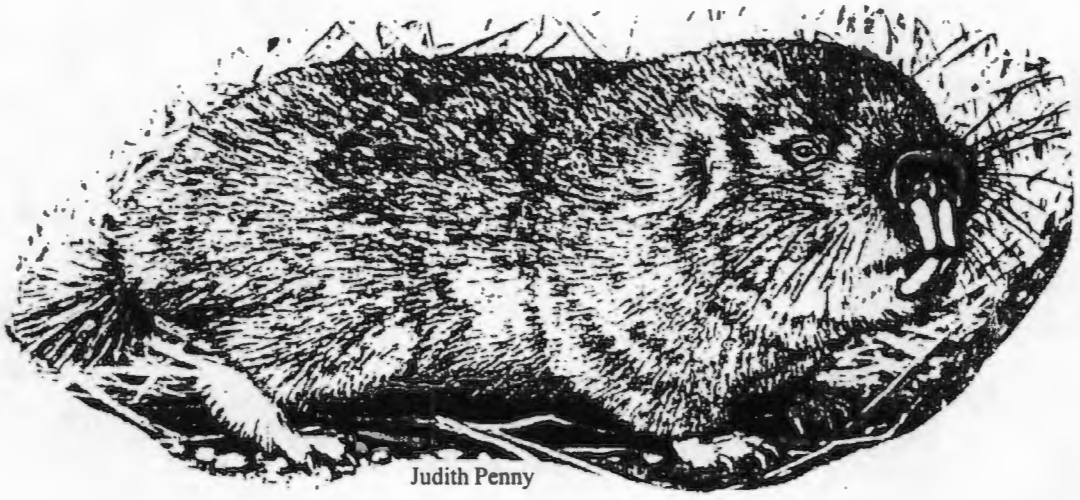
Sociality in the common mole-rat, *Cryptomys hottentotus hottentotus*: the effects of aridity



by Andrew Charles Spinks

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requirements for the Degree of Doctor
of Philosophy

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Declaration

This thesis reports the results of original research I conducted under the auspices of the Zoology Department, University of Cape Town, between 1993 and 1997. All the assistance that I received has been fully acknowledged. This work has not been submitted for a degree at any other university.

Signed by candidate

Dedication

I dedicate this thesis to my wife Sioban, without whose love, support and tolerance I would not have prevailed, and to the "little grey fur-balls", who have captivated me so with their wonderful ways.

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Abstract

Spinks, A.C. 1998. Sociality in the common mole-rat, Cryptomys hottentotus hottentotus: the effects of aridity. PhD thesis, University of Cape Town.

This study addresses the extrinsic factors which have shaped the evolution and maintenance of sociality in the African mole-rats. Specifically, the common mole-rat was used as a model to assess the Aridity Food-Distribution Hypothesis (AFDH), as an explanation for the evolution of bathyergid sociality. The AFDH correlates mole-rat sociality with habitat aridity and the pattern of food distribution. Aspects relating to ecological constraints, foraging behaviour, population demography, reproductive biology and aggressive behaviour were compared between an arid and a mesic population of *C. h. hottentotus*, to assess how inter-habitat divergence in ecological attributes has influenced social behaviour within these two populations.

In evaluating the AFDH as an explanation for the evolution of sociality within *C. h. hottentotus* two broad questions were addressed: (1) do the assumptions of the AFDH hold true *i.e.* do arid and mesic habitats exhibit ecological differences, specifically with regard to the pattern of resource dispersion and the energetic costs of foraging, which influence foraging risks and consequently the costs of dispersal? and (2) do these inter-habitat differences have implications for bathyergid social evolution *i.e.* do the common mole-rat populations inhabiting arid and mesic areas exhibit regional differentiation in social behaviour?

Substantial inter-site divergence in ecological characteristics, notably climate and resource attributes, were revealed in this study. Rainfall at the arid site was markedly lower and more sporadic, and evaporation levels significantly higher, than at the mesic site. Moreover, thermal constraints were more limiting at the arid site. These features will greatly elevate the costs of soil excavation and the risks of hyperthermia, severely restricting the occurrence of suitable burrowing opportunities at the arid locality. Consequently, foraging will be severely constrained in this area. At the mesic site, higher, more predictable rainfall, low evaporation rates and reduced thermal constraints will translate into more suitable burrowing opportunities for much, if not all, of the year.

