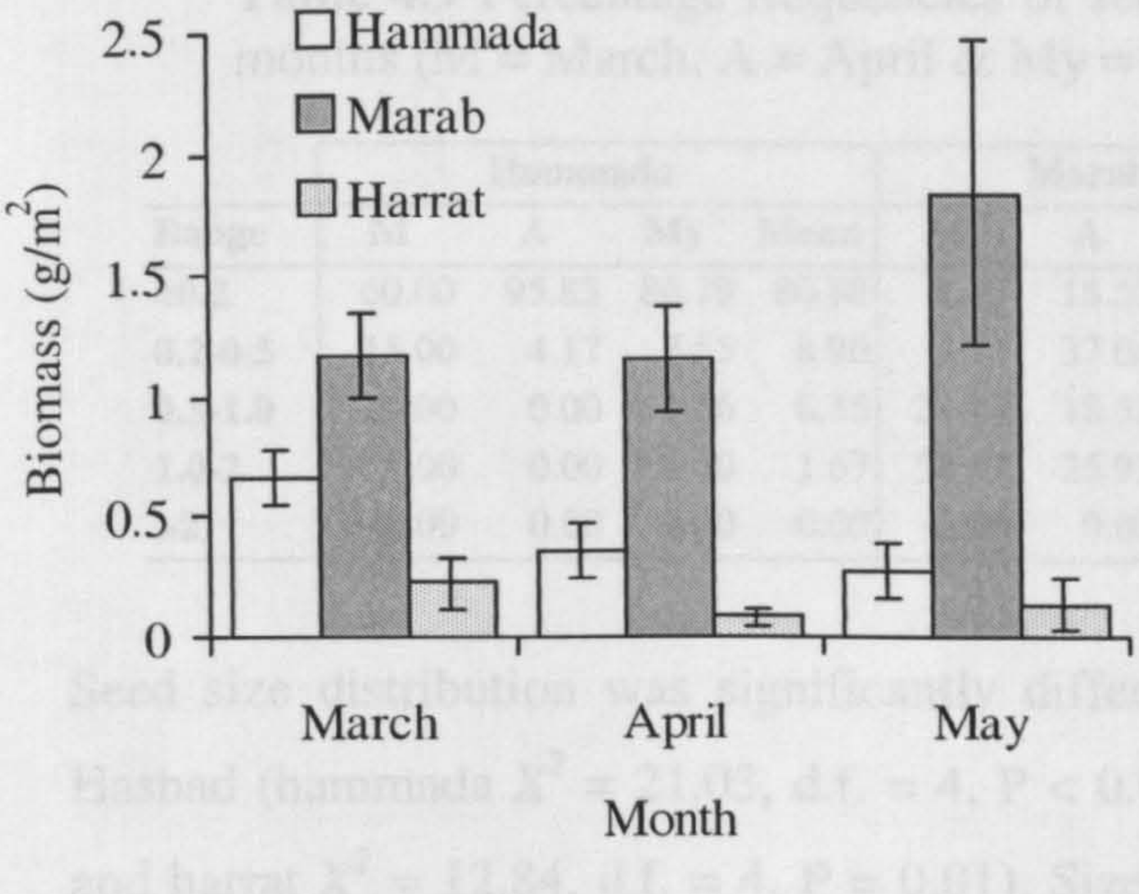
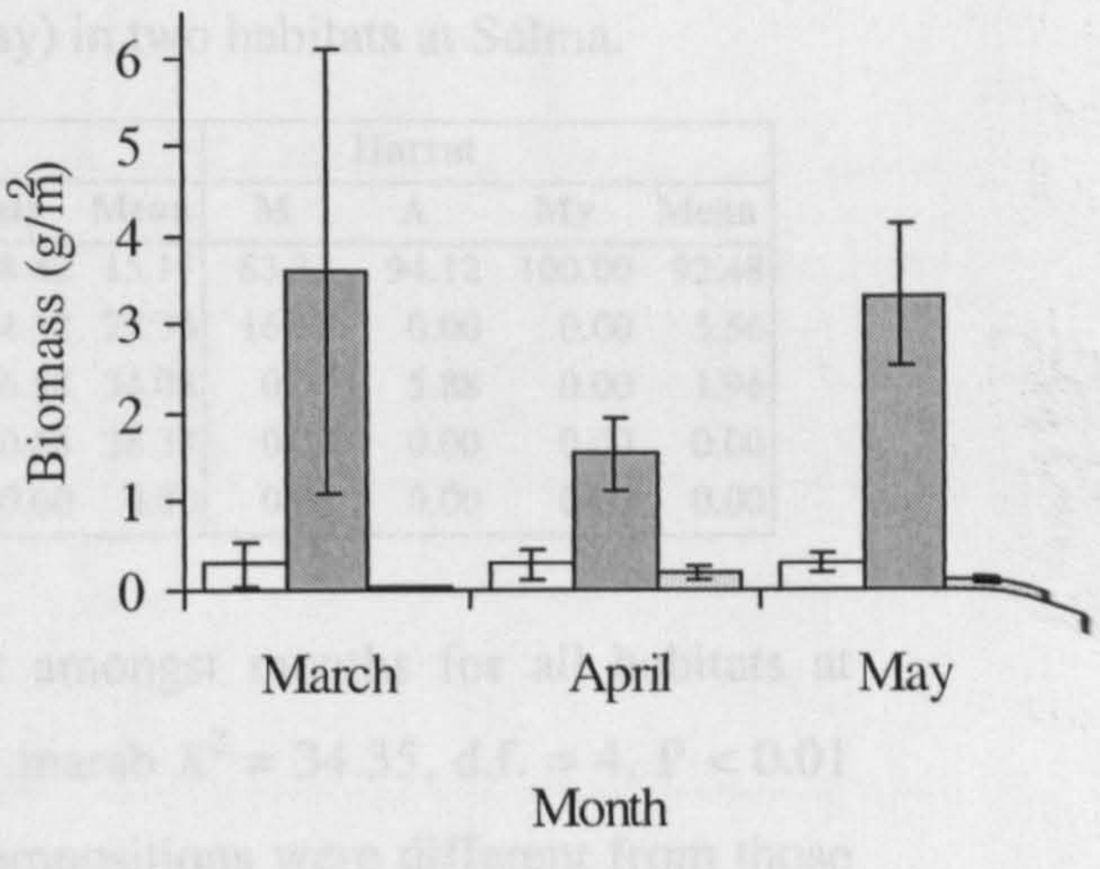


Figure 4.13 Soil seed bank biomass (g/m^2) measured over three months for a) Hashad and b) Salma, (n = 5 and S.E bars are shown)

4.13a Hashad



4.13b Salma



Initial statistical tests showed data were not normally distributed (Kolmogorov-Smirnov test: $P < 0.05$) and had unequal variances (F_{max}: $P < 0.05$). Hence, biomass values were normalised with a log transformation before using a parametric test (Three-way ANOVA). Figures 4.13 a and b clearly illustrate the differences in seed bank biomass amongst habitat types ($F = 24.14$, $P < 0.01$), with marab habitats showing the greatest seed biomass both at Salma and Hashad. Contrary to expectations (from the differences shown between sites for both seed production and seed rain), the difference

in the seed bank biomass between sites was not significant (F = 0.66, P = 0.419). Additionally, none of the differences amongst monthly seed bank biomass estimates were statistically significant (F = 1.10, P = 0.337).

4.3.3.2. Size distribution within the soil seed bank

To enable comparisons with seed production and seed rain, size distributions, and to investigate potential seed size selection by granivores, total seed bank densities were separated into categories of seed size. Results for the two sites and each habitat type are shown in Tables 4.8 & 4.9. Seed size distributions within the seed bank (no./m^2) were also plotted for individual species (n = 23, ranked in order of increasing size) for March, April and May in each site-habitat locality (Figures 4.14 j-r).

Table 4.8 Percentage frequencies of seed sizes within the seed bank over three months (M = March, A = April & My = May) in two habitats at Hashad.

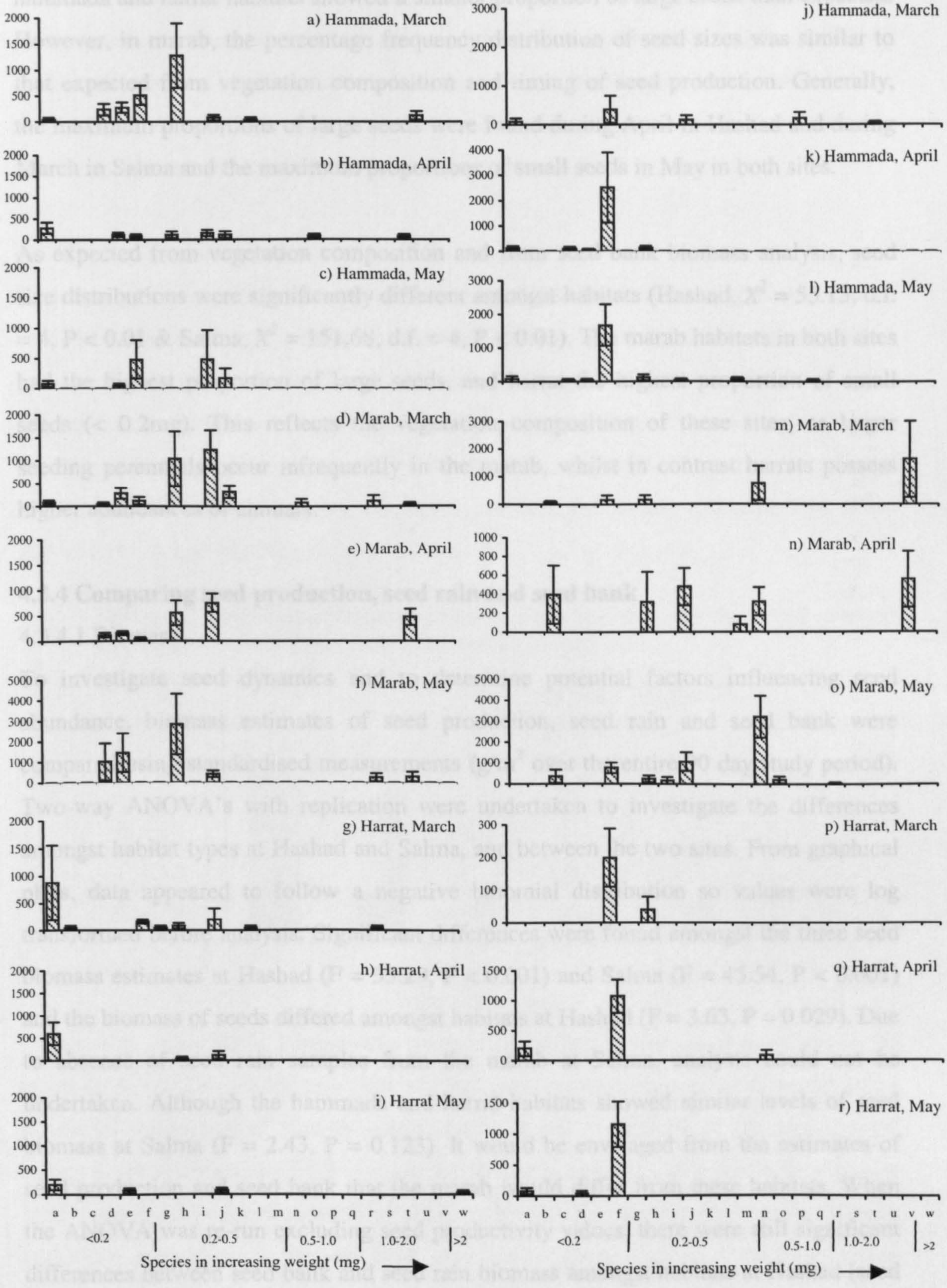
	Hammada				Marab				Harrat			
Range	**M**	**A**	**My**	**Mean**	**M**	**A**	**My**	**Mean**	**M**	**A**	**My**	**Mean**
<0.2	41.50	46.15	48.39	45.35	15.48	15.09	39.35	23.31	75.68	78.95	70.00	74.87
0.2-0.5	53.85	38.46	51.61	47.98	77.38	62.26	52.26	63.97	21.62	21.05	20.00	20.89
0.5-1.0	0.00	7.69	0.00	2.56	2.38	0.00	0.00	0.79	0.00	0.00	0.00	0.00
1.0-2	4.62	7.69	0.00	4.10	4.76	22.64	8.39	11.93	2.70	0.00	0.00	0.90
>2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	3.33

Table 4.9 Percentage frequencies of seed sizes within the seed bank over three months (M = March, A = April & My = May) in two habitats at Salma.

	Hammada				Marab				Harrat			
Range	**M**	**A**	**My**	**Mean**	**M**	**A**	**My**	**Mean**	**M**	**A**	**My**	**Mean**
<0.2	60.00	95.83	86.79	80.88	8.57	18.52	18.42	15.17	83.33	94.12	100.00	92.48
0.2-0.5	15.00	4.17	7.55	8.90	5.71	37.04	24.32	22.36	16.67	0.00	0.00	5.56
0.5-1.0	20.00	0.00	5.66	8.55	27.14	18.52	56.58	34.08	0.00	5.88	0.00	1.96
1.0-2	5.00	0.00	0.00	1.67	58.57	25.93	0.66	28.39	0.00	0.00	0.00	0.00
>2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Seed size distribution was significantly different amongst months for all habitats at Hashad (hammada X^2 = 21.03, d.f. = 4, P < 0.01, marab X^2 = 34.35, d.f. = 4, P < 0.01 and harrat X^2 = 12.84, d.f. = 4, P = 0.01). Size compositions were different from those expected from the plant density estimates (Table 4.1) and the timing of seed production (Fig. 4.5) in each habitat. In the hammada and marab habitats larger seeds were found less frequently in May than expected, whereas in the harrat habitats the proportion of large seed was greater than expected. It can been seen from Figure 4.14 that this is the result of the presence of *Bromus* spp.

Figure 4.14 Soil seed bank seed density (no./m^2) for Hashad (a-i) and Salma (j-r) in hammada marab and harrat habitats over three months (n = 5, S.E. bars are shown). a = *M. picta* , b = Grass C, c =*T. bovei* , d = *L. leyseriodes* , e = *D. hara* , f = Grass A, g = *A. factorovskyi* , h = *A. herba-alba* , i = Spp. R, j = *R. descursiva* , k = *P. eriocarpa* , l = *Crepis* spp., m = *R. vesicarius* , n = *P. ovata* , o = *S.linearis* , p = *T. stellata* , q = *E. glomeratum* , r = *E. deserti* , s = *P. rugulosum* , t = Spp.C., u = *L. album* , v = *M. laciniata* and w = *Bromus* .spp.



At Salma, significant differences in size distribution occurred between months (hammada, $X^2 = 48.655$, d.f. = 4, $P < 0.01$; marab, $X^2 = 108.14$, d.f. = 6, $P < 0.01$). The hammada and harrat habitats showed a smaller proportion of large seeds than expected. However, in marab, the percentage frequency distribution of seed sizes was similar to that expected from vegetation composition and timing of seed production. Generally, the maximum proportions of large seeds were found during April in Hashad and during March in Salma and the maximum proportions of small seeds in May in both sites.

As expected from vegetation composition and from seed bank biomass analysis, seed size distributions were significantly different amongst habitats (Hashad, $X^2 = 55.15$, d.f. = 4, $P < 0.01$ & Salma, $X^2 = 151.68$, d.f. = 4, $P < 0.01$). The marab habitats in both sites had the highest proportion of large seeds, and harrat the highest proportion of small seeds (< 0.2mg). This reflects the vegetation composition of these sites, as larger seeding perennials occur infrequently in the marab, whilst in contrast harrats possess higher abundances of annuals.

4.3.4 Comparing seed production, seed rain and seed bank

4.3.4.1 Biomass

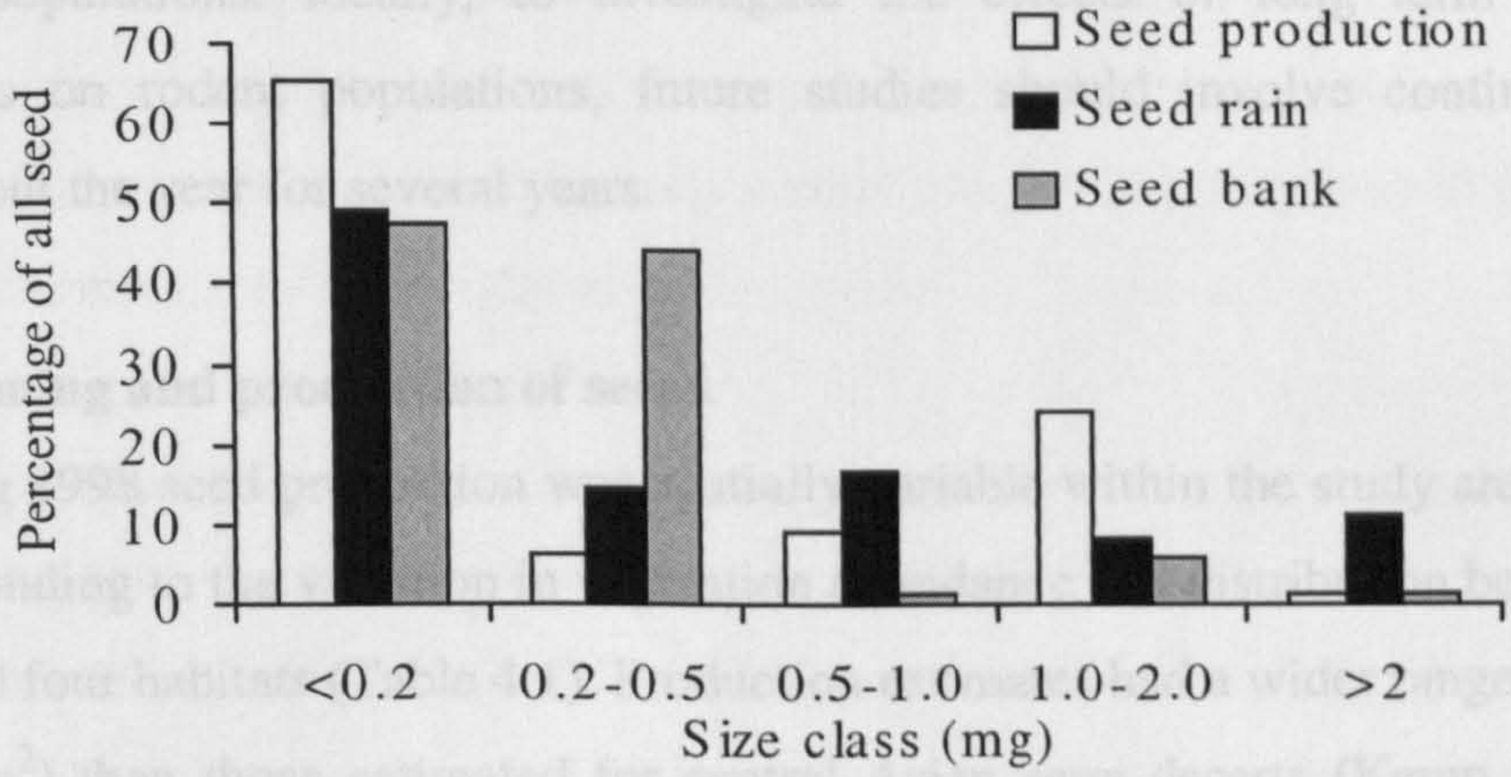
To investigate seed dynamics and to determine potential factors influencing seed abundance, biomass estimates of seed production, seed rain and seed bank were compared using standardised measurements (g/m^2 over the entire 90 day study period). Two-way ANOVA's with replication were undertaken to investigate the differences amongst habitat types at Hashad and Salma, and between the two sites. From graphical plots, data appeared to follow a negative binomial distribution so values were log transformed before analysis. Significant differences were found amongst the three seed biomass estimates at Hashad ($F = 35.29$, $P < 0.001$) and Salma ($F = 45.54$, $P < 0.001$) and the biomass of seeds differed amongst habitats at Hashad ($F = 3.63$, $P = 0.029$). Due to absence of seed rain samples from the marab at Salma, analysis could not be undertaken. Although the hammada and harrat habitats showed similar levels of seed biomass at Salma ($F = 2.43$, $P = 0.123$). It would be envisaged from the estimates of seed production and seed bank that the marab would differ from these habitats. When the ANOVA was re-run excluding seed productivity values, there were still significant differences between seed bank and seed rain biomass amongst habitats at Hashad (seed source, $F = 8.93$, $P = 0.003$; habitats $F = 6.51$, $P < 0.002$) and at Salma ($F = 5.54$, $P = 0.021$).

Spearman rank correlations were undertaken to see if spatial patterns of density estimates were similar between the three seed estimates. The densities of seed production and seed rain were significantly correlated ($r = 0.9$, $P = 0.037$), whereas there was no correlation found between seed rain and seed bank ($r = 0.1$, $P = 0.873$) or seed production and seed bank ($r = 0.371$, $P = 0.468$). This suggests that within a habitat the seed crop directly influences the seed rain, but neither seed rain or seed crop directly determine the numbers of seeds found in the seed bank.

4.3.4.2. Seed size distribution

To investigate the overall seed size frequency distribution between seed production, seed rain and seed bank, samples for Hashad were pooled and expressed as the percentage of seeds occurring in the different size categories (Figure 4.15). Chi-squared analysis showed there were significant differences in seed size frequency distribution between seed rain and seed bank ($X^2 = 80.74$, d.f. = 4, $P < 0.01$), seed rain and seed production ($X^2 = 63.92$, d.f. = 4, $P < 0.01$), and seed production and seed bank ($X^2 = 260.401$, d.f. = 4, $P < 0.01$).

Figure 4.15 Percentage frequency distribution of seed production, seed rain and seed bank for pooled samples from Hashad, spring 1998.



During the spring study period seed production contained the greatest proportion of small seeds (<0.2mg). Seed rain sizes differed from seed production sizes by containing a smaller proportion of smaller seeds and a greater proportion of the larger seeds (>2mg). Seed rain and seed bank sizes held similar proportions of seeds in the smallest seed category, a larger proportion of seeds in the 0.2-0.5mg category in the seed bank and lower proportions in the seed bank than the seed rain of all seed categories above 0.5mg.

4.4 DISCUSSION

This discussion focuses on the three sources of seeds which may be exploited by rodents; seeds on the plant, on the ground surface (seed rain) and in the soil seed bank. The main objective was to examine by how much and why the abundance and size of seeds varied between the two sites and four habitat types in spring 1998 and to discuss the implications of resource variations for rodent ecology.

4.4.1 Timing of investigation

Desert rodent populations have been shown to respond to temporal fluctuations in resource abundance, particularly the annual seed crop (Whitford, 1976). It is therefore assumed that resources in late-winter to spring, at a time when the majority of species in the Badia require additional resources for breeding (Harrison & Bates, 1991), may have the most pronounced effects on rodent population density and dynamics (Price & Joyner, 1997). My study was undertaken in spring when vegetation cover, seed production and seed dispersal are usually at their maximum after winter rains (Gutterman, 1993; Kemp 1989). Resource abundance is dynamic and it is probable that at other times of the year this will also have a direct influence on survival and hence rodent populations. Ideally, to investigate the effects of long term variations in resources on rodent populations, future studies should involve continual sampling throughout the year for several years.

4.4.2 Timing and production of seeds

In spring 1998 seed production was spatially variable within the study areas (Table 4.3) corresponding to the variation in vegetation abundance and distribution between the two sites and four habitats (Table 4.1). Production estimates had a wider range (120-111,600 seeds /m^2) than those estimated for central Asian semi-deserts (Kemp, 1989). Direct comparisons with data from other deserts are limited due to the deficiencies in those data and may be inappropriate as year, season and habitat will influence measurements.

Rare and non-seeding species at the time of study were excluded from production estimates. This may have resulted in a slight under-estimate of the actual seed crop. However, rare species are assumed to make a negligible contribution to the overall seed density and biomass. Only spring seeding species were intensively investigated, hence no annual seed production estimates can be made.

Spatial heterogeneity of vegetation (Table 4.1) may have resulted in an over- or under-estimation of plant densities and may have affected results derived from these values, e.g. seed production (Table 4.2). Annuals tend to have a clumped distribution, exhibiting mass germination in depressions where seeds and water accumulate (Kemp, 1983). Perennial shrubs, however, tend to show regular spacing, probably as a result of intra- or inter- specific competition. For example, high seedling mortality in the vicinity of adult plants was observed in the dominant perennial *Artemisia herba-alba*, possibly as a result of competition for water coupled with an inhibitory influence (Friedman & Orshan, 1975). However, when comparing the indices of dispersion of seeding perennials and annuals observed in my study (Table 4.1), there were no apparent differences between the degrees of clumping shown by the two life forms.

The use of direct multiplication techniques to determine seed production assumed that plants seeded only once during the study period, that pods and seeds were counted at the time of maximum seed production, and that the seeds collected were mature (Mallik *et al.*, 1984) and representative of normal seed size and weight (Table 4.2). Seed size can vary depending on the position within seeding structures (e.g. seedpod), position on plant, location of plant and environmental conditions at the time of maturation (Kemp, 1989). To compensate for variations in seed size, seeds and plants were sampled randomly. Since relative (and not absolute) values of seed density and biomass were calculated, inaccuracies incurred by the methodology will be equivalent for all samples and therefore permit direct comparisons.

Timing of seed composition and production of the seed crop (Figures 4.2 & 4.7 respectively) corresponded to previous reports for Negev desert and the observed skew towards smaller seeds was as expected for spring seeding dominated by winter annuals (Kemp, 1989). The tendency of perennials to seed later or produce seeds that are dispersed later in the summer or winter (Gutterman, 1993) was also evident in this study (Figures 4.5 & 4.6). As annuals were common in both sites at the time of study (see Tables 3.4 & 3.5), the overall temporal pattern of seeding tended to correspond at the two study sites (Fig 4.7). Variation in the timing of seed crop between sites suggests that Hashad and Salma experienced differences in environmental factors such as rainfall and temperature that influenced seeding. Correlation in the timing of seeding within Salma suggests that environmental factors regulating timing of seed production were similar between habitat types. Differences in plant community composition, in

individual plant responses to environmental conditions and in distribution of environmental resources within a locality (e.g. moisture) may all account for the differences in seeding time between sites and habitats.

4.4.3 Seed rain

Measures of seed rain (mean maximum of 160 seeds per m^2, 0.24g/m^2) corresponded to the annual averages estimated by Price & Joyner (1997) for a year of above average rainfall in the Mojave Desert: 262 seeds/m^2, 0.26g/m^2. Annual rainfall during my study year was reported to be slightly above average (see Fig. 3.1). Seed rain showed less spatial than temporal variation in the Badia as reported also for the Mojave Desert. However, low temporal variations in seed rain abundance at Hashad were possibly a consequence of low seed counts. The temporal patterns of seed production (Figs 4.5 & 4.6) tended to correspond to fluctuations in the subsequently estimated seed rain. Differences may result from the calculation assumption that seed dispersal was steady over the seeding period however, this may not be the case as seeds may be released *en masse* first and then the fewer remaining seeds dispersed over a longer period of time (Kemp, 1989).

When plant density estimates (Table 4.1), mean seed sizes (Table 4.2) and the timing of seeding (Figs. 4.5 & 4.6) were compared to the monthly changes in seed size distribution in the seed rain in the different habitats at Hashad (Tables 4.6), patterns did not agree with those expected. For example, in the hammada, *L. leyseriodes* (with a seed weight of 0.05mg) seeded during April, but no seeds of this size were found in the seed rain at this time. In the marab, *L. album* (seed size 1.52mg) seeded during May, but no seeds of this size were found during the study period in this habitat. Additionally, in the harrat, density estimates did not record any species with seeds above 0.05mg, but nearly 38% of the seed rain density in this habitat during May had seeds above 2mg. This was also the case at Salma (Table 4.7), in which three species, *P. ovata, E. bryonifolium* and *T. stellata*, all found seeding in the hammada habitat and having seeds in the size range 0.5-1.0 mg, were not found in the seed rain traps at any time during the trapping period. These results suggest that seed rain composition is not solely determined by seed production, but there are other factors that also influence composition, such as, the mechanism and timing of seed dispersal.

Differences in the species contributing to seed production and seed rain, and the low spatial differences in seed rain density between habitats, are possibly consequences of wind dispersal. Wind acts to 'diffuse' seeds from high release concentrations, and deposition into a habitat is dependent on the extent of seed catchment within the habitat type. Distance from site of production and seed dispersal distances will also determine the potential input to a site/habitat. Larger seeds tend to have shorter dispersal distances from parent plants and therefore may be over-represented in a habitat type compared to smaller seeds with greater dispersal distances. Experimental seed traps create artificial depressions in the soil that may increase the catch potential of a habitat that would normally have low input from the seed rain. The trapping apparatus may influence therefore the apparent spatial distribution of seed rain.

The majority of habitats found in the study area (as described in Chapter 3) are generally only sparsely vegetated (Tables 3.4 & 3.5), therefore comparisons of spatial distributions of seed rain amongst microhabitats within a habitat, such as 'open' and 'bush' habitats (Price & Joyner, 1997) were not appropriate for this study. Following the methodology of previous seed rain studies, only 'viable' seeds were recorded in seed extraction. Viability of seeds may be important in germination studies but may have less influence on selective predation by rodents. However, granivores avoided seeds of reduced viability as a result of fungal infection (Crist & Friese, 1993). Seeds less than 0.05mg were also excluded from the analysis, because it has been suggested that seeds of this size are not an important component of rodent diet (Brown *et al.*, 1979, Price 1983). Also, comparisons between seed rain and seed bank exclude this size range from calculations.

4.4.4 Seed Bank

Due to the spatial heterogeneity of seed banks (Reichman, 1984; Kemp, 1989; Price & Joyner, 1997) it would have been informative to collect more than five replicate samples per habitat per month. However, the cost of air transportation limited the sample number in my study.

The largest observed seed bank density and biomass values (6200 seeds/m^2, 3.7 g/m^2, Figure 4.12a), were similar to those previously recorded in open areas of the Mojave Desert during 1973/4 (Nelson and Chew, 1977). However, the seed bank was dramatically less than annual mean seed bank density estimated for the same desert by

Price & Joyner (1997), 106,000 seeds/m^2 or 38g/m^2 and less than the ranges given for North American hot deserts overall (8000-30000 seeds/m^2). It is difficult to compare values between deserts, particularly due to the inconsistency in sampling and the natural temporal and spatial fluctuations of the seed reserves. As the timing of seeding and germination varies between species, the timing of sample collection will affect the composition of the seed bank. Extended periods of germination may cause lower densities of seeds in the seed bank. As a consequence of above average and prolonged rainfall (Fig 3.1), seed density measured in my study may be lower than the mean annual estimates for this desert. However, it may be that the Jordanian desert is comparatively sparse in soil seed resources.

The size of the soil seed bank was similar over the three-month study period and showed similarities in overall biomass between the two sites. However, from the peaks in biomass (Fig 4.13 a & b), which varied between habitats and sites, patterns of change in seed bank biomass can be related to the timing of annual and perennial seeding. The harrat and hammada habitats at Hashad showed the largest mean biomass in March, corresponding to the timing of seeding of annual species, which were more abundant in these habitats than perennial species. Conversely, the marab at Hashad had its largest value in May, which would correspond to the tendency of perennials, the dominant life form in this habitat, to seed later (May-July). Spatial variability in the seed bank has been recorded previously (e.g. Price & Joyner, 1977) and has been the focus of several investigations into resource partitioning and habitat preferences (Price & Heinz, 1984; Price & Reichman, 1987) as mechanisms of co-existence in desert rodents (Brown *et al.*, 1979). Seed production (no.s/m^2) and the extent of granivory within a habitat will together determine the amount of newly produced seeds entering the seed bank.

4.4.5 Relationships between seed production, seed rain and seed bank

Seed production, seed rain and seed bank showed temporal and spatial variation in the seed sizes they contained. Larger seeds composed a greater proportion of the seed production than the seed rain (Figure 4.15). Differences in the size distribution between the seed bank and the seed rain may be the result of selective predation of larger seeds in the seed rain (Price & Joyner, 1997). Larger seeds are considered higher ranking prey items in foraging behaviour (Reichman, 1975) and may be easier to locate and manipulate than smaller seeds (Abramsky, 1984). Selective foraging by rodents would also cause an under-representation of large seeds in the seed bank (Reichman, 1975).

Dispersal mechanisms may facilitate the movement of seeds from one habitat type to another and may result in species compositions and size distributions in the seed rain and seed bank that differ from those in the seeding vegetation present (Tables 3.2, 3.3 & 4.1), e.g. harrat habitats where no perennial species were present had perennial seeds present in the seed bank (e.g. *P. rugulosum*). As most plant species occur in clumps, seed production is also clumped in space, whilst seed rain is more evenly distributed throughout a habitat. This redistribution from clumps to even spread accounts for the lower seed densities in the seed rain than measured for seed production. Particular species occurred in the seed rain soon after they were observed seeding. For example, *E. boveana* was found in seed traps in May (Fig. 4.11i), corresponding to the time of seeding (Fig 4.5d). Patterns of occurrence in the seed bank were less predictable, e.g. in Hashad, *L. leyseriodes* seeded in late April to May (Fig. 4.5g), was found in seed traps in May (Fig. 4.11c) but was present in the seed bank in March (4.12a), presumably from previous seedings. Species with smaller seeds (Table 4.2), e.g. Gramineae, *D. hara* & *R. descursiva,* did however tend to occur in the seed bank immediately following seeding (Figs. 4.5c, 4.5c & 4.5j, respectively).

4.4.6 Effects of resource abundance and seed size distribution on rodent foraging

Habitat selection by a foraging rodent will determine the resources available to it. These have been shown to be temporally and spatially variable between and within sites. In general, marab habitats possessed the most abundant seed resources in spring 1998 and offered additional protection to rodents against predation by a greater degree of shrub cover than other habitats (Abramsky *et al.*, 1996).

It has been suggested that the annual seed crop and the ability to harvest and store seeds may be important in determining fecundity and mortality in rodents. Therefore, temporal variation in the seed crop will be more important than spatial variation in the seed bank in determining rodent populations within a site (Price & Joyner, 1997). However, as most studies of spatial variation of resources have examined the microhabitat scale within habitats (and not between sites or macro-habitats), they provide little information on factors governing larger scale rodent community compositions. Within a habitat temporal variations in seed production may be important in determining rodent presence and abundance but between sites, overall levels of resource abundance, in terms of seeds and vegetation, could also be crucial. The effects

of resource abundance on the timing and output of reproduction will be examined in Chapter 5.

Lack of statistically significant temporal variation during spring in the seed bank density and the lack of correlation between the densities of seed production and seed bank in different localities, indicate that the sizes of the seed crop and seed rain have little effect on the seed bank. However, observed changes in species composition of the seed bank (Fig. 4.12) indicates that this resource is dynamic even if the density appears stable.

Utilisation of a proportion of the seed rain before it enters the seed bank may result from foraging economics of the rodents, as the seed rain tends to posses a higher proportion of energetically higher-ranking seeds than does the seed bank. As seed dispersal of annual and perennials tends to occur in different seasons, utilisation of the seed rain may be evident throughout the year, particularly in productive years. The seed bank may be a 'reserve' resource and become important only when vegetation and seed rain sources are scarce. Rodents have been shown to switch seed sources as their abundance changes and use different food types from month to month (Reichman, 1979). Seasonal changes in seed resources may also cause a shift in rodent activity and habitat use (M'Closkey, 1983). The temporal fluctuations in seed rain were more obvious in the wadi and marab habitats in Hashad and the marab and harrat habitats in Salma than in other habitats. If foraging behaviour followed resource availability these sites would be utilised more in the spring. Shifts in habitat use have been reported for *M. crassus* in response to seasonal changes in vegetation abundance (Krasnov *et al.*, 1996b). However, a preliminary study of habitat utilisation by *M. crassus,* at Hashad during the summer, showed that different habitats within the home range were equally utilised during foraging bouts (Maddox, pers comm.). This would be expected, if the spatially consistent seed rain was the main source of food during the summer. However, lack of habitat preferences during foraging may also be a consequence of abundant seed caches from the recent spring seed rain, which may act as the primary food source.

Temporal and spatial variation in the distribution of seed sizes may influence foraging behaviour. The seed rain (the suggested main seed source for rodents) in marab and hammada habitats held a wider range of seed sizes and a greater proportion of larger seeds than the harrat habitats at Hashad (Table 4.6). In the overall seed bank, the

hammada at Hashad and the marab at Salma possessed the greatest proportions of larger seeds. For a foraging rodent to maximise returns of larger (and therefore potentially higher ranking) seeds, these localities would need to be exploited more frequently during foraging than others. Utilisation of the different types of seed 'sources' by rodents is recommended as a future field study.

CHAPTER 5

THE INFLUENCE OF RESOURCE ABUNDANCE ON THE TIMING AND OUTPUT OF BREEDING IN DESERT RODENTS

5.1 INTRODUCTION & OBJECTIVES

This chapter reports investigations into the influence of natural resources on breeding in desert-living rodents. Firstly, it describes breeding patterns of several species in relation to the natural temporal and spatial variations in resources and secondly, the effects of supplementary feeding in one habitat type on the timing and extent of breeding in *M. crassus*.

5.1.1 Breeding studies

Periods of reproductive activity in Arabian small mammals have been deduced from observations of pregnancy or testicular development in the field, or from captive-bred animals (Harrison & Bates, 1991). Morphological descriptions of breeding condition for both male and female rodents are given in Gurnell & Flowerdew (1990). Similar classifications of sexual development have been used in studies of reproduction of desert rodents. For example, *M. crassus* females were classified as sexually active if the vagina was open or plugged, or the animal showed signs of lactation or pregnancy (Krasnov *et al.*, 1996b). The reproductive period of rodents inhabiting a study area varies depending on the species and the time and place where the individuals were trapped (Harrison & Bates, 1991). For example, the timing and duration of reproduction in *M. crassus* (see Krasnov *et al.*, 1996b) and other desert species have been shown to vary in different sites throughout Arabia (Harrison & Bates, 1991). Sex-related differences in the timing and extent of breeding within a species are also common, e.g. in *G. dasyurus* (Shenbrot *et al.*, 1997). The temporal and spatial variability in breeding activity in small mammals has frequently been associated with variations in food abundance.

5.1.2 Timing of reproductive activity in desert rodents

Reproduction in mammals is affected by the nutritional, physical and social status of the animals involved (Bronson, 1985). As reproduction and rearing offspring incurs high energetic costs, food availability will set a limit to the extent of these activities. Several

small mammals, particularly in tropical zones, breed throughout the year, suggesting that temporal changes in food availability are not limiting. Continuous breeders are opportunistic and use their present nutritional condition to determine the extent to which breeding should occur. In temperate regions where many resources fluctuate seasonally breeding is limited to specific times of the year at which reproductive success is assured (Nelson *et al.*, 1997), often associated with the periodic increases in food abundance. Timing of reproduction in seasonal breeders will therefore rely on cues and signals that accurately predict fluctuations in food (see Chapter 6).

As emphasised in previous chapters, desert environments tend to have less predictable fluctuations in food supply than other temperate habitats. As a consequence, to maximise reproductive success, the timing of reproductive activity should be linked to reliable cues that predict the abundance of necessary resources, for example to rainfall which influences new vegetation growth, which will in turn affect the seed crop. The relationship between rainfall and the onset of breeding has been demonstrated in several desert-living rodents from Africa (Perrin, 1980), Asia (Rogovin, 1985) and North America (Kenagy & Bartholomew, 1985). An opportunistic reproductive strategy has been proposed for desert-living rodents, as an adaptation to unpredictable resources (White & Bernard, 1999). This has been demonstrated in some heteromyid species (e.g. *Dipodomys merriami*) in which the females can reproduce at any time of year in response to rainfall and subsequent changes in resources (Degen, 1997). In opportunistic breeders the timing and control of reproduction is dependent on fluctuations in the resource, the species and sex of the individual and the population and habitat in which it occurs (White *et al.*, 1997).

It has been noted that many desert rodents tend to breed during the spring following precipitation-induced increases in plant growth and seeding. It would therefore be expected that, overall, rodents would exhibit similar patterns of annual breeding activity, but vary between years in relation to resource abundance. Species show different responses to environmental fluctuations (Shenbrot *et al.*, 1999), therefore potential variations in the precise timing of breeding activity between species would be expected. Additionally, sexes may differ, as females are more reliant on nutritional condition for breeding, i.e. resource abundance, whereas males tend to show more sexual opportunism.

5.1.3 Supplementary feeding experiments

As demonstrated in previous chapters, assessment of natural resource availability in the field is difficult. An alternative technique of investigating the effects of resource abundance on reproduction is to manipulate food abundance experimentally (Boutin, 1990). Such experiments have been used to investigate the structure of desert rodent communities (Brown & Munger 1985; Bowers *et al,* 1987), since the type and amount of food added influenced competition between species and therefore community composition. To date few experiments involving supplemental feeding have been undertaken in the field to investigate the effects of resources on breeding in arid-zone rodents (Neal & Alibhai, 1991; Hall & Morrison, 1998).

Various experimental methodologies have been used, but in general artificial food is supplied *ad libitum* spread evenly over an area at feeding stations. Supplementary feeding in one area should be run in parallel with a control area possessing similar species densities and composition and comparable levels of natural resources (e.g. Akbar & Gorman, 1993a). The size of the experimental area needs to be appropriate to the questions posed for the study species, and the duration of the experiment should depend on the time needed to influence the parameters under investigation. Total grid areas used in small mammal studies have varied from 24ha to less than 0.2ha, and have been conducted over time periods from 21 days (Neal & Alibhai, 1991) to several years. Long-term experiments over several years are required to address regulation of populations and demographic effects of food supply (Boutin, 1990).

Studies of the effects of resource abundance on small mammals have shown that an increase in food may have several effects on their behaviour and ecology. Supplementary food tends to decrease home range size (Broughton & Dickman, 1991; Akbar & Gorman, 1993b), a parameter directly related to the resource requirements of the individual and resource availability (McNab, 1963). However, addition of food to an area tends to attract other animals and therefore increase intruder pressure, which will also influence home range size (Boutin, 1990). Social organisation can also be affected by additions of food; for example, in Californian voles (*Microtus californicus*) females became aggregated and less territorial (Ostfeld, 1986). In general, food addition results in a two- to three-fold increase in rodent population density, depending on the environmental conditions at the time of application (Boutin, 1990). The increase in density is usually the result of direct nutritional affects on one or several stages in

reproduction. In supplementary-fed animals breeding tends to be advanced (Duquette & Millar, 1995), the length of the breeding season extended (e.g. Watts, 1970) and the proportion of adult breeding females increased (e.g. Sullivan *et al.*, 1983). In small mammals extra food provided has been shown to increase the number of offspring (Negus & Berger, 1977) and to increase juvenile body weight at birth, growth rate and survivorship (Sullivan & Sullivan, 1982). Food quality can also effect growth rates (Gross *et al.*, 1985) and social contact can effect densities (Batzli *et al.*, 1977). However, supplementary feeding experiments do not always have a significant effect on rodent populations (Krebs & De Long 1965; Duquette & Millar, 1995), particularly where food abundance is not considered an important factor limiting density.

5.1.4 Reproductive activity of *Meriones crassus*

In Israel, breeding in *M. crassus* occurs seasonally between February and September (Krasnov *et al.*, 1996b). Pregnant females have been caught throughout the year in the Negev desert, but the highest level of breeding occurred from February to May (Krasnov *et al.*, 1996b). Spring peaks were also recorded from studies throughout Arabia (see Harrison & Bates, 1991). Therefore it has been suggested that breeding may be under the control of changes in vegetation and seed abundance in relation to rainfall, or of photoperiod, or of a combination of the two (see Chapter 6). These and other factors may have further effects on specific stages of reproduction such as development and sexual maturity of juveniles.

It has been suggested that the life history strategy and population structure of *M. crassus* varies geographically, as this species has been reported to be both colonial (e.g. Lay 1967; Harrison & Bates, 1991) and solitary (Krasnov *et al.*, 1996b). The most detailed study from Arabia was undertaken in the Negev Highlands, Israel (Krasnov *et al.*, 1996b), where densities varied spatially and temporally with highest densities occurring on sand dunes. However *M. crassus* has been found frequently on open gravel plains (hammada) in Algeria (Daly & Daly, 1975, in Harrison & Bates, 1991), southern Israel (Zahavi & Wahrman, 1957), western Sahara (Petter, 1951, in Harrison & Bates, 1991) and eastern Iran (Petter, 1961, in Harrison & Bates, 1991). In Israel, sex-related differences were noted in body mass, which varied seasonally and annually in relation to winter temperature and rainfall. Young animals, in which the sex ratio was approximately equal, were observed from March to September following reproduction. Individuals were seasonally territorial, with a mean distance of 25.0m between

recaptures. Krasnov *et al.* (1996b) noted an activity pattern he described as 'residing-relocating-residing' with an average distance of relocation of approximately 50m. Short-term home ranges in *M. crassus* are thought to consist of the vicinity around a burrow and movement between burrows with longer-term home ranges incorporating several burrow systems. In a study undertaken during October–November, neither the duration of time spent in the vicinity of a burrow nor the distance of relocation varied between the sexes (Krasnov *et al.*, 1996b).

5.1.5 Objectives

In this chapter, data collected during1996-1997, on the timing and extent of breeding in male and female rodents, and the timing of juvenile recruitment are used to investigate spatial, temporal, sex-related and species variations in breeding performance. From these results, hypotheses are formulated on the effect of variations in food supply on breeding in males and females of different species. Secondly, spatial differences in breeding are described for two sites, Hashad and Salma, for spring 1998. The timing of breeding and of juvenile recruitment will be compared with the changes within the different habitat types in vegetation and seed abundance, as assessed in Chapters 3 and 4. Supplementary feeding experiments in hammada habitats at Hashad were undertaken to assess the effects of seed abundance on breeding activity in male and female *M. crassus*, and on the timing of juvenile recruitment.