Regional differentiation in food resource characteristics was also evident. Although geophytes were clumped at both study localities, the density of geophytes was lower and the distance between geophytes or geophyte clumps concomitantly greater at the arid relative to the mesic site. Differences in resource dispersion in turn influenced the patterns of foraging. In response to the low geophyte density and associated longer foraging distances, burrow systems were notably longer and more linear at the arid site. Furthermore, food storage and *in situ* harvesting were essential components of cooperative foraging in *C. h. hottentotus* as they minimised the risks of starvation, particularly in arid habitats. Thus resource characteristics together with the climatic restrictions on burrowing in arid areas may have a marked impact on foraging behaviour, imposing severe constraints on the mole-rats occurring there and ultimately shaping their foraging responses. Together, these factors satisfactorily account for the underlying premise of the AFDH, that arid and mesic habitats exhibit ecological differences with regard to the pattern of resource dispersion and the energetic costs of foraging, which are likely to influence foraging risks and the costs of dispersal.

In evaluating the AFDH, the second question which needed to be addressed was whether the study populations exhibited divergence in their social behaviour. The populations revealed no differences in absolute group size or in reproductive characteristics which were related to the effects of aridity *per se*. However, distinct inter-population

divergence was readily apparent in phenotypically plastic traits such as dispersal behaviour and xenophobia. Clear differences were evident between the arid and mesic sites in both the quantitative and qualitative nature of dispersal; dispersal was markedly constrained at the arid site and colonies demonstrated greater temporal stability, with more predictable temporal group membership. The ecological constraints on successful foraging at the arid site will curb opportunities for dispersal and promote cooperation in the *C. h. hottentotus* occurring there. Colony members should therefore maximise their inclusive fitness by natal philopatry, delayed dispersal and cooperative foraging.

Inter-site differences were also apparent in the response of colony members to foreign conspecifics. Common mole-rats from the arid site were markedly more xenophobic than those from the mesic site, and aggressively rejected foreigners. For arid-occurring populations, the fitness penalties for failing to exclude foreigners from the colony burrow system and associated resources, will be more severe than for mesic-occurring populations, resulting in heightened levels of xenophobia. Again colony cohesion and cooperation in arid areas are essential to individual survival and inclusive fitness. The regional differences in dispersal patterns and xenophobia revealed in this investigation may reflect adaptive variation in social behaviour between the study populations, and the results suggest that delayed dispersal and cooperation may be more crucial to individual survival in arid than in mesic areas. As such these findings provide support for the underlying contention of the AFDH that ecological constraints on foraging in arid areas have promoted a greater degree of social elaboration in mole-rats occurring there.

This study provides persuasive support for the AFDH as an explanation for the adaptive significance of social behaviour and cooperation in the common mole-rat, and together with other investigations, suggests that the AFDH provides a valid explanation for the evolution of group-living in the Bathyergidae.

Acknowledgements

As befits any investigation of social behaviour the research presented in this thesis represents a lesson in co-operation and without the support and guidance of numerous people this dissertation would not have been possible. I wish to thank my supervisors, Jenny Jarvis and Nigel Bennett, who originally conceived the project. Throughout the course of my research Jenny and Nigel have motivated, encouraged and supported me. Their tireless efforts in the field always made them a blessing on any field-trip, and their wealth of knowledge and experience has been crucial in unravelling the intricacies of mole-rat social behaviour.

I am deeply indebted to the Foundation for Research Development who provided me with the major funding during the course of this research (doctoral bursaries). In addition financial support was also provided by the Bob Blundell Memorial Trust (scholarship), the Cape Tercentenary Foundation (special grant), the Ernst and Ethel Erikson Trust (bursary) and the University of Cape Town (Research Associateship).