5.2 METHODS

5.2.1 Study sites and trapping

Data collected on the breeding status and population structures of various species from the 1996 and 1997 studies (see Table 2.1 for study sites) were collated. The trapping grids used in the breeding studies were also used to track resource abundance in Hashad and Salma in 1998 (Table 3.1). Trapping methodology was similar to that described in Chapter 2 (see section 2.2.2.1), except that due to limited trap numbers, the grid configuration was reduced to 4 x 5 trapping stations at 20m intervals, with only one trap per station instead of two. (This was considered sufficient as previous results showed that only rarely were two individuals caught per trapping station). At Hashad an additional two 'half' grids (2 x 5 configuration) were also set up, one in hammada (HA) and one on harrat slope (Hslope). Trapping was undertaken for three consecutive nights in each of the grids. At Hashad four grids (three full and one half) were trapped for three nights and then traps were moved to the other four grids for the next three nights. This paralleled vegetation surveys and resulted in nine trapping periods at ten-day intervals, from 23rd February until 31st May 1998 (see Table 5.1). Half-grid trapping was initiated slightly later than other grids due to unavailability of traps. At Salma, due to time limitations, three grids were trapped simultaneously at monthly intervals (9th to 11th day of each month).

Table 5.1 Trapping times at for grids at Hashad, where H1, H2, H3, H4 and HA = hammada habitats, Har. = harrat, Mar = marab and Hsl = Harrat slope.

	Grids 1						Grids 2				
	Date	H2	H4	Har.	HA		Date	H1	H2	Mar	Hsl
1	3rd – 5th March	•	•	•		1	6th- 8th March	•	•	•	
2	13th- 15th March	•	•	•	•	2	16th- 18th March	•	•	•	•
3	23rd- 25th March	•	•	•	•	3	26th - 28th March	•	•	•	•
4	3rd- 5th April	•	•	•	•	4	6th- 8th April	•	•	•	•
5	13th - 15th April	•	•	•	•	5	16th - 18th April	•	•	•	•
6	23rd – 25th April	•	•	•	•	6	26th- 28th April	•	•	•	•
7	3rd – 5th May	•	•	•	•	7	6th- 8th May	•	•	•	•
8	13th – 15th May	•	•	•	•	8	16th -18th May	•	•	•	•
9	23rd –25th May	•	•	•	•	9	26th- 28th May	•	•	•	•

5.2.2 Breeding status, age and growth

Breeding condition and age was assessed for all individuals. Age was determined from body mass and breeding condition (e.g. Krasnov *et al.*, 1996b). Three age categories were identified, adult, sub-adult and juvenile. Table 5.2 shows the body mass ranges and breeding condition for each age group of four species. Where data on particular species were unavailable from the literature, age was determined from knowledge of adult body weight, breeding condition, pelage and relative body proportions, since juveniles tend to have larger heads in proportion to body size than adults.

Table 5.2 Size categories and characteristics in age classifications of four desert rodent species.

Age	Juvenile	Sub-adult	Adult	Reference
M. crassus	< 25g	25 -50g	50 – 60g & sexually mature or > 60g	Krasnov *et al.* (1996b)
G. dasyurus	< 15g	15 - 18g	19 – 21g & sexually mature or > 21g	Shenbrot *et al.* (1997)
G. henleyi	-	< 9g	> 9g	Shenbrot *et al.* (1994)
J. jaculus	< 40g	-	> 40g	Happold (1967)

Males were deemed reproductively active if their testes were either slightly descended or developed, and non-reproductive if testes were abdominal or reduced. Females were considered to be reproductively active if there was an indication of recent copulation (perforate vagina; vaginal plug), pregnancy (distended abdomen; swollen vagina; obvious nipples) or lactation (milk production; nipple halos), and considered non-reproductive if the vagina was imperforate and showed none of the above signs. Animals of sub-adult body weight were classified as adult if reproductively active (Krasnov *et al.*, 1996b). Growth (g/day) was calculated from juvenile recaptures by dividing the net gain in body weight (g) by the number of days between consecutive captures.

5.2.3 Supplementary feeding experiments

5.2.3.1 Feeding stations

This experiment attempted to assess the effects of additional food supplementation on the timing and output of breeding, and subsequent juvenile development in *M. crassus*,

of which a population was maintained at the University of Durham to undertake comparative laboratory experiments (see Chapter 6). To obtain sufficient data, hammada habitat was selected since trapping has demonstrated high densities of *M. crassus;* up to 8 individuals/ha were found within this habitat type (see Appendix II).

At Hashad three treatments were applied to five grids in hammada habitat (see Table 5.3). The grids were surveyed initially for burrows of *M. crassus,* to ensure potentially comparable densities between replicates. An 'early' supplementation of barley seed was applied to two hammada grids (H3 & H4) at the onset of the study, 24th February 1998. A second 'late' application was applied to two grids H1 & H2 in mid-April and the final grid received no supplementation (Control). Supplementary seed was left *in situ* for approximately 41 days after which it was excavated and deposited away from the study site.

Table 5.3 Timing of application and duration of seed supplementation in five hammada grids at Hashad during spring 1998.

	Treatment	Application	Extraction	Duration (days)
HA	Control	Nil	-	83
H1	Late	14th April 1998	25th May 1998	41
H2	Late	10th April 1998	22nd May 1998	42
H3	Early	24thFebruary 1998	6th April 1998	41
H4	Early	24th February 1998	6th April 1998	41

Within each treatment grid 12 alphabetically coded feeding stations were marked out, each station being situated in the middle of each square formed by the trapping grid configuration (Fig 5.1). Feeding stations consisted of a square depression, (50cm x 50cm by 5 cm depth) lined with a plastic sheet, to which 1.5 kg of barley seed was added (18kg in total). Seeds were then covered with a layer of soil, submerging them 2cm below the soil surface (Fig 5.2).

Figure 5.1 Arrangement of feeding stations (squares) within the trapping grid area. Points represent trapping stations. Not to scale.

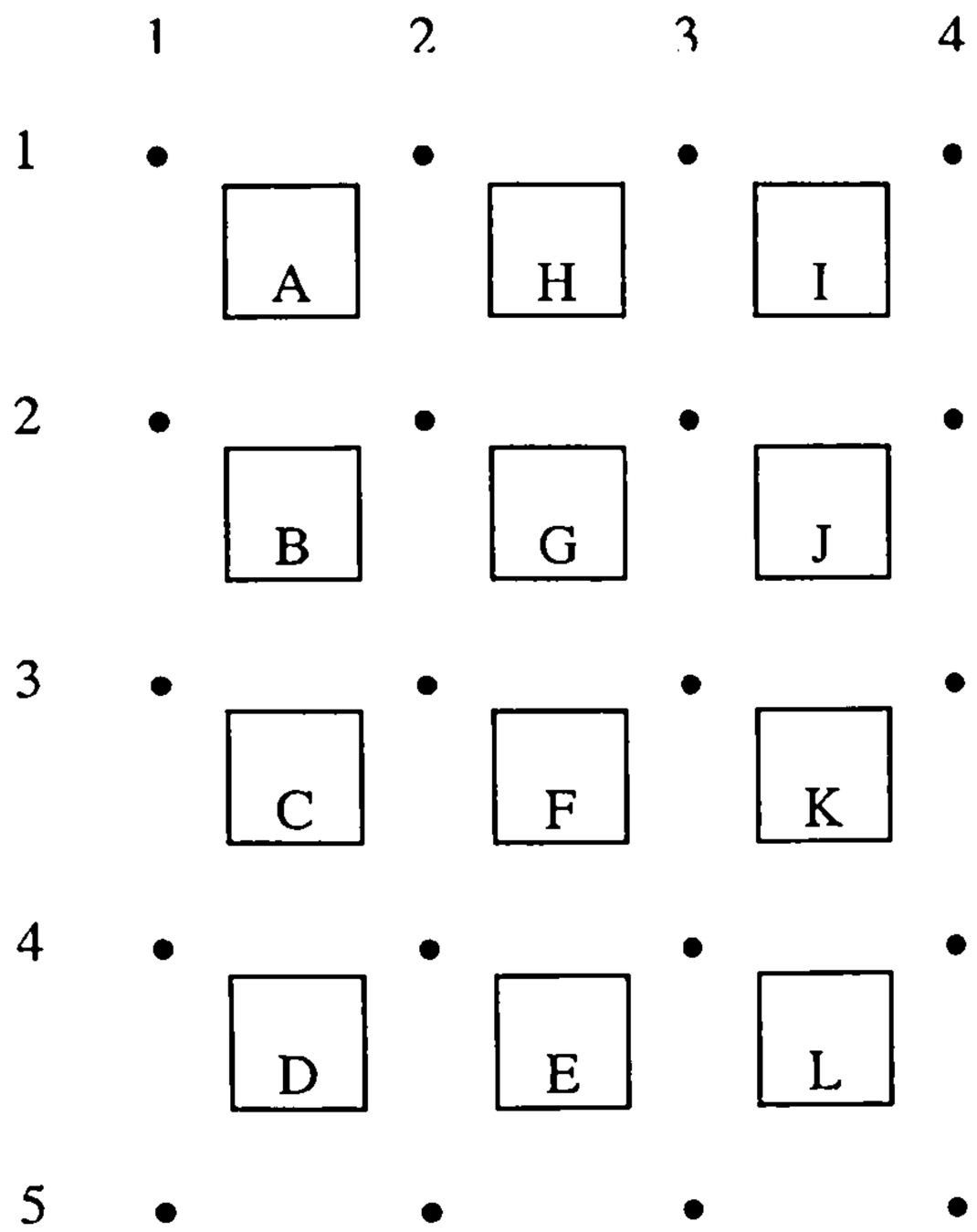
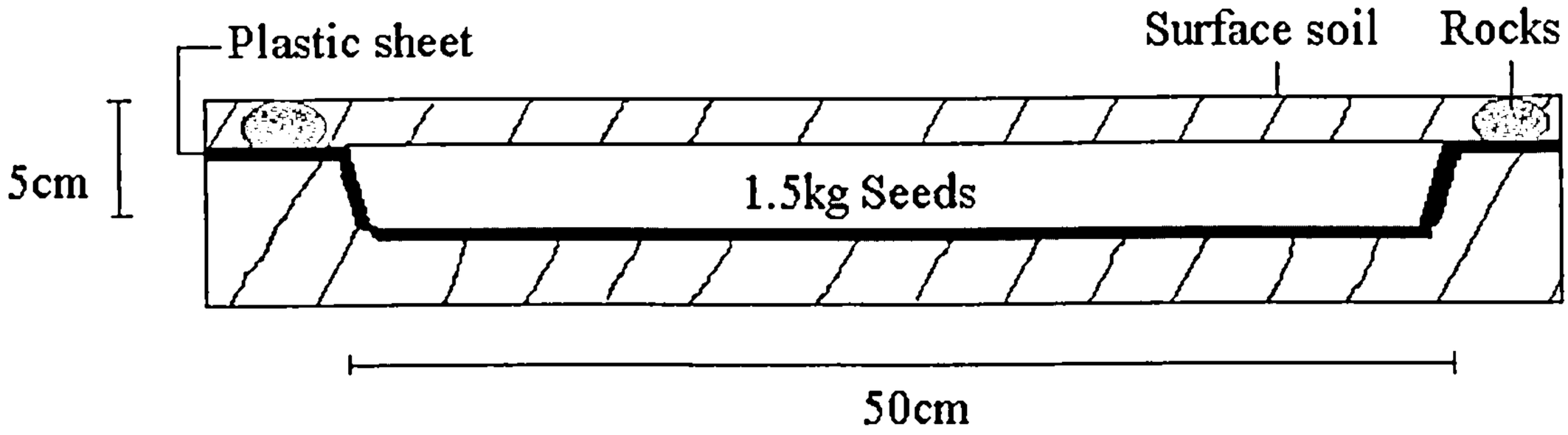


Figure 5.2 Cross-section view of a feeding station.



5.2.3.2 Preliminary observations to assess predation at feeding stations

It has been previously reported that both granivorous ants and birds forage predominantly on surface seeds (Brown *et al.*, 1979). Therefore, to prevent/reduce predation by granivores other than rodents, seeds were buried. However, from preliminary observations it was evident that due to nightly excavations by rodents, seeds were regularly left exposed on the soil surface, where they were vulnerable to ant and bird predation. In an attempt to reduce predation, seeds were re-buried by smoothing each station with a trowel each morning, so that no seeds were visible. 'Smoothing' was undertaken whenever possible.

5.2.3.3 Bird predation

Four feeding stations, two undisturbed and two artificially disturbed (using a trowel) were set up to investigate bird predation on smoothed and non-smoothed areas. Stations were covered with a plastic sheet over-night to prevent rodent predation and left uncovered during the day (approximately 8 hours). Every evening for three days evidence of diurnal bird activity was assessed from the number of bird footprints and scratches. From these observations there was little or no predation from birds at the non-disturbed stations. Therefore, smoothing was considered to reduce, but not wholly prevent bird predation and incorporated into the methodology.

5.2.3.4 Ant predation

From initial observations, ant predation appeared low and tended to occur on disturbed rather than non-disturbed feeding stations. However, in the later stages of the experiment, possibly as a consequence of warmer weather (and the abundant seed resources provided), several feeding stations were clearly heavily foraged by ants. Ant predation was not exclusively diurnal and sites appeared to be localised but unpredictable. Therefore no obvious method of prevention was available during the study period. The localities of heavily foraged grids were recorded and excluded from the analysis.

5.2.3.5 Rodent predation

The smoothing of feeding stations also enabled monitoring of rodent utilisation over-night. In early March the number of digs, the species identity of prints and the presence of husks were noted for each station for five consecutive mornings (Appendix IV). Rodent prints were identified from observations of actual prints formed by the rodent during release after trapping. As husking by either birds or ants is uncommon, this was deemed as evidence of rodent granivores utilising the stations. Visual observations confirmed that *M. crassus* were frequently utilising the feeding stations.

5.2.3.6 Assessing the amount of seed taken from feeding stations

It was initially intended to re-weigh the seed remaining in the feeding station to calculate predation rates and confirm that the amount of seed available to rodents throughout the time period was *ad libitum*. Sieving and floatation techniques were attempted but proved neither feasible nor practical. Therefore a sub-sampling method was devised;

The content of one randomly selected feeding station was excavated, mixed thoroughly and the total weight measured. Five sub-samples, approximately 1% of the total weight, were taken randomly from the seed-soil mix and the seed content of each sorted by hand. The percentage weight of seed in each sub-sample was measured and the mean, standard error and 95% confidence intervals calculated. These values were then extrapolated for the whole station. Additionally, one whole feeding station was sorted by hand and the total *actual* seed weight measured. The technique was considered reliable if the proportion of the seed content in the whole sample fell within the 95% confidence limits calculated from the sub-samples (see results for worked example). This method was then used to calculate the remaining seeds in six randomly selected feeding stations from each grid.

5.3 RESULTS

5.3.1 The natural timing and output of breeding – data from 1996 and 1997

A pilot study was undertaken to investigate the seasonal changes in the proportions of breeding females, breeding males and juveniles of all species, using data from field based community studies undertaken in 1996 and 1997 (Chapter 2). Tables 5.4 and 5.5 show the proportion of sexually active adult males and females in spring 1996 and 1997 and summer 1996.

Table 5.4 Proportion of males showing sexual activity during the study period 1996-1997, N = number of individuals examined.

Species	Spring 96		Summer 96		Spring 97	
	Proportion	N	Proportion	N	Proportion	N
G. dasyurus	0.38	24	0.73	11	0.89	18
G. nanus	1.00	12	0.38	8	0.40	5
G. henleyi	1.00	1	-	0	1.00	3
G. cheesmani	1.00	1	0.20	5	1.00	5
A. russatus	-	0	-	0	0.67	3
J. jaculus	0.50	2	-	0	0.50	2
M. tristrami	1.00	1	-	0	-	0
M. crassus	0.64	11	0.29	7	0.90	10
M. libycus	1.00	4	0.00	2	1.00	2

Table 5.5 Proportion of females showing sexual activity during the study period 1996-1997, N = number of individuals examined.

Species	Spring 96		Summer 96		Spring 97	
	Proportion	N	Proportion	N	Proportion	N
G. dasyurus	0.53	17	0.60	5	0.94	17
G. nanus	0.17	12	0.13	15	0.82	11
G. henleyi	1.00	1	-	0	1.00	7
G. cheesmani	0.25	4	0.50	2	0.67	3
A. russatus	1.00	1	-	0	0.80	5
J. jaculus	0.57	7	-	0	0.80	10
M. tristrami	1.00	1	-	0	-	0
M. crassus	0.00	5	0.00	2	1.00	10
M. libycus	0.20	5	0.00	1	1.00	1

Tables 5.4 and 5.5 show differences between species in the proportion of animals breeding during each study period. For example, in spring 1996 all the *G. nanus* males examined were sexually active, whereas only 38% of male *G. dasyurus* were sexually active; in 1997 *G. dasyurus* males were more sexually active than *G. nanus* males. For males of each species examined, with the exception of *G. dasyurus*, there was a decrease in the proportion of males breeding between spring and summer 1996 and

except for *G. nanus* an increase in breeding from summer 1996 to spring 1997. However, there was no consistent difference between species in male sexual activity between the two springs. All species except *A. russatus* showed similar or higher proportions of breeding females in spring 1997 compared to spring 1996. Data were too sparse for summer 1996 to compare female breeding between seasons in 1996, but for the few species for which data were available, there appeared to be little difference in the proportion breeding. There was no significant difference in sexual activity between males and females of all species during either spring 1996 (U = 20.5, n = 8, n = 9, P = 0.115, non parametric Mann-Whitney U test), summer 1996 (U = 10.0, n = 5, P = 0.597) or spring 1997 (U = 28.0, n = 8, P = 0.666).

The proportion of adults breeding was followed at two sites, Salma and Hazim, during spring 1997 (March, April and May). It was expected that there would be a decrease in sexual activity later in the spring, however Tables 5.6 and 5.7 show that for the individuals captured there was no general decrease in the proportion of animals breeding for either males or females during the three months. Data were too sparse to allow statistical analysis. Table 5.8 shows the proportion of juveniles captured during spring 1996, summer 1996 and spring 1997, and Table 5.9 shows the proportion of juveniles over three months during spring 1997.

Table 5.6 Proportion of adults reproductively active in three species at Salma during spring 1997, (-) indicates no data available, N = number of individuals examined.

	Sex	March	N	April	N	May	N
G. dasyurus	Male	1.00	6	0.75	4	1.00	5
	Female	1.00	6	1.00	3	0.92	6
A. russatus	Male	1.00	1	0.50	2	-	-
	Female	0.50	2	1.00	1	1.00	2
M. crassus	Male	-	-	-	-	1.00	1
	Female	-	-	-	-	-	-

Table 5.7 Proportion of adults reproductively active in six species at Hazim during spring 1997, (-) indicates no data available, N = number of individuals examined.

	Sex	March	N	April	N	May	N
G. henleyi	Male	0.33	3	-	-	1.00	1
	Female	0.67	3	1.00	4	0.50	2
M. crassus	Male	1.00	1	0.50	2	1.00	2
	Female	1.00	3	-	-	1.00	2
G. nanus	Male	1.00	1	1.00	1	1.00	1
	Female	1.00	2	1.00	2	1.00	3
M. libycus	Male	-	-	1.00	1	1.00	1
	Female	-	-	-	-	-	-
G. cheesmani	Male	-	-	1.00	1	1.00	1
	Female	-	-	-	-	1.00	1
J. jaculus	Male	-	-	1.00	1	-	-
	Female	-	-	0.50	2	-	-

Table 5.8 Proportion of juveniles in captures in all sites during the study period 1996-1997, N = number of individuals captured.

Species	Spring 96		Summer 96		Spring 97	
	Proportion	N	Proportion	N	Proportion	N
G. dasyurus	0.03	31	0.06	30	0.16	37
G. nanus	0.26	17	0.35	17	0.24	16
G. henleyi	0.00	5	-	0	0.00	10
G. cheesmani	0.00	7	0.00	7	0.25	3
A. russatus	0.00	1	-	0	0.20	8
J. jaculus	0.00	9	-	0	0.29	10
M. tristrami	-	0	0.50	1	-	0
M. crassus	0.00	13	0.20	4	0.31	18
M. libycus	0.00	5	0.00	2	0.20	4

Table 5.9 Proportion of juveniles in captures during March, April and May 1997 in Hazim and Salma study sites only. N = the total number of animals captured.

Species	March		April		May	
	Proportion	N	Proportion	N	Proportion	N
G. dasyurus	0.00	12	0.11	9	0.22	18
G. nanus	0.14	7	0.00	4	0.5	6
G. henleyi	0.00	3	0.00	3	0.00	4
G. cheesmani	0.00	0	0.00	1	0.33	3
A. russatus	0.00	3	0.40	5	0.00	2
M. crassus	0.25	4	0.00	2	0.41	17
M. libycus	0.00	1	0.00	1	0.00	2

There were differences in the proportion of juveniles captured amongst species (Tables 5.8 and 5.9). For three species, juveniles formed a higher proportion of the number of animals captured in summer 1996 than spring 1996 and in seven species juveniles

formed a larger part of the animals trapped in spring 1997 than in spring 1996. In general, juveniles comprised a greater proportion of the captures in May, except for *A. russatus*, which had the largest proportion of juveniles during April, and *M. libycus*, for which no juveniles were caught.

5.3.2 Breeding data from 1998 field studies

As habitats contain different resource abundance, it should be possible to investigate the effects of resources on rodent density and breeding activity in the field by comparing areas of high and low abundance. However in practice this is more difficult, as the extent of breeding varies between species and, as demonstrated in Chapter 2, habitats vary in the rodent species they contain. Furthermore, I have previously shown that resources are spatially and temporally variable within and between sites and habitats.

5.3.2.1 Resource abundance and rodent density

The density of rodent species in each of the trapping grids was calculated to allow comparisons between habitat types during spring 1998 (Table 5.10).

Table 5.10 Density per hectare of four species (MC = *M. crassus*, G.D = *G. dasyurus*, M.L. = *M. libycus* and AR = *A. russatus*), for each of the trapping grids during spring 1998. Hslope = harrat slope and H1-4 are hammada replicates. Hashad n = 9 trapping periods and Salma n = 3 trapping periods.

	Hashad								Salma					
	M.C.		**G.D.**		**M.L.**		**A.R.**		**M.C.**		**G.D.**		**M.L.**	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
H1	5.41	0.81	0.41	0.30	0.00	0.00	0.00	0.00	0.00	0.00	1.25	0.73	0.00	0.00
H2	1.80	0.43	0.41	0.30	0.41	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
H3	6.11	1.16	0.14	0.14	0.28	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
H4	8.60	1.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Marab	1.80	0.43	0.41	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.41	0.24
Harrat	1.95	0.66	2.36	0.44	0.14	0.14	0.00	0.00	0.41	0.24	5.84	0.64	0.00	0.00
Hslope	0.00	0.00	11.78	2.46	0.00	0.00	10.36	1.48	0.00	0.00	0.00	0.00	0.00	0.00

It can be seen from Table 5.10 that sites and habitats differed in species composition and density. Density data were not normally distributed ($P < 0.01$, Kolmogorov-Smirnov test). There was a significant difference in the density of *M. crassus* in the four hammada replicates ($X^2 = 15.196$, d.f. = 3, $P < 0.01$ Kruskal-Wallis) and significant differences between habitats within Hashad in the density of both *M. crassus* ($X^2 = 17.08$, d.f. = 2, $P < 0.01$) and *G. dasyurus* ($X^2 = 5.272$, d.f. = 2, $P = 0.072$). Within the

Hashad harrat habitat there were significant differences in *G. dasyurus* densities between the harrat slope and plain (U = 1, n = 7, n = 9, P = 0.001, Mann-Whitney U). *Gerbillus dasyurus* densities in the harrat at Hashad and Salma also showed differences between the two sites (U = 1.5, n = 9, n = 3, P < 0.05).

Individual species densities (excluding *A. russatus* for which data were deficient) and the total density of rodents within each habitat were compared with the mean cover of annuals (Table 3.7), perennials (Table 3.8), the summed total vegetation cover, seed density and seed biomass (Table 4.3). Using Spearman rank correlation there were no significant correlations at the 5% level of probability between densities of individual species and vegetation cover of annuals (*M. crassus*, r = -0.646, P = 0.060; *G. dasyurus*, r = 0.218, P = 0.573; *M. libycus*, r = -0.032, P = 0.934), but total rodent density was significantly negatively correlated with this (r = -0.678, P = 0.045). Likewise individual species were not significantly correlated with vegetation cover of perennials (*M. crassus*, r = -0.268, P = 0.486; *G. dasyurus*, r = 0.164, P = 0.672; *M. libycus*, r = 0.345, P = 0.363) and total rodent density was correlated only at the 7% level (r = -0.627, P = 0.071). There were significant negative correlations between overall vegetation cover and (i) *M. crassus* and (ii) total rodent densities (*M. crassus*, r = -0.681, P = 0.044; Total, r = -0.717, P = 0.03, Spearman rank correlation).

High vegetation cover and very low rodent densities in the marab at Salma could have biased results, so analyses were re-run excluding this habitat type. The reduced data sets showed no significant correlations between rodent densities and vegetation cover of annuals (*M. crassus*, r = -0.536, P = 0.176; *G. dasyurus*, r = 0.675, P = 0.066; *M. libycus*, r = -0.453, P = 0.260; Total, r = -0.539, P = 0.168) or of perennials (*M. crassus*, r = -0.013, P = 0.976; *G. dasyurus*, r = 0.143, P = 0.736; *M. libycus*, r = 0.058, P = 0.891; Total, r = -0.457, P = 0.255). Additionally, there were no correlations between total vegetation cover and rodents for *M. crassus*, (r = -0.587, P = 0.126), *M. libycus*, (r = -0.453, P = 0.260) or total rodent density (r = -0.595, P = 0.120), but a marginally significant positive correlation with *Gerbillus dasyurus* was found (r = 0.708, P = 0.050). Overall, rodent densities were not positively correlated with vegetation abundance within the immediate habitat where the species was trapped.

Meriones crassus densities were significantly negatively correlated with both density (r = -0.986, P < 0.001) and biomass of seeds (r = -0.841, P = 0.036). No other densities of

individual species or total rodents were correlated with either seed density (*G. dasyurus*, r = -0.203, P = 0.700; *M. libycus*, r = 0.338, P = 0.512; Total, r = -0.657, P = 0.156) or seed biomass (*G. dasyurus*, r = -0.232, P = 0.658; *M. libycus*, r = 0.169, P = 0.749; Total, r = -0.371, P = 0.468).

5.3.2.2 Breeding activity and juvenile emergence in 1998

Data were processed to enable the proportion of juveniles within the population and the proportion of breeding males and females to be calculated for each trapping session in 1998. These parameters were then compared between species and habitats, and with changes in vegetation cover. As only three monthly samples were taken at Salma, correlation analysis was not undertaken. Data were also too sparse to attempt to correlate any of the breeding parameters of *M. crassus* and *G. dasyurus* within harrat habitat. On the harrat slope there was no significant correlation between *A. russatus* and *G. dasyurus* in the timing of breeding of males (r = 0.385, n = 7, P = 0.394, Spearman rank correlation) or in the proportion of juveniles (r = 0.737, n = 7, P = 0.059) trapped, although the latter was close to normally accepted levels of significance. This suggests that offspring of the two species may have occurred at similar times, in early April. Unfortunately, as this was a supplementary study site, no changes in vegetation parameters were tracked. In the harrat, *M. crassus* juvenile recruitment (the proportion of juveniles amongst all animals trapped) was not correlated with changes in vegetation cover (r = -0.607, n = 7, P = 0.149).

There was no significant correlation between the proportions of juveniles among *A. russatus* and *M. crassus* trapped on different dates on the hammada (r = -0.211, n = 7, P = 0.650) or on the harrat (r = -0.685, n = 7, P = 0.090). On the harrat *M. crassus* juveniles were more prevalent in the trapped population later in the spring, i.e. in May, whereas in the hammada they were consistently present between March and May. Hence, there was no correlation between juvenile presence in the two habitats (r = 0.652, n = 7, P = 0.057). In comparison *A. russatus* showed a bimodal pattern in the proportion of juveniles trapped, one peak occurring during early April and the second during late May. There was no significant correlation between the proportions of juveniles among *G. dasyurus* and *M. crassus* trapped on different dates on the hammada (r = -0.476, n = 7, P = 0.280) or in the harrat (r = -0.516, n = 7, P = 0.236), as *G. dasyurus* juveniles were trapped only in early April. All other data were insufficient for analysis. In general the timing of breeding activity and juvenile emergence as judged

from trapping during spring 1998 differed between species, and within species between habitat types. Neither the timing of breeding nor juvenile recruitment were correlated with changes in vegetation cover.

5.3.3 Manipulation of seed resources

5.3.3.1 Assessing seed remains at feeding stations

Estimates of mean weights of seed remaining after approximately 40 days of predation, and hence of the mean seed loss per night, were made at six randomly selected feeding stations per grid. None of the stations selected had previously suffered extreme levels of predation by ants. On one occasion heavy rain occurred immediately before sub-sampling, which might have altered the validity of the technique. To allow for water content of the soil-seed mix, the sub-samples were separated into soil and seed fractions, and then weighed before and after drying (for approximately 1 week to constant weight). The water content was then allowed for, when the seed content of the whole sample was calculated.

5.3.3.2 The sub-sampling technique: A worked example

Table 5.11 shows sub-sample weight (g), the proportion of the total soil-seed mix weight, the seed content (g) and the proportion of seed in each of the five sub-samples. The total weight of the soil-seed mix was 3475g.

Table 5.11 Parameters recorded during sub-sampling to estimate the remaining seed content of feeding stations. Numbers 1-5 are the sub-samples.

No.	Weight of sub-sample (g)	Proportion of total weight	Seed content of sub-sample (g)	Proportion of seed in sub-sample
1	35	0.010	5	14.3
2	37	0.011	8.5	23.0
3	41	0.012	10	24.4
4	53	0.015	11	20.8
5	49	0.014	10	20.4

Proportion of seed in the sub-sample (mean = 20.58 & S.E. = 1.73).

Therefore, 95% confidence limits = Mean ± (S.E.*1.96)

= 20.58 ± (1.73 *1.96)

= 17.189 to 23.971

Total weight of soil-seed mix = 3475g,

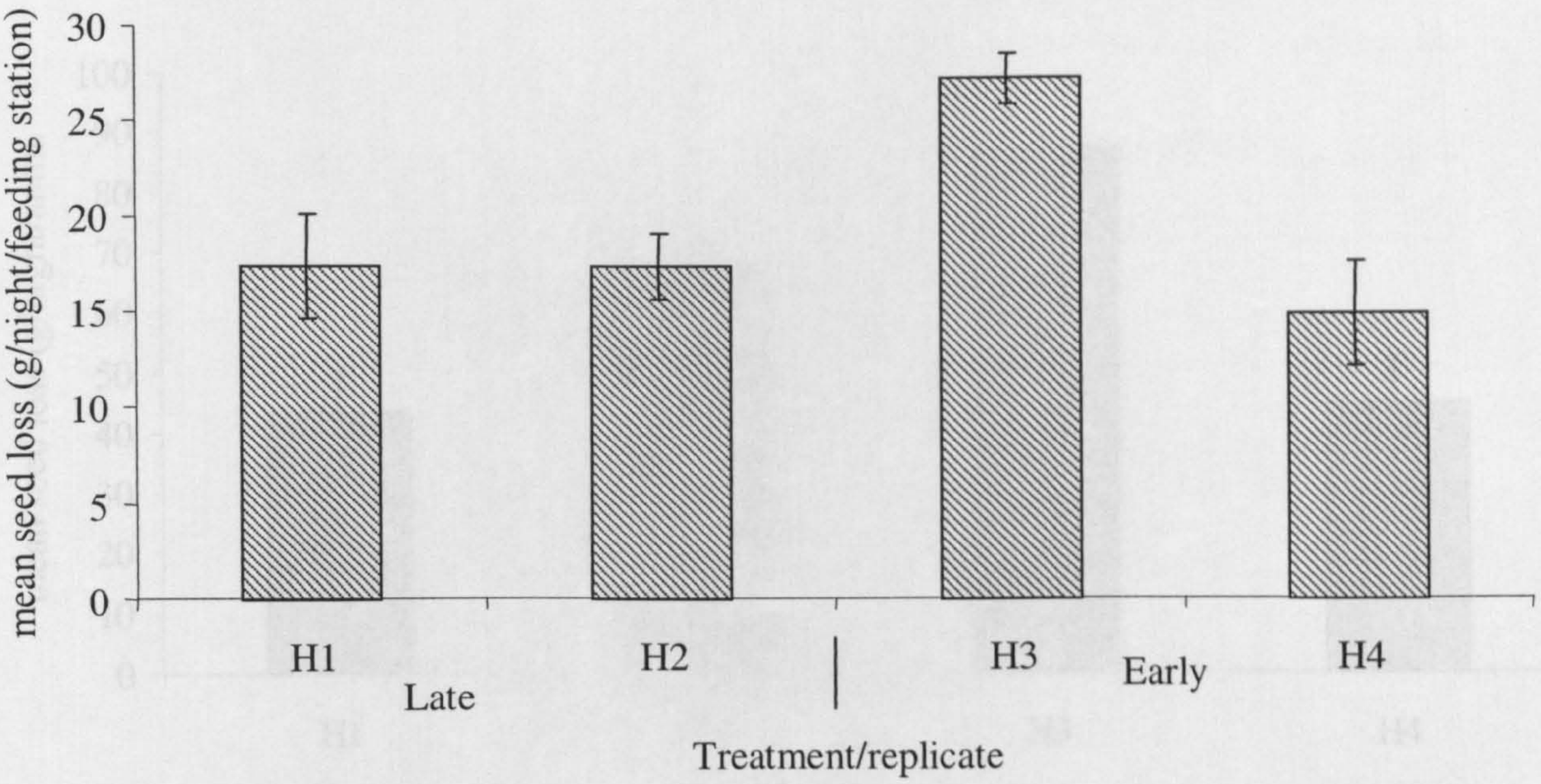
Therefore, 95% confidence limits

of the weight of seed in the mix =597.3 to 833.0 g

Actual seed weight was 830g, which falls just within the confidence limits i.e. the sub-sampling technique can estimate seed remaining within feeding stations within 95% accuracy.

For each grid the mean and standard error of the nightly seed loss per station were calculated. Figure 5.3 shows the nightly losses in each hammada treatment grid.

Figure 5.3 Mean nightly seed losses (g/night/feeding station) in the four hammada supplementary feeding treatments, n = 6 feeding stations.

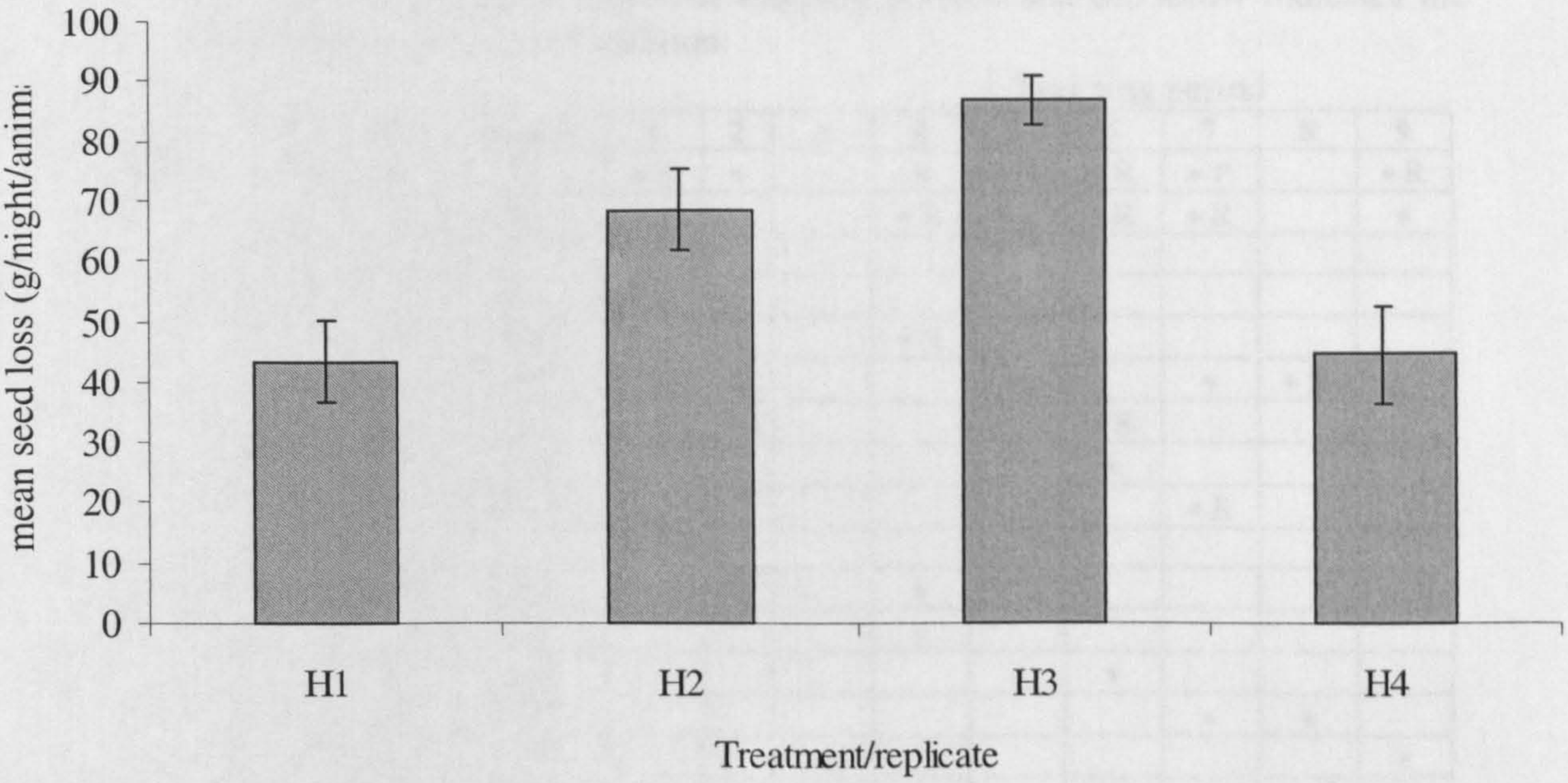


Data were shown to be normally distributed (P = 0.686, Kolmogorov-Smirnov test), but as a Levenes test (Norusis, 1998) revealed variances to be significantly different (P < 0.05) non-parametric tests were used. These revealed a significant difference between the amount of seed removed from each treatment (X^2 = 9.727, d.f. = 3, P = 0.021, Kruskal-Wallis), but not in the extent of seed removal between early and late applications (U = 49.0, n = 12, P = 0.184, Mann-Whitney U). To allow for the difference in rodent density between grids, mean weight of seed removed by each rodent per grid was calculated by multiplying the seed loss by the total number of feeding stations within the grid area (12) and dividing by the mean number of animals trapped within the grids during the time of supplementation (Table 5.12).

Table 5.12 Mean numbers of animals in the trapping grid area (0.8ha) during the appropriate period of seed supplementation.

	M. crassus		*G. dasyurus*		*M. libycus*		
	Mean	**S.E.**	**Mean**	**S.E.**	**Mean**	**S.E.**	**Total**
H1	4.80	0.30	0.00	0.00	0.00	0.00	**4.80**
H2	1.80	0.26	0.75	0.48	0.50	0.50	**3.05**
H3	3.50	0.14	0.00	0.00	0.25	0.25	**3.75**
H4	4.00	0.74	0.00	0.00	0.00	0.00	**4.00**

Figure 5.4 Mean nightly seed losses (g/night/animal) in the four hammada supplementary feeding treatments, n = 6 feeding stations.



Data were normally distributed (P > 0.50, Kolmogorov-Smirnov test) and a Levenes test revealed equal variances (P > 0.05); therefore parametric tests were used. There was a highly significant difference between the amount of seed taken from each grid when values were corrected for the total number of rodents within the trapping area (0.8ha) at the time of supplementation (F = 9.93, d.f. = 23, P < 0.001, One-way ANOVA). However, there was no significant difference in the extent of individual granivory between early (H3 & H4) and late (H1 & H2) applications (t = 0.990, d.f. = 22, P = 0.333, independent t-test). It can be seen from Figure 5.4 that in H2, individual animals removed over 85g of seed in one night, which is greater than expected. Because seed remained after treatments, the level of seed application was assumed to be above the

rodent requirements, and therefore sufficient to alleviate any restrictions normally imposed on breeding activity by natural seed abundance.

5.3.3.3 The influence of supplementary feeding on timing and output of breeding.

Captures of *M. crassus* on each hammada grid are summarised to show the number and identity of males, females and juveniles within the population during each trapping period. Pregnancies of females (P) and breeding activity of males and females (R = reproductive) were also noted. Tables 5.13a-e show data for *M. crassus* individuals (each with lettered codes) caught on H1 and H2 (seed provided late), H3 & H4 (seed provided early) and HA (control) (for timing of trapping period see Table 5.1).

Table 5.13a *Meriones crassus* captures in H1 (late seed application), during spring 1998. Where F = female, M = male, P = pregnant, R = sexually active and • = captures. Numbers represent trapping periods and the arrow indicates the approximate time of seed addition.

↓ Trapping period

Age	Sex	No.	Animal	1	2	3	4	5	6	7	8	9
Adults	F	1	H	• P	•		•	• R	• R	• P		• R
		2	FG				• R	• P	• R	• R		•
	M	3	AC	• R								
		4	ABC				• R					
		5	ABE					•		•	• R	
		6	ACF						• R			
		7	ADE						•			
		8	BCD							• R		
Juveniles	F	9	EG				•					
		10	EI				•					
		11	ACI						•			
		12	BCF							•	•	
		13	BDF									•
		14	BDG									•
	M	15	I	•		• R						
		16	AH			•	•					
		17	CFH				•					
		18	BEH							•		
		19	BCG							•	•	•
		20	BCI								•	

An apparently uneven sex ratio (1:3) of *M. crassus* was found on H1, with more adult males captured than females. Females tended to persist in the same locality, whereas males appeared to be more transient and were usually caught on only one or two occasions. Breeding activity of both males and females appeared not to be synchronised, as no more than one breeding adult male or female was caught during a

single trapping period. Offspring showed a sex ratio of 1:1 and juveniles may have moved away from the grid as recaptures were uncommon after the initial emergence.

Table 5.13b *Meriones crassus* captures in H2 (late seed supplementation).

↓ Trapping period

Age	Sex	No.	Animal	1	2	3	4	5	6	7	8	9
Adults	F	1	A	• R	•							
		2	CF			• P						
		3	EH							•		
	M	4	ABE					• R			•	
		5	ABF					• R				
Juveniles	F	6	ABH						•			
		7	BB							•		
	M	8	DI				•	•		•	•	

The population structure in H2, inferred from the smaller number of animals caught, was quite different from that in H1. Sex ratio was biased towards females and neither males nor females persisted in the grid for long periods (or they avoided traps after the initial capture). Only one juvenile male was caught within the grid, but on several occasions.

Table 5.13c *Meriones crassus* captures in H3 (early seed supplementation).

↓ Trapping period

Age	Sex	No.	Animal	1	2	3	4	5	6	7	8	9
Adults	F	1	G	• R		• P	• R	• R	• P	• R	• R	
		2	BD			• P					•	•
		3	HI				• R	• R	• R	•		
		4	GH									• R
	M	5	AB	•	• R			• R	•	•		
		6	AD	•								
		7	AE	• R				• R				
		8	CE		•	• R	•					
		9	CF		• R			• R				
Juveniles	F	10	A'					•				
		11	B					•	•			
		12	ACE						•	•	•	
		13	ADF						•			
		14	ADH						•			
	M	15	FI				•	•	•			
		16	ADG						•		•	
		17	ADI						•			
		18	AEI						•			
		19	BDE								•	

The population structure in H3 (Table 5.13c) shows that more adult males were captured than adult females. Several females and males were frequently recaptured within the grid and both males and females were in breeding condition at the same time. As in H1, juvenile sex ratio was equal and recapture of juveniles was uncommon.

Table 5.13d *Meriones crassus* captures in H4 (early seed supplementation).

↓ Trapping period

Age	Sex	No.	Animal	1	2	3	4	5	6	7	8	9
Adults	F	1	BG		• P		• R		• P		• R	•
		2	BH		• P			• R	•	• P	•	•
		3	DF				•	• R	• P	•	•	
		4	ABD					• R	• P	•	•	•
		5	DH				• R					
	M	6	C	•								
		7	BI		•			•	• R	• R		
		8	DI				•	• R				
		9	ABG						• R	• R		
		10	AFH							•		
		11	AGI							• R		
		12	AB									•
Juveniles	F	13	B	•						• P		
		14	E	•	•							
		15	CH				•					
		16	GHI								•	
		17	AAB									•
		18	AFI							•		
		19	AGH							•		
		20	DE				•					
	M	21	ACD						•			
		22	F	•	•							
		23	DG				•					
		24	AA							•		
		25	BB							•		
		26	DD							•		•
		27	EE							•		
		28	FF							•		•

H4 showed similar population characteristics to H3, i.e. females were recaptured more often than males and both several males and several females were in breeding condition simultaneously. Again juveniles consisted of equal numbers of the two sexes and juvenile recaptures were uncommon. However, one juvenile female was re-caught within the grid as a breeding adult two months after the first capture.

Table 5.9e *Meriones crassus* captures in HA (no seed supplementation). Note grid area was half of the size used for H1-H4.

				Trapping period								
Age	**Sex**	**No.**	**Animal**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Adults	F	1	A	• P								
		2	B		• P							
		3	C		• P							
	M	4	G	•								
		5	AG		• R	• R		•				
		6	EH				• R	• R		• R	•	•
Juveniles	M	7	ABE		•							
		8	ABG						•	•	•	•
		9	AEG						•	•	•	•
		10	BDH									•

The control grid appeared to contradict previous observations, in that adult sex ratio was equal, whereas juvenile sex ratio was not. Additionally, all adult females were caught only once whereas two males were caught frequently throughout the study period. Male breeding activity appeared not to be synchronised, whereas the three females were probably pregnant simultaneously. The juveniles that first appeared in the grid during trapping period 6 resided within the grid for over a month.

In general, females resided within grids during the study period whereas males tended be more mobile and individuals were not recaptured frequently. As a possible consequence of this, the number of individual males trapped was generally greater than females. In some grids there appeared to be some form of staggering of reproductive activity within both males and females. The ratio of juvenile males to juvenile females was equal, and from recaptures it is suggested that juveniles remain in the vicinity of the maternal burrow for a few weeks after emergence, after which they disperse or are lost to predation.

To test the effects of supplementary food on the extent of breeding, the number of non-breeding and breeding males and females were counted on each grid during two time periods; 'early' and 'late' (Tables 5.14 & 5.15). Trapping periods 2-4 were classified as 'early' and trapping periods 6-9 were 'late'. It is assumed that there would be no immediate effect on breeding; therefore trapping periods 1 and 5 were excluded from the analysis.

Table 5.14 The number of females breeding and not-breeding in the early and late trapping periods, with (Supple.) and without (No. supple.) supplementary seeds.

Treatment	Early (2-4)				Late (6-9)			
	Breeding	%	Non-breeding	%	Breeding	%	Non-breeding	%
Supple.	8	88	1	12	5	71	2	29
No supple.	4	57	3	43	10	45	12	55

Table 5.15 The number of males breeding and not-breeding in the early and late trapping periods, with (Supple.) and without (No. supple.) supplementary seeds.

Treatment	Early (2-4)				Late (6-9)			
	Breeding	%	Non-breeding	%	Breeding	%	Non-breeding	%
Supple.	3	43	4	57	3	50	3	50
No supple.	4	100	0	0	5	55	4	45

Due to low values a chi-squared test could not be performed and therefore the effects of supplementary food could not be investigated for late and early time periods individually (see Tables 5.14 & 5.15). Counts of breeding and non-breeding animals for food supplementation and non-supplementation were combined for the two time periods to enable analysis of males and females separately (Table 5.16). Supplementary feeding caused an increase in breeding in females ($X^2 = 9.64$, d.f. = 1, $P < 0.01$, Chi-squared test) but not males ($X^2 = 1.58$, d.f. = 1, $P > 0.05$).

Table 5.16 The number of males and females breeding and not-breeding with (Supple.) and without (No. supple.) supplementary seeds.

Treatment	Females		Males	
	Breeding	Non-breeding	Breeding	Non-breeding
Supple.	13	3	6	7
No. Supple.	14	15	9	4

From laboratory observations juveniles should be trappable at approximately 20-30 days after the female has been recorded pregnant. Therefore the mean litter size may be estimated by dividing the number of juveniles in the population by the number of

pregnant females 20-30 days prior to juvenile captures. Mean litter size per pregnant female was calculated during periods with and without supplementation for each of the grids (Table 5.17). Pregnancies during trapping periods 1 or 5 were excluded from the analysis.

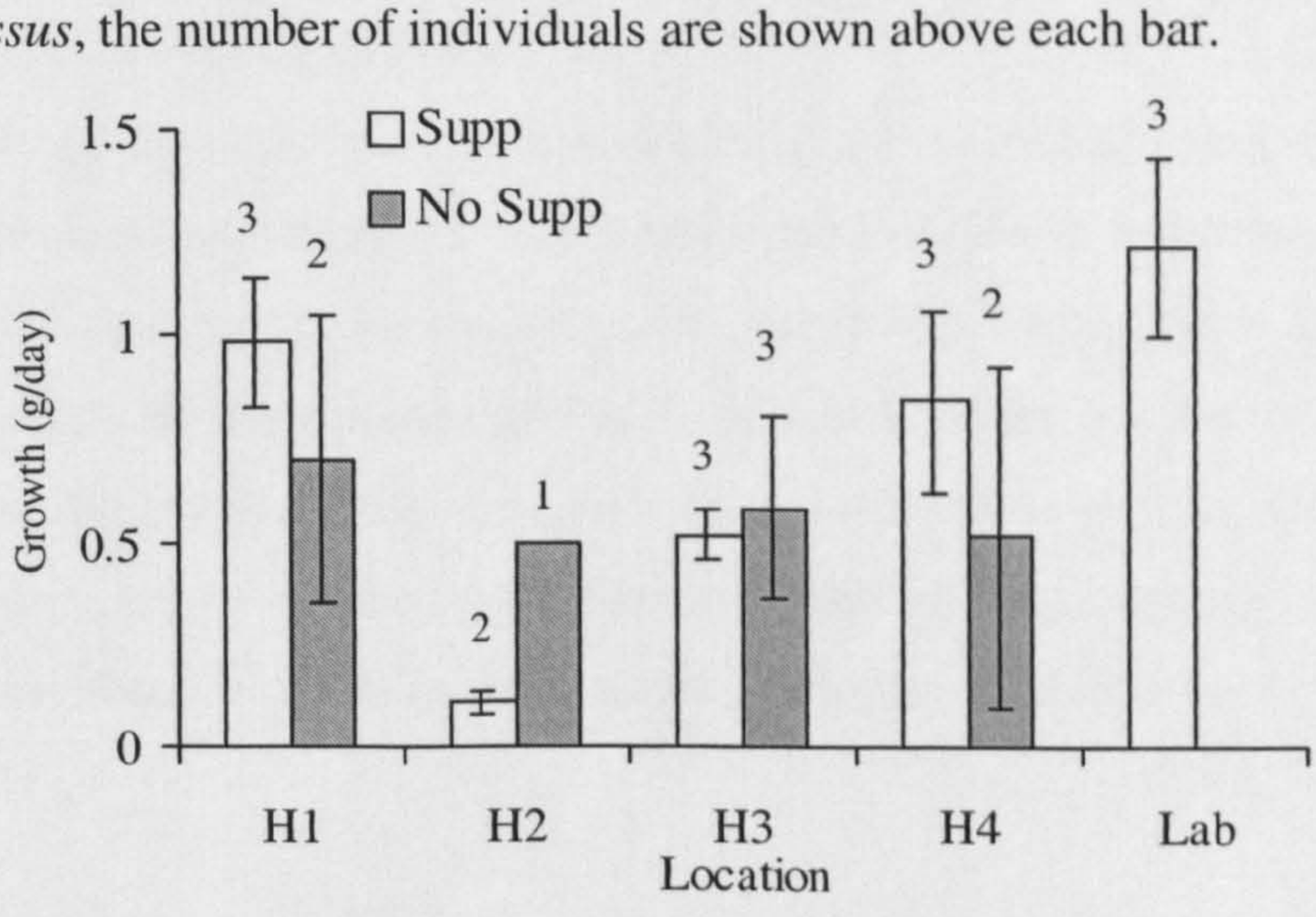
Table 5.17 The mean litter size per pregnant female with (Supple.) and without (No. supple.) food supplementation in each of the treatment grids.

	Supple.	**No supple.**
H1	3.0	4.0
H2	2.0	-
H3	4.5	3.0
H4	3.0	2.7
HA	-	1.0
Mean	3.13	2.68
S.E.	1.03	1.24

The number of young per litter with and without food supplementation had equal variances ($P > 0.05$, F-test), therefore a t-test assuming equal variances was undertaken which showed that supplementary food did not significantly increase the mean litter size in the treatment grids ($t = 0.556$, d.f. = 6, $P = 0.598$).

The effect of seed abundance on juvenile development was investigated by comparing juvenile growth rates (g/day) before and after seed supplementation for each hammada replicate. These results were also compared to juvenile growth rates in laboratory animals, which were considered to be free of dietary constraints (Figure 5.5).

Figure 5.5 Effects of supplementary feeding on growth of juvenile *Meriones crassus*, the number of individuals are shown above each bar.



Data were normally distributed ($P > 0.05$) and Levene's test showed equal variances ($F = 0.554$, $P = 0.467$). There was no significant difference in the growth of juveniles between periods of supplementary feeding and non-supplementary feeding ($t = 0.461$, d.f. = 17, $P = 0.651$, t-test). However, due to the low number of recaptures of juveniles, following development to adulthood was not possible. The highest number of juvenile recaptures was four times, three individuals were caught three times, ten were caught twice and 27 were trapped once.

5.4 DISCUSSION

5.4.1 Limitations to the study

Overall, trap availability and time limited the number of grid replicates that could be undertaken by one person. Ideally more replicate grids would have been used as 'controls' and the control grid would not have been of a different configuration to other grids to avoid the potentially greater 'edge effect' (Sutherland, 1996). It would also have been desirable to undertake trapping studies at Salma more frequently than monthly.

It is difficult to define precisely the age of an individual, even using body weight criteria given by previous researchers, as this can vary between populations (see section 2.3.1.2). For the purpose of analysis two main categories were defined, adults and juveniles. Adults were of high body weight for the species and/or reproductively active. If body weight was less than half the maximal adult weight, individuals were classified as juveniles. The 'sub-adults' were up-graded to adults if sexually active and down-graded to juveniles if body weight was relatively low and they were not sexually mature. Sub-adults that did not fall into either category were excluded from the breeding/juvenile emergence analysis. It is accepted that this may lead to some biases; however, this methodology was applied consistently to all samples

Breeding status was also difficult to assess precisely. For example, pregnancy is often detectable only in the later stages of gestation. An animal early in pregnancy may be imperforate (as the vagina can heal a few days after copulation) and so show no obvious signs of pregnancy (Gurnell & Flowerdew, 1990). In my classifications this animal would be classified as non-breeding.

5.4.2 Preliminary studies in 1996-1997

From the 1996-7 data there was an indication that the timing and extent of breeding was species-dependent; this suggests that species show different responses to changes in environmental conditions, such as resource abundance. Males showed a reduction in breeding activity in the summer (Table 5.4), which might be due to the changes in resource availability between seasons. There was however no distinct seasonal difference in the extent of breeding in females, although this comparison was limited by the available data. Vegetation was more abundant in 1997 than 1996 (personal

observation) and sexual activity varied in extent between years, i.e. generally greater in 1997 than 1996, indicating that annual fluctuations in resources may have effected breeding activity. There were no distinct differences in the timing and extent of breeding activity between males and females. Comparisons of breeding activity between habitats were limited as species tend to show clear habitat preferences and only a few species are found in more than one habitat type (e.g. *J. jaculus,* see Chapter 2).

The timing of the investigation may have had some influence on the results obtained, as in 1996-97 annual and seasonal replicates were undertaken systematically but not at specific time intervals, i.e. consecutive sampling dates in one site may differ slightly to the next site. In general, my results agreed with previous findings in that the timing of breeding activity is species dependant (see Harrison & Bates, 1991) and temporally variable (Degen, 1997).

5.4.3 Habitat comparisons using 1998 data

There was a great deal of spatial variability in rodent densities, between habitats and within sites. For example, in the hammada at Hashad densities of *M. crassus* varied from 2-9 animals per hectare (Table 5.10). If population density is resource dependant and vegetation and seed abundance within the trapping grid were important food sources, higher densities of rodents should be found in areas where vegetation and seeds were more abundant. However in general, rodents were caught less often in areas with greater vegetation cover, and very high vegetation cover appeared to deter rodents from inhabiting the area, i.e. marab at Salma. Additionally, *M. crassus* densities were negatively correlated with seed availability (section 5.3.2). One explanation for this could be that rodents were more trap-prone in areas where seeds were least abundant. However, from the supplementary feeding grids there was no indication that rodent trappability decreased with an increase in seed abundance (Tables 5.13a-e).

Several explanations can be suggested for this observation. It would be expected that rodents would utilise the 'best' areas first, therefore some areas may have the most abundant resources, but may not necessarily be the best habitat for a rodent to inhabit. Habitat selection has been suggested to be a compromise between the availability of food resources, competition and anti-predatory protection (Brown *et al.,* 1988). Therefore factors additional to resource abundance should be considered as density determinants.

The intensity of habitat utilisation may not be reflected in the trapping results. For example, a pilot radio-tracking study conducted in summer 1996 showed *M. crassus* to utilise a range of habitat types, but were less frequently trapped in these habitats compared to hammada where their burrows were located. Therefore results may reflect the aggregation of animals in areas suitable for refuge but not where they may forage. The effect of captures on an individual's movements has previously been commented on when estimating home ranges from trap results (Bergstrom, 1988).

Resource abundance and accessibility are not necessarily equivalent. Areas may be highly vegetated with toxic or unpalatable plants, or seeds may be more readily available on the soil surface in habitats were the seed bank is low. Additionally, measured resource abundance may be a *consequence* of high rodent densities, i.e. seed densities and vegetation cover may be lower in areas where they have been heavily fed upon. Either vegetation availability prior to the investigation or the abundance of other resources not in the immediate vicinity of the trapping grid may have also accounted for the lack of correlation in rodent density and resource abundance. Therefore, it would be advisable that further habitat utilisation and diet studies should be undertaken, to check whether the overall resource availability from the different habitats within the home range of an individual, rather than the immediate resources surrounding the burrow may influence density and breeding activity. Long term studies investigating the food availability throughout the life history of an individual should also be considered if further studies are made in the Badia.

5.4.4 Supplementary feeding experiments

The first seed application was made in February, near the start of the annual breeding period in *M. crassus* (Krasnov *et al.*, 1996b), when it was assumed that vegetation would be abundant following the recent winter rainfall. The late application was given at the predicted time of reduction in vegetation, as estimated from observations in 1996-1997. However, it was clear from the results (Table 5.13d) that some breeding had occurred prior to food addition. It was further noted that vegetation was more prevalent in May 1998 than previously recorded in 1996 and 1997.

Rodent density varied between grids, irrespective of the number of burrow systems within the area, which had been used to assess approximate densities before grid selection. From the vegetation survey (Chapter 3) it was shown that all hammada

replicates had similar levels of vegetation cover. Heterogeneity of the area limited the grid size used, and time available restricted the study period to within one season. It is assumed that the added seed was freely available to all individuals; however it has been reported that resource allocation between individual mammals may not be even as dominant individuals may monopolise the food source (Monaghan & Metcalfe, 1985). It was also assumed that the duration over which the seed was available (6 weeks) was adequate to permit a physiological response (breeding) to occur.

Due to the tendency of unattended equipment to "go missing", feeding stations were designed to allow rodents access to seeds, but which were not visible. Grids were spaced at a distance >250m, which was considered large enough for spatial independence. This distance was estimated from preliminary telemetry studies (Maddox, pers. comm.) and reports from Krasnov *et al.* (1996b). Only on one occasion was an individual rodent previously recorded on one grid captured on another.

It was noted that seed continuously available at one site over a long period attracted other granivores such as birds and ants. It is recommended for future studies that anti-granivory precautions are employed on both feeding stations and traps laid, to prevent this interference. Although non-rodent predation was evident it was assumed that overall this would not effect the *ad libitum* seed abundance. This was verified by calculation of the seeds remaining within the feeding stations after excavation (Fig 5.3). Although soil smoothing appeared to reduce predation, this could not be undertaken every day, therefore feeding stations were open to more predation when I was not resident at this site.

As there was no significant difference between the mean nightly food consumption per individual rodent following early and late seed application (Figs 5.3 & 5.4), it is suggested that their energetic requirements did not differ between the two time periods. However, this is debatable as it is unknown which granivore species, or how many individuals, were actually utilising the supplemented food. Additionally, the increase in the availability of natural seed in the latter part of the investigation did not appear to effect exploitation of feeding stations. In all feeding stations the quantity of seed taken (>40g) was above the amount required for the daily energetic expenditure of the rodents present within the grid. This could potentially be the result of predation by other granivores or caching. (It has been noted that when resources are abundant, *M. crassus*

caches food within its burrow system (personal observation)). If caching did occur, seed abundance within the grid would be above the level of natural abundance, even after the feeding stations were excavated.

Investigating the number and population structure of animals within a specific locality over a period of time can give an indication of their life history strategy (Tables 5.13a-e). However, sample sizes in this study were small and gave only a small and possibly unrepresentative structure of the population as a whole. The population structures and dynamics of Arabian desert rodents are not well documented; hence, detailed information is required to enable comparisons between spatial and temporal samples. As aggregation in *M. crassus* has been reported to differ geographically (Harrison & Bates, 1991), mating systems might differ in relation to colony density, which is dependant on food availability.

Density of *M. crassus* appeared to be higher in this study (6/ha) than in habitats with the greatest density in Israel (4/ha). This may be a consequence of competition from co-existing species found in dune habitats in Israel; the hammada habitats in this study were inhabited predominantly by *M. crassus*. Contrary to previous reports (Krasnov *et al.*, 1996b) there appeared to be sex-related differences in the time an individual stayed within the vicinity of a burrow. Females were frequently re-caught near burrows, recaptures of males within a grid were less common, indicating they tended to be more mobile or trap-shy than females. This may be due to breeding activity, as many animals become more territorial during breeding and Krasnov's investigation was undertaken outside the breeding season. It is suggested that the requirement of a burrow for rearing young would require females to reside within one locality for longer. Observations of equal sex ratio in juveniles agree with previous observations for this species (Krasnov *et al.*, 1996).

For analysis within-treatment grids were assumed to be similar; however, the natural resources within the grid or factors other than resources, e.g. social dynamics of rodents within the grid, or adjacent habitat resources, may result in differences within treatments. Increased food availability may have resulted in higher densities of females within the grids by reducing competition for resources, decreasing territorial behaviour and increasing overlap in home ranges (Ostfeld, 1986; Ims, 1987).

As females tend to reside within a grid, these animals should show a greater response to supplementary feeding compared to transient males, which would only have a short exposure to supplementary food. Supplementary feeding caused an increase in breeding activity in females. In the early seed supplementation this would have been expected to result in a higher proportion of females breeding and in the late application an extension in breeding period. Data however were too few to investigate the effects of the timing of application. It can be suggested that under natural circumstances, seed abundance would have similar effects to supplementary feeding in extending the breeding period in years of plenty.

Juveniles were not re-caught frequently within a grid, a result of either high predation or mortality, or dispersal. Dispersal may be a response to resource availability or a strategy to promote genetic dilution (Begon *et al.*, 1990). However, juveniles were re-captured more frequently after weaning in late supplementary feeding grids. This suggests that dispersal is influenced by resource abundance and therefore acts as a potential mechanism of reducing intra-specific competition for resources. There was no significant difference in the growth of juveniles between periods of supplementary feeding and non-supplementary feeding (Figure 5.5); however, recapture rates for juveniles were low and derived from different stages in development in which growth rates may differ. The lack of significant increase in litter size or juvenile growth rate suggests that factors other than seed abundance may influence these. Both have been related to water availability for lactation (Kam & Degen, 1994). Therefore vegetation abundance as a water source may be an important determining factor.

There were no apparent effects of supplementary feeding on males. This may be due to the mobility of males, which would not have as much exposure to food supplementation, or males being less dependent on resources in controlling their breeding activity. Sexual activity in males did show a general decrease during later trapping periods, suggesting that some factor other than resource availability reduced breeding activity. As males showed a decrease despite the extended breeding season in females in H1 (Table 5.13a), it is suggested that the extent of female breeding period does not directly effect male sexual activity. The decrease in vegetation cover during the late-spring months may account for the decrease in male sexual activity, if sexual activity is influenced by a vegetation component such as water, nutrients or a secondary compound.

The level and distribution of supplemental food can have an effect the overall social organisation, foraging behaviour and the spatial relationship between males and females (Boutin, 1990). The effect of food supplementation will differ depending on environmental conditions. If they are good, additional feeding is less likely to cause a response. The application of food may make animals more vulnerable to predation (Boutin, 1990) and the increase in population density in prey species may attract predators to an area (Boutin *et al.*, 1986). Overall, results from experimental feeding grids partially agreed with observations from other small mammal studies in temperate regions, in which additional food influenced female breeding season, but had little effect on males.

CHAPTER 6

ENVIRONMENTAL CONTROL & ENERGETICS OF BREEDING IN DESERT RODENTS

6.1 INTRODUCTION & OBJECTIVES

Chapter 5 demonstrated that seed abundance influenced the extent of breeding in *M. crassus* and suggested that the availability of natural resources, such as vegetation, also appeared to play an important role in determining the timing and extent of breeding. This chapter describes studies investigating the role of vegetation as a proximate trigger for breeding in *M. crassus* and the importance of vegetation in breeding and juvenile development. Additionally, it describes attempts to determine energy requirements of *M. crassus* of different ages and sexual status to investigate how food (energy) requirements of breeding and development can be matched to natural fluctuations in resource abundance.

6.1.1 Timing and cues for breeding in desert-living rodents

Many desert rodent species are considered to be seasonal breeders (see Table 1.1), but to date, there have been few investigations of the proximate triggers controlling the timing of breeding or to what extent breeding is limited by food or water supply. It has been suggested that plants, as a water source (Pinter & Negus, 1965) or as a reproductive cue (Degen, 1996), can influence reproduction in rodents and it is well documented that food supply limits breeding in many temperate small mammals (Boutin, 1990). Chemical substances within plants can act a cue to stimulate or inhibit sexual activity. Studies of the montane vole, *Microtus montanus* (Negus & Berger, 1977), showed that a plant-derived cyclic carbamate 6-methoxybenzoxazolinone (6-MBOA) stimulated reproduction. Treatment resulted in the higher instances of pregnancy and levels of testicular growth compared to controls. The results were thought to be a response to the plant substances acting as an environmental trigger, indicating that the abundance of vegetation was increasing.

Investigations have also been undertaken on desert rodents to assess which environmental cues are involved in seasonal breeding. White & Bernard, (1996, 1999) proposed that seasonal breeding occurred in response to multiple environmental cues or

was controlled directly by energetic and metabolic constraints. El Bakry *et al.* (1998) found in laboratory studies that desert rodent species were responsive to manipulation of day length, but changes in photoperiod alone did not induce dramatic differences in reproductive status. In further experiments of the effects of photoperiod and free-water deprivation on the reproductive status of male and female *Meriones shawi*, neither testes mass nor spermatogenetic activity (males), nor uterine mass nor folliculo-genesis (females) were significantly affected by changes in either photoperiod or vegetation (El Bakry, 1999). It is still unclear what initiates and controls breeding in desert rodents, as the evidence so far appears to indicate a combination of photoperiod, vegetation availability and physiological state, possibly controlled by resource availability. It is also unclear whether environmental cues are universally used amongst desert species or are species-specific.

6.1.2 Photoperiodic effects on breeding in small mammals

Photoperiod is a reliable environmental cue in predicting seasonality and it is thought to act as a proximate trigger in controlling the timing of breeding in many species of mammals and birds (e.g. Wingfield & Farner, 1993; Bronson & Heideman, 1994). In temperate deserts, photoperiod would be a reliable cue for predicting changes in seasons i.e. food shortage and colder temperatures during winter, but an unreliable cue for changes in food abundance. In general, shorter day lengths that signal a reduction in food abundance under natural conditions tend to inhibit reproduction. However, the processes behind this response are not yet fully understood. Short day inhibition has been demonstrated in field voles, *Microtus agrestis* (Baker & Ranson, 1932) where above a threshold photoperiod of between 12-14 hours of light, sexual development was more rapid (Breed & Clarke, 1970). In hamsters, short days (<12.5 hours of light per 24 hours) also stimulated gonad regression (Hoffman, 1973). It has been demonstrated for laboratory rodents that day length can also have effects on other stages of reproduction, such as gestation length (Racey, 1981). However, photoperiod as an environmental cue for breeding is species dependent, as not all species are reproductively responsive, e.g. cane mice (*Zygodontomys brevicauda*) in Venezuela did not respond reproductively to changes in photoperiod (Bronson & Heideman, 1992). To date few studies have been undertaken to investigate the direct effects of photoperiod on breeding in desert-living rodents (see 5.1.2).

Photosensitivity will influence an animal's ability to respond to photoperiod and the processes underlying this are physiological. The pineal gland produces anti-gonadal substances including melatonin, and although the understanding of the process is not clear, many species including gerbils and rats do show anti-gonadal effects in response to melatonin, with the extent varying between species (e.g. Steinlechner & Niklowitz, 1992). Elliott *et al.* (1972) showed that in initiating a response to photoperiod the timing of light or dark in relation to circadian rhythms of photosensitivity was more important than the actual day-length received. Sicard *et al.* (1992) further demonstrated that different rodent species showed circadian rhythms of photosensitivity even when only small variations in day length were experienced. Therefore potential circadian rhythms of photosensitivity must be considered when manipulating photoperiod.

6.1.3 The influence of other individuals on breeding

The chemical, auditory or tactile signals from conspecifics may also alter reproductive activity. Champlin (1971) demonstrated suppression of oestrus in grouped female mice (*Mus mus*) and that chemosensory stimulation by fertile males is needed in order to induce solitarily females into oestrus (Moffatt *et al.*, 1991). Male urine has been shown to act as a chemical synchroniser of female oestrus (the Whitten Effect) and may also stimulate female puberty in several species of rodent, e.g. prairie voles, *Microtus ochrogaster* (Carter *et al.*, 1980).

6.1.4 Nutritional and water requirements for breeding in small mammals

Nutritional constraints on reproduction in small mammals have often been investigated in the laboratory. In females, malnutrition during pregnancy can cause implantation failure, underweight young and other effects such as the selective or total mortality of young (Flowerdew, 1987). Limited food and water during lactation can result in a reduced milk production by laboratory rats, (Widdowson & Cowan, 1972), which can depress the growth rates of suckling young (Kam & Degen, 1994). Green vegetation can act as an important water source, especially for species inhabiting arid environments. For example, in 'fat sand rats' (*Psammomys obesus*), body mass at birth and juvenile growth rates were both affected by the water availability in green vegetation consumed by pregnant and lactating females (Kam & Degen, 1994). Kirkpatrick (1988) also showed that food quality and water availability, along with litter size, can influence the growth rate and survival of offspring. Food limitation can extend the period between oestrus in females and delay sexual maturity in sub-adults, as juvenile growth rates and

development control the timing of puberty (Myers & Poole, 1962). In male *Tatera leucogaster*, for example, it has been suggested that increased nutrition accelerated the maturation and recrudescence of reproductive organs (Neal & Alibhai, 1991). In other male mammals, deficiencies in nutrients, such as Vitamin A, have been shown to inhibit spermatogenesis and depress the quality of semen (Flowerdew, 1987).

6.1.5 Energetic requirements and metabolism

The basal metabolic rate (BMR) is the minimum energetic cost of maintaining cells and organs (Ricklefs *et al.*, 1996) and is defined as the minimum rate of energy expenditure by a non reproductive, non-growing animal measured under post-absorptive and thermoneutral conditions during inactivity (Aschoff & Pohl, 1970). Metabolic rate is affected by body mass (BM), such that for mammals, BMR (Kcal/day) = 73.3 BM (kg) $^{0.74}$ (Kleiber, 1932). Interspecifically, metabolic rates tend to lie close to a regression line with a slope of 0.75; this is termed the Brody-Kleiber law (Brody *et al.*, 1934). Metabolic rate is also affected by body composition, as metabolic heat is generated mainly by lean tissues (Scott *et al.*, 1996).

6.1.6 Metabolic studies of desert rodents

Basal metabolic rate of rodents is affected not only by body mass but also by environmental conditions, such as climate, seasonality (McNab, 1980), habitat (Corp *et al.*, 1997) and diet. Metabolic rates appear to be lower in granivorous than omnivorous rodents (McNab, 1986; Degen, 1994). BMR and daily existence energy (DEE) tend to be higher than expected in species which experience energetically costly climatic conditions (McNab, 1979). Seed-eating rodent species inhabiting arid environments tend to have lower BMR than that predicted for their body mass, according to the derived allometric equations (Kleiber, 1975). These metabolic rates are suggested to be adaptations to arid environments (McNab, 1966; Degen *et al.*, 1986; Haim, 1987).

Pregnancy incurs additional energy requirements of the animal (Gittleman & Thompson, 1988). However, in small mammals the difference in energy intake between pregnant and non-pregnant females has been shown to be minimal (e.g. *Acomys cahirinus*, Degen, 1997). However, in some cases metabolic rates of small mammals have been shown to vary with breeding activity (e.g. Stephenson & Racey, 1993). In studying metabolic costs of sexual activity or growth, the metabolic rate of the individual at rest (resting metabolic rate (RMR)) is used for comparisons rather than the

basal rate. In reproduction, lactation is considered the most energetically costly phase, due to production of milk (Kam & Degen, 1993). Nutritional energy intake by lactating rodents can be up to 400%, compared to non-lactating females (e.g., *M. musculus*, Konig & Markl, 1987) and some species have demonstrated an elevated level of metabolism during both gestation and lactation (e.g. *Monodelphis domestica*, Thompson & Nicoll, 1986). In golden hamsters (*Mesocricetus auratus*), gestation and lactation showed an increase in resting metabolic rate with the highest metabolic demands during lactation (Garton *et al.*, 1994).

6.1.7 *Meriones crassus*

The diet of *M. crassus* is mainly granivorous, although it is known to incorporate green vegetation selectively when available. When given a choice between green vegetation and seeds *ad libitum*, over 80% of the dry matter intake (DMI) was seeds (Kam *et al.*, 1997). Seasonal changes in the vegetation component of the diet could act in several ways, as direct increases in food and in water availability or as a cue to trigger sexual activity through chemical stimulation, e.g. by 6-MBOA. Khokhlova *et al.* (unpubl. data & pers. comm.) suggest that green vegetation (e.g. *Atriplex halimus*) is important for almost all stages of reproduction, although it is not known why, or to what extent. They have also demonstrated that the oestrous cycle in *M. crassus* is approximately 4.5 days, extending in response to a reduction in available energy but eventually ceasing if food is limited. The ratio of water intake (WI) to metabolizable energy intake (MEI) in pregnant females increases with higher numbers of foetuses. The WI increases by 5 % at the beginning and to 14% above normal within the last 10 days of pregnancy. However, the MEI increases by only 6% in the last 10 days of pregnancy. Parental diet directly affected the growth rate of pups, but not the developmental stages of offspring, or litter size (Khokhlova, pers. comm.).

In an experiment (Haim & Rubal, 1993) investigating seasonal acclimatisation in thermoregulatory mechanisms, *M. crassus* was found to be responsive to photoperiod. In response to short day lengths *M. crassus* significantly increased Digestible Dry Matter Intake (DDMI) and Digestible Gross Energy Intake (DGEI). It was suggested that these results were in response to a photoperiodic cue signalling forthcoming food shortage. Seasonal changes in body weight were also observed in *M. crassus*, possibly as a response to changes in day-length (Khokhlova *et al.*, 1994). Therefore, photoperiod seems to be important in *M. crassus* in predicting potential forthcoming food shortages,

but it is not known whether this cue also stimulates breeding. *Meriones crassus* has many physiological attributes thought to be adaptations to arid environments. It is able to maintain energy balance even on low quality diets with no significant difference in the rate of O_2 consumption (Yahav & Choshniak, 1989). As is true for many desert rodents, it has lower daily energy expenditure (by 33%) than predicted for its body mass (Haim & Rubal, 1993) and during pregnancy it lowers its osmotic threshold for vasopressin and thirst (Baddouri & Quyou, 1991). From these studies *M. crassus* would seem to be less dependant on water and food abundance than most small mammals, including many desert-living species.

6.1.8 Objectives

The objectives of the work described in this chapter were to: i) to test whether photoperiod and/or vegetation availability act as proximate triggers for reproduction in *M. crassus*; ii) investigate the effects of supplementary vegetation on gestation length, litter size, survivorship and juvenile growth and development before and after weaning; iii) determine the energetic costs of breeding in males and females, and of juvenile growth.

6.2 METHODS

6.2.1 Study animals

A breeding colony of ten *M. crassus* were loaned to me courtesy of Mike Jordan (Animal Management and Care Section, Sparsholt College, Hampshire, UK). From 9th November 1998, the colony was housed in Durham within an observation room, maintained at approximately 25°C. Individuals were kept in sawdust lined cages (45 x 28 x 20cm) with shredded paper for bedding. Water and dry rodent pellets (Expanded Rat and Mouse No.3, Special Diet Services, Wytham, Essex) were available *ad libitum*. In mid-November the breeding colony was split into two groups, A and B, each consisting of equal number of males and females, which were paired and immediately bred to increase numbers prior to experiments. Supplementary feeding was undertaken every two to three days (Pinter & Negus, 1965), at which time all individuals received approximately 10g of husked sunflower seeds and animals in Group B received an additional 10g of fresh carrot (see section 6.2.2).

6.2.2 Food requirements

Atriplex halimus vegetation, which has previously been used in feeding experiments on *M. crassus* (Khoklova, pers. comm., 1998) was not readily available in Britain. Carrot (*Daucus carota*) has been used as a supplementary food for captive desert rodents by Choshniak & Yahav (1987) and Downs & Perrin (1990) and was therefore used for the present study. Approximate daily food requirements were assessed using carrot and sunflower seeds (*Helianthus annuus*) (see Appendix V for nutrition composition). An experiment to determine food requirements of *M. crassus* showed that during a 16 hour overnight foraging period, on average 5-6 grams (approximately 130kJ) of husked seed were consumed per night. In the presence of sunflower seeds, 13-14g (approximately 18.5kJ) of carrot was ingested per night (Sykes, pers. comm.). These values were used to derive appropriate feeding regimes in supplementation experiments (section 6.2.3). Light regimes during the experiments were maintained at 12:12, room temperature was kept at approximately 25°C and no free water was available.

6.2.3 Photoperiod and supplementary feeding experiments

Breeding experiments were carried out between March and November 1999. Initially nine pairs of adult *M. crassus* were used in the experiments, but this varied throughout the experiment depending on the number available. Reproductive photoresponsiveness

was investigated by gradually altering (increasing or decreasing) the day length of the housing unit by 2 hours at weekly intervals (see Gorman, 1995). Both groups of animals experienced the same day-length changes simultaneously. Animals were housed separately at the experimental photoperiod for 1 week before pairing. Photoperiod was kept constant over the breeding period. Day-length was initially changed from a 12:12 LD cycle to 16:8 LD, after which shortening and lengthening were alternated. This was undertaken twice for each photoperiod, once commencing in parallel with the natural photoperiod and once opposite to the natural photoperiod (Table 6.1).

Table 6.1 Outline of the experimental protocol for photoperiod and supplementary feeding experiments.

	Onset	**Stage 1**	**Stage 2**	**Stage 3**	**Stage 4**
Photoperiod	12:12	LD 16:8	SD 8:16	LD 16:8	SD 8:16
Natural photoperiod	Short day	Short days	Long days	Long days	Short days
No vegetation	Group A	Group A	Group A	Group A	Group A
Vegetation	Group B	Group B	Group B	Group B	Group B

6.2.3.1 Breeding and copulation

Animals were paired on the basis of kinship. If this was unknown it was assumed individuals were unrelated. The breeding period was initiated by placing one male in the cage of one female for two weeks. After this time males were separated from females and returned to their own cages. On nine randomly selected days during pairing, body mass (g) and sexual status of both males and females were recorded. Reproductive activity for both males and females was assessed as described in section 5.1.1. Recent copulation events were recorded if the female was either perforate or possessed a vaginal plug. However vaginal perforation can also result from oestrus (Krasnov *et al.*, 1996). Imperforate status indicated no recent copulation.

6.2.3.2 Pregnancy

Initially females were monitored every other day after males were removed; body weight and any signs of pregnancy (see 5.1.1) were noted. However, as maternal infanticide frequently occurred during pregnancy, this method was abandoned in an attempt to prevent unnecessary disturbance. In later experiments females were regularly monitored, visually, to record parturition dates. After parturition females were left undisturbed for up to one week to prevent infanticide, after which juveniles were

counted, sexed and body mass recorded. For reasons of female sensitivity to disturbance, RMR of pregnant or lactating females was not measured.

6.2.3.3 Juvenile development

Development of juveniles was assessed visually at regular intervals after birth and body mass recorded every few days, commencing one-week after birth. Developmental stages were categorised following Krasnov *et al.* (1996) (Table 6.2). Animals were maintained in constant photoperiod throughout juvenile development and weaning. Offspring were removed from their maternal cage when fully weaned. Once animals had reached adult status the photoperiod manipulation experiments were continued.

Table 6.2 Developmental stages in *M. crassus*, adapted from Krasnov *et al.* (1996).

Stage No.	Characteristics
1	Ear pinnae free
2	Dorsal hair presence
3	Ventral hair presence
4	Eyes open
5	Weaned
6	>50g Sub-adult
7	>60g Adult
8	Sexual maturity

6.2.4 Resting Metabolic Rate (RMR)

It was intended to use respirometery to investigate the energetic requirements of *M. crassus* of different ages, sex and breeding condition, i.e. non-reproductive animals, reproductive active males, pregnant females, lactating females and juveniles. Diet of individuals, i.e. with or without supplementary carrot, was also investigated as a factor that could potentially effect RMR. The extent of this investigation was dependent on obtaining a number of animals sufficient for statistical comparisons, i.e. more than five pregnant females and five young.

Between 25 February 1999 and 8 March 1999 the metabolic rate during resting was measured for eighteen animals, nine males and nine females. Total body mass (TBM) in grams was measured to an accuracy of 0.1g using an electronic balance (OHAUS 200,

Cottenham, Cambridge) every day for five days immediately before open-flow respirometery. Methodology followed that described in Selman (1998) using the same respirometry train.

Animals were deprived of food for 4-6 hours (Degen *et al.*, 1988) before measurement, to ensure that they were post-absorptive. This prevented any effect on O_2 consumption which might have been caused by the heat increment of feeding (Selman, 1998). Individuals were placed in a clear, but slightly frosted Perspex metabolic chamber (77.9 x 11.5 x 127 cm, volume 1154ml) with a small amount of inert bedding and left in the temperature control unit (LMS, Sevenoaks, Kent) for two hours to equilibrate. Measurements were taken over 2-3 hours under artificial fluorescent light and at a constant temperature within the thermo-neutral zone for *M. crassus* (25°C has been previously used for *M. crassus* and other desert rodent species by Degen *et al.* (1988)).

Oxygen consumption and carbon dioxide production were measured using a paramagnetic oxygen analyser (Servomex plc, Crowborough, East Sussex, Model 1111D/OOO) and an infrared gas analyser (Mine Safety Appliances Company, Pennsylvania, USA, Lira 3000) respectively. Air dried over silicate was drawn through the metabolic chamber at a rate of 60 l/h using mass flow controllers (Brooks Instruments, Netherlands, 5878 & 5850 TR series).

Gas analyses were performed on samples of both inlet and outlet gases, which were dried prior to measurement by passing them through columns of dried silica gel. Calibrations of the two analysers were carried out prior to measurements using 100% N_2 (BOC), and a certified mixture of 20.9% O_2 and 0.03% CO_2 in N_2 (SIP Analytical Ltd). The levels of O_2 and CO_2 measured during the BMR run were recorded directly onto a flatbed recorder (Kipp and Zonen, Delft, Netherlands, Model BD112).

From the trace (an example of which is given in Appendix VI), three ten minute periods in which the animal was at rest were identified (i.e. the baseline of the graph was flat), from which ten measurements of O_2 consumption were derived. Cursory checks of activity were possible through a peep-hole in the temperature control unit, which were then recorded on the trace at the approximate time of activity (response time of Servomex oxygen transducer is 4/sec from N_2 to 100% O_2 at 80ml/min flow, Servomex User Manual). RMR (mlO_2/g /hr) was calculated using equation 6.1.

$$\mathbf{RMR} = \frac{((\mathbf{V} \times 0.23) \times 10) \times 60}{\mathbf{TBM}} \qquad \text{Equation 6.1}$$

Where **V** is the measurement from the graph in cm, 0.23 and 10 are correction factors imposed by the respirometery equipment (see Selman, 1998), **TBM** is the total body mass of the individual and 60 is to convert values from minutes to hours.

6.3 RESULTS

6.3.1 Effects of photoperiod and supplementary vegetation on breeding attempts

In *M. crassus* breeding activity has been shown to be highest during spring, following the winter precipitation. If the onset of breeding activity were under photoperiodic control it would be expected from natural patterns in breeding activity that changes from short day to long day would stimulate activity, whereas the changes from long day to short day would inhibit activity. The increase in vegetation abundance at the time of breeding has also been suggested to stimulate breeding directly by supplying supplementary water for lactation. Therefore both these factors could have some influence on controlling the onset of breeding and supplementary water could aid lactation and therefore enhance juvenile survivorship, growth and development.

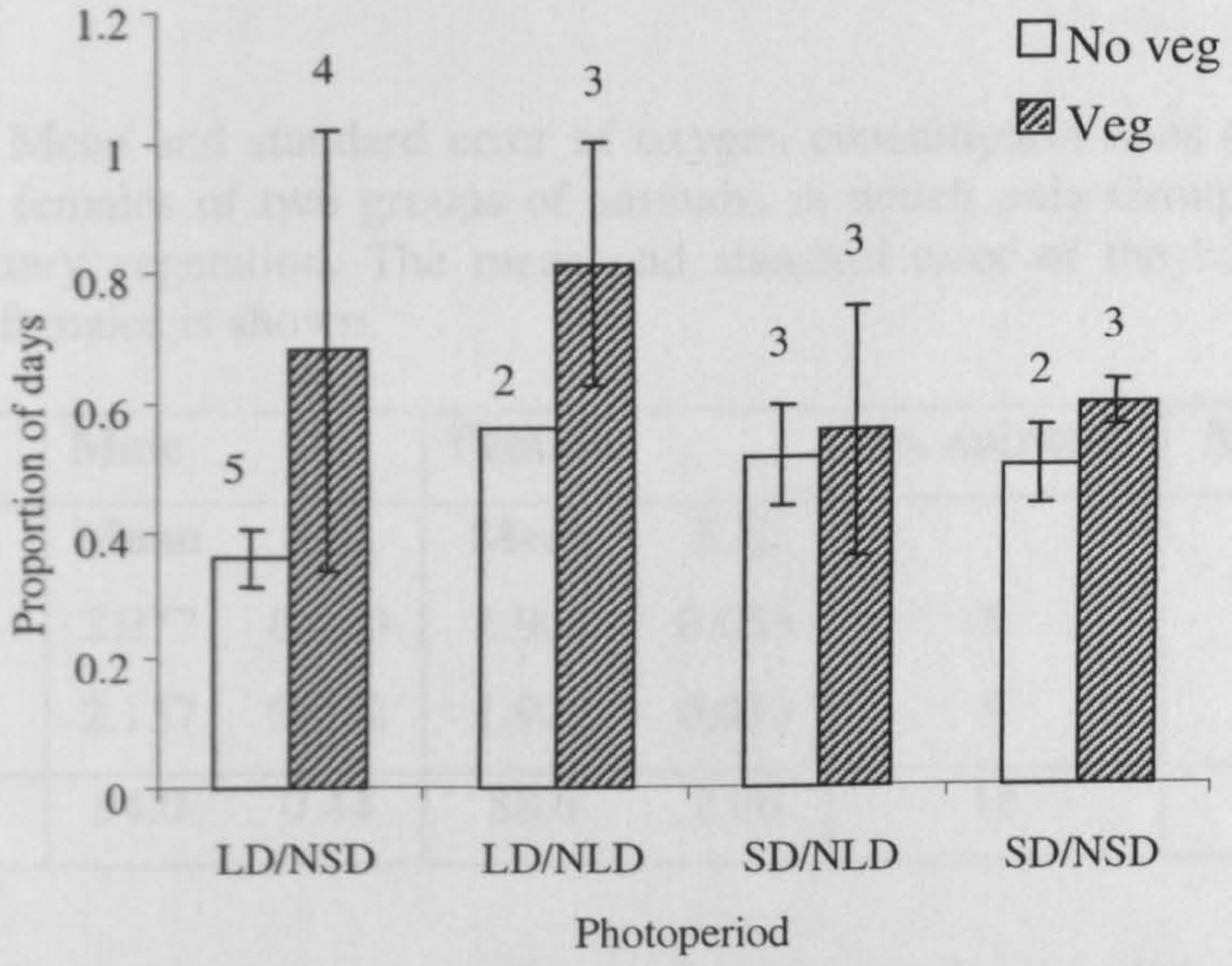
Six pregnancies were observed, of which three litters were devoured by their mothers a few hours after birth and one litter was still-born. In total three offspring of the two successful litters survived to adult status, one animal from the supplementary vegetation treatment and two from the other treatment. This sample size was not adequate to investigate the effects of vegetation on breeding parameters and therefore this topic will not be discussed further.

Copulation attempts, as assessed from female status, were used as an indication of breeding activity between treatments. Figure 6.1 shows the proportion of copulation attempts measured for animals on the two diet regimes exposed to two photoperiods. Long day and short day photoperiods were experienced twice, in parallel and in opposition to the natural photoperiod. It should be noted that the two successful litters, one from each diet regime, occurred during long artificial days in parallel with natural long days.

As data were expressed as proportions, non-parametric tests were used. Overall there were significantly more copulation attempts in animals that received supplementary vegetation compared to those that did not ($U = 37.5$, $P = 0.026$, $n = 12$, $n = 13$, Mann-Whitney U test). During long day photoperiods there was a significant difference in breeding activity between animals on different diets ($U = 6.5$, $P = 0.020$, $n = 7$), whereas, during short day photoperiods the difference in copulation attempts was not statistically significant ($U = 10.5$, $P = 0.402$, $n = 5$, $n = 6$). Overall there was no

significant difference in breeding activity between photoperiods for either animals without vegetation (U = 10, n = 7, n = 5, P = 0.213) or those with (U = 14, n = 7, n = 6, P = 0.315).

Figure 6.1 The proportion of days in which copulation attempts were noted during pairing, under the different photoperiods and vegetation supplement regimes. LD = long day, SD = short day, NLD = natural long day, NSD = natural short day. N is the number of females with each group.



Overall breeding attempts appeared to be slightly elevated when it was in parallel with natural breeding condition, but there was no statistical significance for either long day photoperiod (U = 10, P = 0.093, n = 9, n = 5) or short day (U = 11.5, P = 0.514, n = 6, n = 5). These results show that in this experiment the abundance of vegetation increased copulation attempts in *M. crassus*. However, the effect of vegetation was significant only when days were long.

6.3.2 Resting Metabolic Rate (RMR)

Due to low breeding success and the observation that breeding females were sensitive to human disturbance, resting metabolic rate was assessed only for non-reproductive animals. The influence of sex and diet regime on metabolic rate, investigated in preliminary studies (Sykes, pers. comm.) showed that seed biomass intakes of males and females were not significantly different, suggesting that the energetic requirements of males and females were similar. However, as mentioned in the introduction, body mass and fat composition influence metabolic rate and therefore males and females may show differences in RMR.

Granivorous rodents tend to have lower metabolic rates than omnivores (McNab, 1986; Degen, 1994); therefore it might have been expected that rodents fed a pure seed diet would have a lower RMR than rodents supplied with supplementary vegetation. However, *M. crassus* is noted for maintaining metabolic rate under different diet regimes (Yahav & Choshniak, 1989), with an oxygen consumption of males ranging from 1.93 to 2.86 ml/g/hr depending on diet. Table 6.3 shows the mean mass-specific RMR for males and females of the two groups under the two diet regimes, in which Group B received supplementary vegetation.

Table 6.3 Mean and standard error of oxygen consumption rates (ml/g/hr) for males and females of two groups of animals, in which only Group B received supplementary vegetation. The mean and standard error of the body mass of males and females is shown.

Group	Male		Female		No. animals	No. samples
	Mean	S.E.	Mean	S.E.		
RMR A: No veg.	2.077	0.020	1.908	0.035	9	150
RMR B: Veg.	2.157	0.032	1.922	0.035	9	120
Body mass (g)	94.0	0.44	88.6	2.06	18	270

Oxygen consumption of males was similar to that previously recorded even though body mass was much greater in my study than the 67.3g ± 4.16 given by Yahav & Choshniak (1989). Data were not normally distributed ($P < 0.05$, Kolomogorov-Smirnov) and attempted transformations did not normalise data (log transformation $P < 0.05$ Kolomogorov-Smirnov). There were significant differences in the median RMR between sexes within Group A ($U = 7939$, $n = 150$, $P < 0.001$) and Group B ($U = 4215$, $n = 120$, $P < 0.001$, Mann-Whitney U test), with males demonstrating a higher RMR than females. Adult males had a significantly higher body mass than females ($P < 0.05$, Kolomogorov- Smirnov, $U = 10.5$, $n = 9$, $P < 0.01$). Diet did not appear to effect metabolism as there was no significant difference between groups with or without vegetation supplementation for either males ($U = 8137$, $n = 150$, $n = 120$, $P = 0.176$) or females ($U = 8476$, $n = 150$, $n = 120$, $P = 0.412$, Mann-Whitney U test).

The large individual variation in the oxygen consumption by *M. crassus* has previously been noted (Yahav & Choshniak, 1989). Individual variation was investigated in this study by calculating the mean and standard error for each animal from 30 measurements of O_2 (Table 6.4). There were significant differences in the median RMR between

individuals of the same sex within Group A males ($X^2 = 21.62$, d.f. = 4, $P < 0.01$) and females ($X^2 = 100.31$, d.f. = 4, $P < 0.01$) and Group B males ($X^2 = 74.12$, d.f. = 3, $P < 0.01$) and females ($X^2 = 52.68$, d.f. = 3, $P < 0.01$), which agrees with previous observations for individual variations in *M. crassus*.

Table 6.4 Mean and standard error of resting metabolic rate ($mlO_2/g/hr$) for male and female individuals of the two groups of animals in which only B received supplementary vegetation, n = 30).

		Males			Females	
Group	**Animal Code**	**Mean**	**S.E.**	**Animal code**	**Mean**	**S.E.**
A	**C**	1.987	0.025	**B**	1.681	0.049
	J	2.048	0.060	**D**	1.532	0.038
	BE2	2.191	0.059	**K**	1.632	0.049
	DE1	2.190	0.042	**BE4**	2.339	0.023
	DE2	1.967	0.025	**BE6**	2.364	0.032
B	**E**	2.220	0.027	**H**	1.954	0.098
	F	2.041	0.044	**I**	2.330	0.015
	G	2.567	0.037	**BE5**	1.763	0.022
	BE1	1.791	0.011	**BE7**	1.642	0.017

6.4 DISCUSSION

6.4.1 Experimental limitations

Carrot was considered suitable as a form of supplementary water source and did not contain secondary compounds previously suggested to stimulate breeding in small mammals, e.g. 6-MBOA (Negus & Berger, 1977). If natural vegetation had been available this would have been preferred. It was assumed that the vegetation supplementation, as estimated from the average amount of carrot taken during one night's foraging (section 6.2.2) was above the amount required to influence sexual activity. In the absence of seeds, animals were shown to ingest carrot in relation to availability. This may be the result of facilitated digestion or nutritional supply, as on average more seeds were ingested in the presence of carrot than seed alone. It was also assumed that total food availability was above the energy requirements. Photoperiod may have increased energy requirements by stimulating energetically costly reproduction or by influencing variations in daily activity patterns, i.e. *M. crassus* is strictly nocturnal in the wild (Harrison & Bates, 1991). Therefore, longer days may decrease the overall period of activity and hence reduce energy requirements. It was assumed that the time over which the photoperiod was manipulated was sufficient to stimulate breeding activity. It would be interesting to repeat the experiment with more pairs of animals and vary the time over which the photoperiod was manipulated. Additionally, if time had allowed the diet of the two groups would be switched and the experiments re-run.

In the pairing experiments it was assumed that breeding attempts were not affected by the level of kinship of the pairs or female sexual selection. The same individuals were paired throughout the experiments, except when individuals died in which case new partners were found. Copulations or breeding attempts were recorded from females possessing vaginal perforation and/or vaginal plugs, however it should be noted that perforation also occurs as a result of oestrus. By selecting random days in which to assess recent copulation it is assumed that the chance of recording perforation resulting from oestrus (compared to recent copulation) was similar for all animals; therefore results would be comparable. However, in most cases, it was obvious that perforation must have occurred from male penetration, i.e. swollen opening to the vagina or the presence of a copulatory plug.

Reproductive success was low in laboratory conditions. Due to the low number of litters and juveniles, RMR studies were not continued during breeding in case they would cause yet more disturbances to a dwindling population. It has been suggested that low breeding success is the result of the presence of *ad libitum* water, as Khokhlova (pers. comm.) recorded an increase in infanticide, embryo re-absorption and a destabilisation of the oestrous cycle in *M. crassus* when free water was available.

6.4.2 Effects of supplementary vegetation on breeding attempts

Supplementary vegetation experiments suggest that the supplementary water increased copulation attempts in *M. crassus*. The effect of supplementary vegetation was significant only when days were long, indicating that photoperiod also influences breeding activity. This suggests that sexual responsiveness to supplementary water availability is affected by day length. Individually, male sexual activity did not appear to differ in the presence or absence of vegetation, which suggests males and females show differences in responsiveness to environmental factors and may use different cues in reproduction. Overall, results suggest that the timing and extent of breeding are controlled by several interacting environmental factors.

6.4.3 Metabolic rate

In estimating the RMR it is assumed that the animals were actually at rest. As the individuals were not in constant view, resting was assumed when there was a basal flattening of the trace. Occasional observations allowed me to check the animals lack of activity, which appeared to correspond with the carbon dioxide production levels at the time of viewing. Some animals did not settle throughout the measurements and in these cases respirometery was repeated until the animal did eventually rest.

There were significant differences in the median mass-specific RMR between sexes within Group A and Group B, with males demonstrating a higher RMR than females (Table 6.3). One explanation for this could be the differences in body composition, i.e. lean body mass (Konarzewski & Diamond, 1995), as lean tissues, such as liver and kidneys have higher metabolic activities per gram than other tissues such as fat (Krebs, 1950). However, estimation of this using TOBEC was not undertaken as no previous data were available on the body composition of *M. crassus* and sacrificing the animals was not permitted. Although all animals were of adult body weight they varied in age, which may contribute to the individual variations in RMR. Metabolic rate is higher

during birth to maturity and decreases in older animals (Blaxter, 1989). Animal husbandry, diet, experimental set-up and the population from which the animals were first taken may have accounted for the differences in body mass and metabolism in my animals compared to previous studies (Yahav & Choshniak, 1989).

Diet did not appear to affect metabolism, as there was no significant difference between groups with or without vegetation supplementation for either males or females. Changes in diet quality have been shown to influence basal metabolism in semi-arid rodents, e.g. *Octodon degus*, such that, greater digestibility increased basal metabolic rate (Veloso & Bozinovic, 1993). Changes in diet in the field are linked to seasonal changes in ambient temperature and photoperiod, which can also independently influence energy requirements (Haim & Rubal, 1993). Seasonality has been shown to influence body weight, fat composition, sexual activity and thermogenesis (Haim & Levi, 1990; Khokhlova *et al.*, 1994). It has been suggested that as an adaptation to arid-environments *M. crassus* can maintain energy balances and O_2 consumption on diets of differing quality (Yahav & Choshniak, 1989). If changes in the availability of vegetation did enhance reproductive activity in males or females, this was not reflected in the resting metabolism.

CHAPTER 7
GENERAL DISCUSSION

This chapter provides a synthesis of all work undertaken, comparing the findings with previous studies of the ecology of desert living rodents; identifying areas of agreement and dissimilarity, and indicating where the present study provides additional knowledge. It discusses the potential applications of the findings to the conservation, management and development of arid environments and suggests ideas for future studies of the ecology of desert-dwelling rodent.

7.1 Limits to the scope of the study

As the north-eastern Badia region of Jordan has received little attention with respect to ecological studies, one of the limitations to the scope of the study was the paucity of background information, including that on the distribution and abundance of animal and plant species. Therefore, one of the aims of thesis was to establish 'baseline' and descriptive data, comparable to similar studies elsewhere, on habitat types, small mammal communities and potential resource abundance. An additional objective was to study several aspects of the ecology of desert rodents. Funding and the interests of collaborating parties imposed further limitations on the scope of the investigations, i.e. the study had to be of relevance and application to arid-land development, management and conservation. The timing of the field work was limited by environmental conditions and logistics, and the field studies themselves were restricted by the levels of disturbance and problems associated with land ownership in the region.

7.2 Species presence and geographical distributions

This thesis reports on small mammal species present in an area of Jordanian desert, previously unstudied. The data collated provides additional information on species' geographical distributions within the Middle East and their adaptations to the particular habitat types represented in this region. The observations on the occurrence of *Gerbillus henleyi* expand the current range for this species, as it has not previously been reported from such a northerly location. The absence or low occurrence of some species (e.g. *Meriones tristrami*) suggests that Badia may lie at the limits of the distribution of these species. This may be due to the presence of the extensive rocky area of black basalt (harrat) which dominates the north of this region and which contains species that have evolved to exploit this habitat type. For example, it is suggested that the darker

individuals of *G. dasyurus* reported in this area possibly represent a local subspecies restricted to the basaltic habitat (Harrison, pers. comm.).

7.3 Mechanisms underlying community organisation

Analyses of community composition supported several previous findings. Firstly, rodent species fell within 'guilds' similar to those described by Shenbrot *et al.* (1999), whereby rodents showed petrophily, psammophily or were habitat generalists. The formation of spatial assemblages related to macro-habitat type has been found for many studies of desert rodents in Asia (e.g. Shenbrot *et al.,* 1999). The distinct habitat preferences, together with size disparity and differences in specialisation and morphology demonstrated within 'guilds', reported in this study, further support ideas of mechanisms involved in resource partitioning, which are thought to underlie community structuring in desert rodent species (Kotler *et al.,* 1993).

In this study rodents showed habitat preferences, with a maximum of three species represented in each guild (Fig. 2.4). This supports the theory of macro-habitat separation as a co-existence mechanism, suggested to be more important in community structure in Asian deserts than North American deserts (Shenbrot *et al.,* 1999). Within the petrophiles there were size differences between the two common species, *Acomys russatus* and *Gerbillus dasyurus*. These species also showed differences in spatial habitat use, i.e. *Acomys russatus* was found in the upper basalt slopes, whereas *G. dasyurus* was found throughout. Both these features may reduce inter-specific competition within the guild. It has also been noted that *A. russatus* is partially insectivorous, whereas *G. dasyurus* is not thought to take insects. Both these species were darker in form in the harrat habitat than in other habitat types (Harrison & Bates, 1991) and the melanic forms may represent anti-predatory adaptations to this black basaltic habitat. This supports the suggestion that predation risk has played an important role in the evolution of morphologies within desert rodent species (e.g. Bowers & Dooley, 1993). Additionally, *A. russatus* was observed to be nocturnal in this area, supporting the suggestion that it is more active at night here than elsewhere, in response to reduced competition from *A. cahirinus,* which was not found within this region. This observation also agrees with the idea that inter-specific competition affects foraging behaviour in desert rodents.

Within the guild associated with open hammada habitats, there were differences in body size and morphology. The differences in morphology between the species of closest body size within this guild, i.e. bipedal *Jaculus jaculus* and quadrapedal *Meriones crassus* (Fig 2.1), may reflect another axis on which resources are partitioned between these two species. The third constituent species of this guild was much smaller in body size than the other two, and therefore indicates that difference in resource utilisation aids co-existence. Overall, the psammophile guild also showed differences in body mass. However, the two species closest in body size, i.e. *Gerbillus cheesmani* and *Gerbillus nanus,* were both quadrapedal (See Fig. 2.1), but the hairy feet of *G. cheesmani* may be a specialisation to sandy habitats, to enable it to exploit different resources. It is likely to be more effective at traversing open sandy areas than *G. nanus*, which may increase its ability to harvest seeds from these areas or reduce the predation risk associated with foraging within them. Additionally, the sandy dorsal coloration of *G. cheesmani* captured in this study was similar to the predominant soil colour in which it was caught. Again, this maybe an anti-predatory adaptation.

Comparison of my data with those from Israeli studies (Krasnov *et al.*, 1996a) indicates that some species are flexible in their habitat preferences in relation to availability of habitat and possibly as a result of inter-specific competition. This is demonstrated by the habitat preferences shown by *G. nanus* and *G. dasyurus*, which appear to be mutually exclusive in Jordan but not in Israel. *G. dasyurus* was observed to be more petrophilic and *G. nanus* more psammophilic in Jordan. Biological factors (e.g. intra- and inter- specific competition, predation and disease) which potentially play a role determining community composition were not specifically addressed in this study.

7.4 Optimising energy returns in an unpredictable environment

Within habitats that were neither predominantly sandy nor rocky, i.e. marab and wadi, community composition differed between months, seasons and years (Fig. 2.5). The observation of temporally dynamic community compositions within habitats suggests that some rodent species respond behaviourally to temporal changes, such as in food abundance, within habitats. Foraging decisions to optimise food returns have to be highly flexible, and are dependent on many factors additional to resource abundance. Flexibility is one way of increasing energy returns in an environment that has unpredictable resources. The spatial and temporal variations, within and between habitats, for both vegetation and seeds were demonstrated in Chapters 3 and 4.

Flexibility in habitat use, i.e. foraging in a variety of habitats as resources became available, would be advantageous only if the benefits of shifting habitat outweigh other costs. For specialist species, shifting habitat may incur additional 'costs', such as increased inter-specific competition and predation risk. For example, *Acomys russatus lewisi*, a melanistic climbing mouse would potentially incur more 'costs', such as increased predation risk, if it were to attempt to exploit resources available in a sandy areas. Changes in community composition in some macro-habitats may be a result of the unpredictable characteristics of desert environments and therefore the temporal fluctuations should be considered in future studies of desert rodent community composition.

Flexibility in diet would be advantageous in an ecosystem where resource availability is unpredictable and can fluctuate dramatically. This has been demonstrated for several desert rodent species (e.g. *M. crassus*; Krasnov, *et al.*, 1996b), where diet varies in relation to resource availability. Although granivory is reported for many desert rodents, this tends to be only the predominant and not the sole diet (Degen, 1997). It is therefore suggested that both granivory and flexibility in diet are important adaptations in desert environments.

7.5 Environmental factors

Vegetation and soil parameters were found to be the environmental factors that most influenced rodent community composition. Vegetation can either provide a food source or habitat structure, which in turn provides niches to facilitate co-existence. Soil composition will influence accessibility to resources, such as seeds and the availability of refuges. Habitat preference is possibly a composite of several of these factors. The importance of soil in determining distributions of species has been noted for desert rodent communities by Shenbrot *et al.* (1994a). The necessity of a refuge from harsh desert conditions and predation appear to have been important in the evolution of many of the observed morphological features of desert rodents (e.g. Webster & Webster, 1971). Additionally, soil texture, moisture content and particle size have been shown to affect foraging efficiencies. A habitat may have high densities of normally inaccessible seeds which become susceptible to foraging from time to time. For example, rainfall may increase olfactory location of seeds by rodents (Vander Wall, 1995), or even change soil properties.

7.6 Influences of vegetation and seed abundance on rodent ecology

If vegetation within a habitat is of major importance to rodents as a food, habitats with more vegetation would be expected to support higher rodent densities than those with less vegetation; however, this was not observed to be the case (see section 5.3.1). Therefore, it is suggested that the availability of refuges and/or suitable soils for burrowing are of greater importance in determining the presence of a particular species within a habitat than resource abundance. This is possibly because, on a smaller scale, rodents can shift their foraging behaviour to incorporate a range of habitat types other than those they burrow in. However, this does not explain why low densities of rodents were found within the marab habitat at Salma, despite this habitat possessing the greatest vegetation and seed abundance recorded of all the study sites. In the marab at Salma, the soil surface was densely covered with vegetation, which may present problems for foraging rodents trying to dig. This habitat was found to be the hardest to penetrate and separate when taking soil cores. The suitability of habitats adjacent to marab habitat could also explain the low density of rodents therein. Habitats suitable for burrowing, e.g. hammada, were limited in the vicinity of the marab at Salma (see Plate C), whereas higher densities of rodents were found in the marab at Hashad, which had large areas of adjacent hammada.

It is evident from the results that the spatial scale at which communities are assessed is important. A rodent may be recorded as present within a 'wadi' system but only utilise a small proportion of the heterogeneous habitats types found within the 'wadi'. The temporal and spatial variability in resource abundance in deserts also depends on the scale and type of resource assessed.

Studies of vegetation showed that composition and abundance varied between habitats. Composition may influence the habitat preference of rodents depending on their species-specific food preferences and its temporal availability. Habitats possessing perennials may be utilised all year round as a vegetation source, but they can vary seasonally in biomass and water content (Degen *et al.*, 1990). Vegetation composition will also determine the time and abundance of the seed crop, which may also account for temporal variations in habitat use by rodents. Figures 4.5 and 4.6 show the differences in the timing of seeding between species. It is suggested that rodents may shift their habitat use to exploit newly produced seed crops, as has been demonstrated for heteromyid rodents in the Sonoran desert, Arizona (M'Closkey, 1983). However,

further studies of rodent diet and micro-habitat use would be required to investigate this in the Badia region.

The temporal availability of vegetation was shown to be important in determining the extent of breeding in a laboratory colony of *Meriones crassus* (see Chapter 6). Extrapolating observations conducted under laboratory conditions to field studies is difficult due to the multitude of factors that potentially affect breeding in the wild and that cannot be controlled in the laboratory, e.g. social interactions, refuge availability etc. However, if rodents in the wild respond similarly to laboratory animals, it may be inferred that the availability of fresh vegetation in the spring would increase breeding activity. It has also been shown that the abundance of vegetation can determine the abundance and number of co-existing species within a habitat, probably by reducing inter-specific competition for resources and enhancing reproductive output (Abramsky & Rosenzweig, 1984; Abramsky, 1988). Habitats that have a predominance of perennial species, e.g. marab, will provide a constant availability of vegetation, and animals that utilise perennials as a food source would be free of marked seasonal variations in food abundance (Daly & Daly, 1975). However, there was no evidence that these habitats were associated with higher abundances' of rodents or changed the timing of thier breeding. It was not possible to manipulate the abundance of vegetation to investigate the effect on breeding in this study. This is recommended for future investigations.

The problems associated with assessing rainfall are emphasised in desert systems, where it may be highly localised and sporadic in occurrence. Furthermore, features such as habitat topography and soil properties make the assessment of moisture availability, which will directly influence vegetation abundance at smaller spatial scales, difficult. Many other factors influencing resource abundance could not be controlled for in this field study (e.g. temperature, humidity etc.) and it is recommended that future studies could consider the influences of additional abiotic factors on changes in resource abundance.

The systematic approach to assessing seed abundance adopted in this study has demonstrated that assessment of individual seed 'sources', such as the seed bank, may provide an incomplete picture of the total seed abundance within an area that is potentially available to rodents. Additionally, the variation in seed abundance in space and time differs between different seed 'sources'. The seed rain was less spatially

variable than the seed bank, whereas the seed bank was more consistent in abundance over time (see Chapter 4). Data were obtained which supported findings of Price & Joyner (1997) that larger seeds occurred more frequently in the seed rain than in the seed bank. During dispersal, seeds are translocated from concentrated areas of production, i.e. the parent plant, and the type of mechanism will determine the dilution of seeds within the area. Hence, within an area, levels of seed abundance do not always correspond with the density of vegetation cover (see Fig.4.12). As with vegetation cover, seed abundance within habitats was not a good predictor of rodent densities, which supports the previous suggestion that resource abundance is not the major factor influencing rodent habitat preferences. Seed abundance in a habitat appeared to be less predictable than vegetation abundance and more evenly dispersed. This may account for the observations that rodents exploit virtually all habitats available and do not appear to show preference for, or higher densities in, areas which visually seem to have higher productivity, i.e. the highly vegetated marab.

7.7 Timing of breeding

Field observations of the timing of breeding generally agreed with previous observations for the species trapped, although a longer study period would be required to compare seasonal breeding patterns. As species show habitat preferences, and within these habitats the timing of resource availability varies, this may account for the observed differences in the extent of breeding between species. The extent of breeding and the timing of juvenile emergence did not correlate with natural resource abundance within the habitat where the animals were captured. Several suggestions can be made to account for this. Rodents may be utilising resources in other habitats or utilising different resources from those assessed; or there may be a lag period between resource abundance and its influence on breeding. Additionally, although the proportion of females breeding was higher in area with supplementary food, this might not necessarily lead to higher densities, as other factors may control the overall density within an area.

Triggers controlling the timing of breeding are likely to vary between rodent species (see Degen, 1997), and may vary geographically within species in relation to environmental conditions. The results of my laboratory experiments support the idea that reproduction in *Meriones crassus* is controlled by the amount of vegetation in the diet (as found also by Khokhlova, pers. comm.). However, it also indicates that this species varies in sensitivity to this cue, and that breeding will be enhanced only if

vegetation is available during increasing day-lengths. This further supports and potentially clarifies recent suggestions that breeding in some desert rodents is determined by a combination of cues from the environment (El Bakry *et al.*, 1998). Photoperiodic involvement in breeding may act as a mechanism to prevent *Meriones crassus* breeding during decreasing day-lengths, i.e. autumn, when the forthcoming environmental conditions may be unsuitable for the survival of offspring. It is predicted that in arid regions with little seasonality, photoperiod would have a less important role in determining the timing of breeding.

Lactation is considered to be costly with respect to energy and water balance; however the differences in metabolic rates of desert rodents in relation to gestation and lactation have yielded conflicting evidence (see Degen, 1997). It was hoped that metabolic studies on *Meriones crassus* would have contributed to this debate and provided an insight into the costs of various stages of reproduction and development. As my investigation was limited by sample size the conclusions were equivocal and it is recommend as a potential future study topic.

7.8 Future investigations on desert rodent ecology: a summary

From this discussion it is clear that there are many areas of research in the Badia region, and desert rodent ecology as a whole, that require further work. For future studies on desert rodent ecology in this area I would recommend investigations into macro- and micro-habitat use, activity patterns and diet in relation to changes in resource abundance over space and time.

Investigations of changes in macro- habitat use by individuals and species in relation to resource abundance would provide further information on the dynamics of desert rodent communities. It would also provide an insight into behavioural responses whereby the rodents attempt to optimising energy returns in an unpredictable environment. Micro-habitat use by different species may elucidate the factors facilitating co-existence within guilds, i.e. the consequences of body size and morphology. Studies of diet and activity patterns may also provide some insight into this. Diet selection by rodents may be a consequence of plant palatability, nutrient content, water content and/or the presence of secondary compounds, potentially involved in initiating breeding. Therefore, it would be informative to investigate the composition of different food sources, their temporal and spatial abundance and dietary preferences of rodent species in relation to resource

type and abundance. Further studies of spatial and temporal variation in rainfall and moisture distributions at different spatial scales could provide information on resource availability patterns.

Annual variations in resource abundance will influence the extent and output of breeding, and therefore it would be interesting to compare breeding in different species between years of above and below average productivity, and/or to manipulate levels of vegetation abundance to investigate its effects on breeding. It has been suggested that some species are less dependent on seed abundance than others (Degen, 1997) and therefore the response of different species to resources would contribute to another level of dynamics in community composition. Additionally, it would also be informative to investigate 'the lag effect' of a previous year's seed and vegetation productivity on breeding and densities of rodents.

A further suggestion for future study would be to investigate predator prey-interactions within this ecosystem. From preliminary studies it appeared that the diet of the red fox (*Vulpes vulpes*) inhabiting this area was more restricted than for *V. vulpes* populations inhabiting less arid areas (Watson, 1976; Richards 1977), and was comprised largely of invertebrates (in 72% of faeces examined), vegetation (62%) and small mammals (52%). The dominance of invertebrates, particularly Coleoptera, in the diet of foxes has been recorded previously in areas of particularly sparse or seasonally fluctuating rodent densities (Blanco, 1986; Cavallini & Lovari, 1994). It is also thought that the high proportion of vegetation maybe a result of aridity and limited resource abundance.

Finally, it would be of interest to investigate the spatial scaling of rodent communities; this would reduce the ambiguity involved in defining a habitat type, or area, relative to individuals and communities, and facilitate comparisons between studies that have used different scales.

7.9 Conservation and development in Jordan

During this century Jordan has suffered losses of wildlife through poor land management (resulting in desertification), development of agriculture and hunting. One example where desertification is already visible in Jordan is an arid rangeland (Al-Mowaqqar) where overgrazing, lack of rotational or deferred grazing, ploughing for barley and wheat cultivation, and uprooting of shrubs for fuel, aggravated by environmental conditions, have resulted in massive land deterioration. In large areas

severe reduction or disappearance of vegetation has occurred (Abu-Taleb & Salameh, 1994).

In the 1980s several nature reserves were set up to conserve and in some cases reintroduce (e.g. oryx) the endemic wildlife of the country. Since their formation, several investigations have been undertaken to assess the effectiveness of reserve establishment and suggest plans for their management. These studies have suggested that 'protection' of areas, i.e. prevention or reduction of human activity, is 'beneficial' to the conservation of many plant and animal species. This was concluded from observations that protection caused an increase in vegetation height and cover, the number of macrophyte species and the density of rodents (Hatough *et al.*, 1986).

The findings in this thesis suggest that the changes in vegetation abundance, composition and habitat structure, resulting from grazing protection will influence the community composition of small mammal fauna of this region. Productivity from vegetation will determine food abundance, both plant material and the subsequent seed bank. Increases in food abundance have been demonstrated to influence the extent of breeding in the desert rodent *M. crassus,* and may result in higher densities of this species and other rodents. Habitat structure has been shown to influence rodent community composition, as changes in vegetation cover, habitat heterogeneity and suitability of burrowing will determine the species presence. Increased vegetation cover will reduce the number of species with preference for open habitats, e.g. bipedal species. Increases in rodent density may not necessarily result in areas of higher species richness. Higher densities of animals will confer increased inter- and intra-specific competition and at high levels of productivity, species diversity has been shown to decrease (Rogovin, 1996). In my study, the habitat containing the highest vegetation abundance, marab at Salma, had the lowest levels of species richness and density of all the habitats studied in 1998.

At the other extreme, changes in habitat structure, vegetation abundance, seed abundance and soil structure, as a result of overgrazing and detrimental land uses (Sankary, 1981), could also potentially influence rodent species community composition, density and richness. Overgrazing results in a decrease in vegetation abundance and can effect the annual seed crop (Milton, 1995), therefore this can decrease food abundance for rodents and consequentially population densities (Hatough

et al., 1986). The effect of grazing was evident in the present study, where a decrease in vegetation cover was recorded at Salma during periods of high Bedouin presence. Changes in habitat features such as soil and cover will influence microhabitat use, foraging behaviour and possibly suitability of habitats for burrow construction and hence will determine the presence and abundance of species within these areas.

Differences in rodent abundance and community composition in response to changes in habitat features will have effects on their prey and predators. Predator populations tend to follow prey abundance and therefore would be expected to decrease following reductions in prey density in response to decreased resource abundance (e.g. Lindström, 1988). The relative availability of different prey will influence predator foraging behaviour and diet selection, and therefore may determine spatial distribution of predator species and predation levels on alternative food sources (e.g. Lloyd, 1975). Plant communities may also be affected, as increased herbivory and granivory will reduce abundance of vegetation and seeds. Selective predation of seeds by rodents, as indicated in the size differences observed in the seed rain and seed bank in Chapter 4 (Price & Joyner, 1997), may also alter plant community composition (e.g. Brown & Heske, 1990a).

Therefore, with respect to conserving wildlife biodiversity within the Badia region, and other desert systems, both overgrazing and 'over-protection' could have detrimental effects on overall species diversity. To maximise the species richness of small mammals within a reserve, the maximal range of habitat types should be represented. Within Jordan, this should include habitats of basaltic desert, due to its individuality as a biome and the presence of endemic and potentially new sub-species. The land management of this area should facilitate the persistence of 'natural' levels of populations of these species by moderating human exploitation to extents that do not result in overall land deterioration. It is suggested that rodent populations may be used to monitor desertification as their populations can reflect recent productivity and therefore habitat status that is not always evident from visual estimation.

7.10 Future studies related to arid land management

To enable recommendations for land management it would appear to be essential for future studies to assess sustainable levels of grazing and habitat exploitation. This has also been recommended by previous studies within Jordan (Hatough *et al.*, 1986) and

this information appears to be critical to implement effective arid-land management. However, this will be influenced by several factors, such as the productivity of the habitat type. It has been demonstrated in this investigation that vegetation abundance can differ dramatically, temporally and spatially, and is dependent on changes in environmental conditions, such as precipitation.

Persistence in the seed bank is an important strategy for the survival of many desert plants (Kemp, 1989). The timing of gazing in relation to the production of the seed crop could be vital in determining the abundance of seeds that are incorporated into the seed bank, hence species survival and therefore, plant biodiversity. It has been shown that selective herbivory during flowering can reduce the number of seeds produced (Milton, 1995). Restricting grazing to periods after seed dispersal by annual plants would maintain the biodiversity and 'productivity potential' of an area. However, this suggestion is complicated by differences in the timing of seed set between species. In this investigation seeding of different annual plant species showed spatial and temporal variation (Figs. 4.5 & 4.6). Overall, seeding appeared to curtail in early May, but vegetation biomass was still relatively high during May. Therefore, grazing immediately after seed dispersal, which has least effect on the seed bank (hence on sequential productivity and species diversity) would still encounter levels of nutrients similar to previous months. Again, this would vary annually in relation to environmental conditions, but may be an approach to conserving plant biodiversity and seed abundance for rodents in grazed areas. Further investigations within deserts ecosystems of the interactions between trophic levels and the impact of changing environmental factors on each level would give a better understand of the ecological consequences of the land management practices employed.

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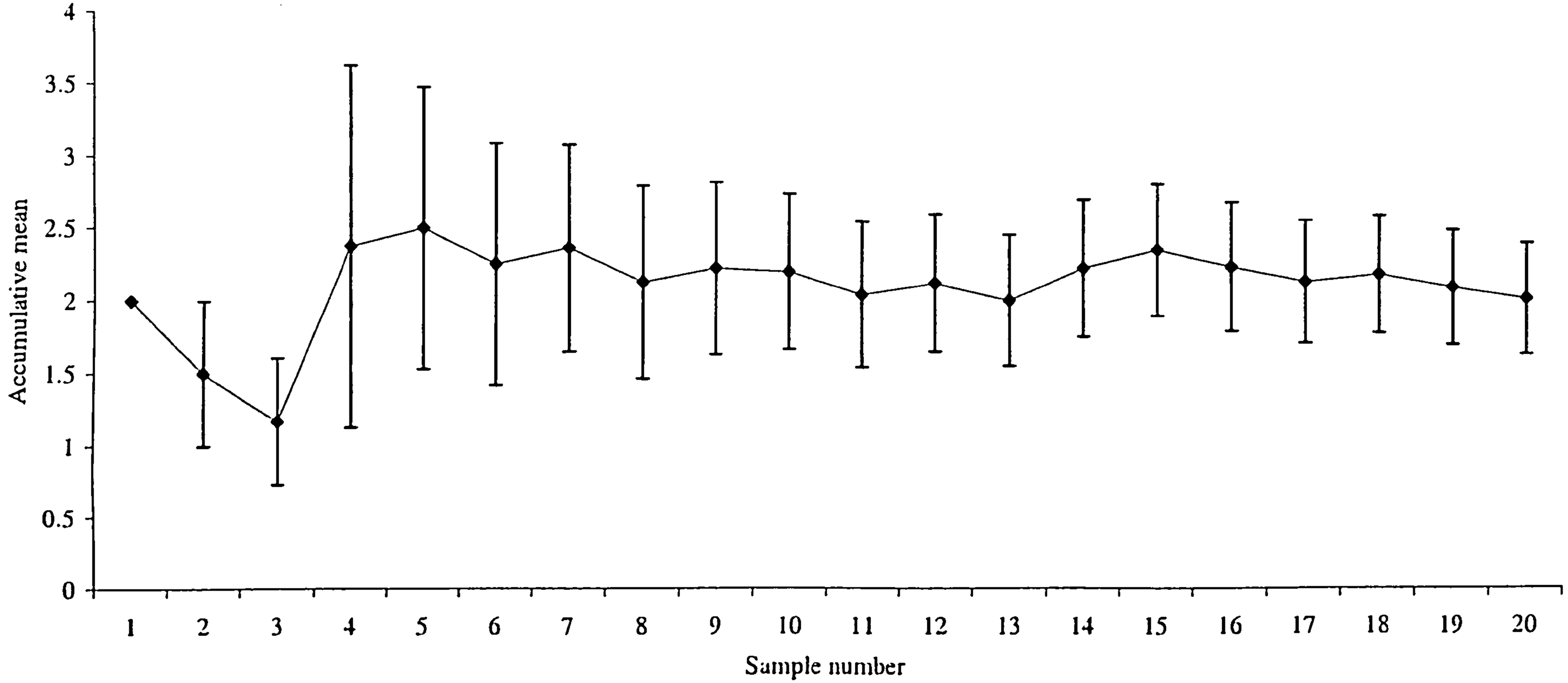
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Appendix I. The accumulative mean and standard error of the percentage cover of ephemerals in the harrat habitat at Salma, from data collected during spring 1998. Results show that the optimum sample size is above 10.



Appendix II. Density estimates (no/ha) per species for each sample site. Samples are coded by site name, season (or month) and year. C = limestone cliffs, D = dunes, RD = red dunes, H = hammada, M = marab, B = Harrat and W = wadi. Rodent species are also coded, JJ = *J. jaculus*, GD = *G. dasyurus*, GN = *G. nanus*, GH = *G. henleyi*, GC = *G. cheesmani*, MC = *M. crassus*, ML = *M. libycus*, MT = *M. tristrami* and AR = *A. russatus*.

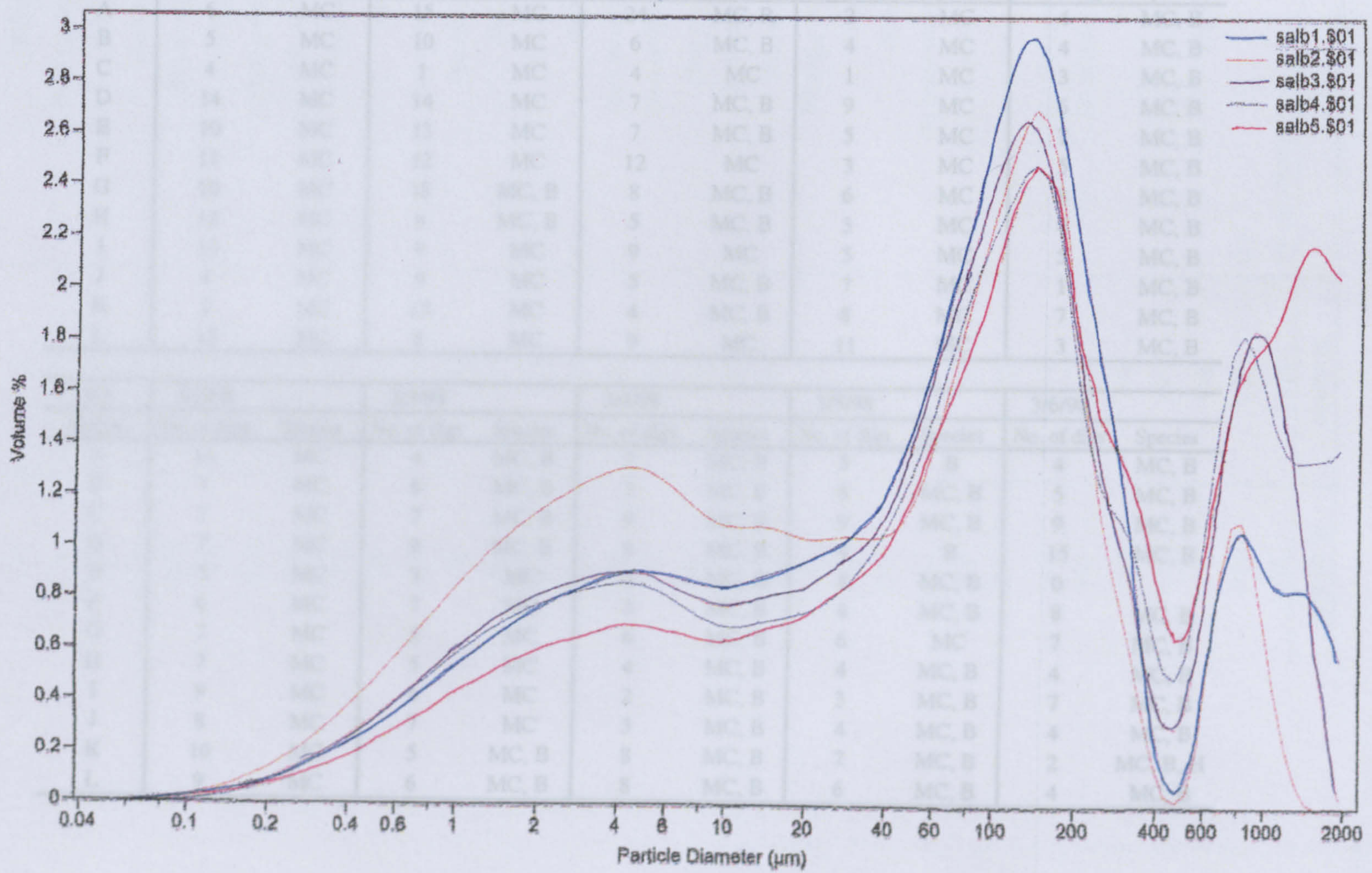
Habitat/site

	RD	C	C	C	D	D	D	D	D	H	H	H	H	M	M	M
Spp.	QDsp97	DHsp96	DHsm96	DHsp97	HZDsp96	HZDsm96	HZD3/97	HZD4/97	HZD5/97	HZH3/97	HZH4/97	HZH5/97	BHsp97	SMsp96	SMsm96	BQsp96
JJ		0.01		0.07	0.12	0.08	0.15	0.12	0.12	0.12	0.09	0.02	0.08	0.04	0.10	0.12
GD															1.04	17.71
GN		6.25	4.17	5.00	21.88	27.08	8.75	5.00	8.75							
GH										3.75	3.75	5.00				2.08
GC	8.75				8.33	8.33		1.25	3.75							
MC					1.04	1.04	1.25	1.25	3.75	3.75	1.25	5.00	1.25	3.13	1.04	2.08
ML		1.04	2.08		6.25	3.13	1.25	1.25	1.25	1.25						
MT																
AR																

Habitat/site

	M	M	M	M	M	M	W	W	W	W	B	B	B	B	B
Spp.	BQsm96	BQsp97	HSAsp96	HSAsm96	HSAsp97	HSBsp97	SWsm96	SW3/97	SW4/97	SW5/97	BUBsp97	SBsp96	SB3/97	SB4/97	SB5/97
JJ	0.12	0.07	0.13	0.04	0.05	0.05									
GD	16.67	5.00	7.29	6.25	1.25	3.75	10.42	5.00	3.75	5.00	1.25	12.50	11.25	10.00	12.50
GN															
GH															
GC															
MC	2.08	2.50	4.17	2.08	6.25	7.50				1.25					
ML	1.04														
MT							2.08								
AR			1.04										3.75	6.25	2.50

Appendix III: An example of soil particle size analysis from the harrat at Salma



Appendix IV. Dig counts and print identification on feeding stations, where MC = *M. crassus*, B = bird and H = Hare (*L. capensis)*

H4	3/2/98		3/3/98		3/4/98		3/5/98		3/6/98	
Station	No. of digs	Species	No. of digs	Species	No. of digs	Species	No. of digs	Species	No. of digs	Species
A	6	MC	15	MC	24	MC, R	2	MC	4	MC, B
B	5	MC	10	MC	6	MC, B	4	MC	4	MC, B
C	4	MC	1	MC	4	MC	1	MC	3	MC, B
D	14	MC	14	MC	7	MC, B	9	MC	6	MC, B
E	10	MC	13	MC	7	MC, B	5	MC	7	MC, B
F	11	MC	12	MC	12	MC	3	MC	5	MC, B
G	10	MC	18	MC, B	8	MC, B	6	MC	8	MC, B
H	12	MC	6	MC, B	5	MC, B	3	MC	4	MC, B
I	13	MC	9	MC	9	MC	5	MC	5	MC, B
J	8	MC	9	MC	5	MC, B	7	MC	1	MC, B
K	2	MC	15	MC	4	MC, B	8	MC	7	MC, B
L	15	MC	8	MC	9	MC	11	MC	3	MC, B

H3	3/2/98		3/3/98		3/4/98		3/5/98		3/6/98	
Station	No. of digs	Species	No. of digs	Species	No. of digs	Species	No. of digs	Species	No. of digs	Species
A	11	MC	4	MC, B	2	MC, B	5	B	4	MC, B
B	7	MC	6	MC, B	3	MC, B	8	MC, B	5	MC, B
C	7	MC	7	MC, B	9	MC, B	9	MC, B	9	MC, B
D	7	MC	9	MC, B	8	MC, B	4	B	15	MC, B
E	5	MC	3	MC	4	MC, B	4	MC, B	0	
F	6	MC	7	MC	3	MC, B	4	MC, B	8	MC, B
G	7	MC	5	MC	6	MC, B	6	MC	7	MC, B
H	7	MC	5	MC	4	MC, B	4	MC, B	4	MC, B
I	9	MC	4	MC	2	MC, B	3	MC, B	7	MC, B
J	8	MC	7	MC	3	MC, B	4	MC, B	4	MC, B
K	10	MC	5	MC, B	8	MC, B	7	MC, B	2	MC, B, H
L	9	MC	6	MC, B	8	MC, B	6	MC, B	4	MC, B

Appendix V. Nutritional composition per 100g of carrot (*D. carota*) and sunflower seeds (*H. annuus*) used in supplementary feeding experiments. Taken from Holland *et al.*, (1991), where Tr is trace and N is nil.

	D. carota	*H. annuus*
Energy: (Kcal)	32.5	581
(kJ)	135.5	2410
Water (g)	89.3	4.4
Protein (g)	0.65	19.8
Fat (g)	0.4	47.5
Carbohydrate (g)	6.95	18.6
Total Nitrogen (g)	0.11	3.74
Fatty acids: Saturated (g)	0.1	4.5
Monounsaturated (g)	Tr	9.8
Polyunsaturated (g)	0.25	31.0
Starch (g)	0.25	16.3
Sugars (g)	6.5	1.7
Dietary Fibre (g)	2.5	N
Sodium (mg)	32.5	6.0
Potassium (mg)	205	710
Calcium (mg)	29.5	110
Magnesium (mg)	6	390
Phosphrous (mg)	20	640
Iron (mg)	0.35	6.4
Copper (mg)	0.02	2.27
Zinc (mg)	0.15	5.1
Cholrine (mg)	36	N
Manganese (mg)	0.1	2.2
Se (µg)	1	49
Iodine (µg)	2	N
Carotene (µg)	6722.5	15
Vitamin E (mg)	0.56	37.8
Thiamin (mg)	0.07	1.6
Riboflavin (mg)	0.02	0.19
Niacin (mg)	0.2	4.1
Tyrpt (mg)	0.1	5.0
Vitamin B6 (mg)	0.11	N
Folate (µg)	20	N
Pantothenate (µg)	0.25	N
Biotin (µg)	0.6	N

Appendix VI An example of a trace produced in respirometry experiments showing periods of flattering in O_2 consumption from which 30 values were measured.