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Chapter 1

General introduction: sociality in the African mole-rats

THEORETICAL BACKGROUND

The social insects exhibit an unparalleled social organisation, particularly with respect to social cohesion, caste specialisation and individual altruism (Wilson 1971). Consequently they have fascinated scientists for decades and explanations for social evolution within this group previously monopolised sociobiological thinking (*e.g.* Hamilton 1964a; 1964b; Wilson 1971; Alexander 1974; West Eberhard 1975; Evans 1977; Bartz 1979; Andersson 1984; Pamilo 1984). Probably as a result the social vertebrates initially tended to attract less attention. Although less dramatic, group-living is widespread amongst vertebrates, especially in birds and mammals which display a remarkable array and degree of social elaboration (Boorman & Levitt 1980; Jarvis 1981; Emlen 1982a; 1982b; 1984; Jennions & Macdonald 1994). This realisation has subsequently generated considerable interest in vertebrate social evolution, and has stimulated significant conceptual discussion (e.g. Brown 1978; Stacey 1979; Emlen 1982a; 1982b; 1984; Wrangham & Rubenstein 1986; Arnold 1990; Jennions & Macdonald 1994). Within the broad sphere of research into cooperatively breeding vertebrate societies, the African mole-rats (Bathyergidae), a family of subterranean hystricomorph rodents endemic to sub-Saharan Africa, have emerged as a key model system to test hypotheses relating to the evolution and maintenance of sociality (Jarvis 1981; Jarvis & Bennett 1990; 1991; Bennett & Faulkes in prep.).

The bathyergids are unique amongst subterranean mammals (Jarvis & Bennett 1990; 1991). While most subterranean taxa are aggressively solitary and highly xenophobic (Nevo

1979; 1982; Jarvis & Bennett 1990; 1991), the Bathyergidae include two social[1] genera. Moreover, this family probably displays the widest range of sociality known for any mammalian family, ranging from strictly solitary species (*e.g.* the Cape dune mole-rat, *Bathyergus suillus*) through loosely social species (*e.g.* the common mole-rat, *Cryptomys hottentotus hottentotus*) to eusocial species (*e.g.* the naked mole-rat, *Heterocephalus glaber*) (Jarvis 1981; Bennett 1989; Jarvis & Bennett 1990, 1991). Eusociality (*sensu* Michener 1969; Wilson 1971), has evolved independently in no fewer than two bathyergid species (Allard & Honeycutt 1992; Jarvis & Bennett 1993; Faulkes *et al.* 1997a) and one of these species, *H. glaber*, probably represents the pinnacle of vertebrate social specialisation (Lacey & Sherman 1997).

Darwinian selection favours individuals that "strive" to maximise their own fitness. Consequently, social systems, in which the cooperating organisms forgo their own "selfish" desires in the interest of group co-ordination, demand explanation in terms of current evolutionary theory. Several theories have been proposed to elucidate the origin and evolution of sociality within the mole-rats (Jarvis 1985; Lovegrove & Wissel 1988; Burda 1990; Alexander 1991; Lovegrove 1991; Jarvis *et al.* 1994; Lacey & Sherman 1997). Of these, current consensus holds that the Aridity-Food Distribution Hypothesis (AFDH)[2] represents the most convincing and comprehensive explanation.

The Aridity-Food Distribution Hypothesis

The AFDH as an explanation for the evolution of group-living within the African mole-rats, represents the culmination of almost two decades of philosophical and empirical input by several workers (Jarvis 1978; 1985; Brett 1986; 1991; Lovegrove & Painting 1987; Bennett 1988; Lovegrove & Knight-Eloff 1988; Lovegrove & Wissel 1988; Alexander 1991; Jarvis &

[1] For the purposes of this thesis Boorman and Levitt's (1980) definition of social is adopted *i.e.* a species is social if its members engage, at any point in the life cycle, in sustained intraspecific cooperation that goes beyond parental care and the continued association of mated pairs.

[2] Although Jarvis (1978; 1985) first suggested a link between mole-rat sociality and aridity, it was Lacey and Sherman (1997) who coined the term Aridity Food-Distribution Hypothesis. This term is used throughout the thesis as it is informative and because no suitable alternative exists.

Bennett 1990; 1991; 1993; Lovegrove 1991; Honeycutt 1992; Jarvis *et al.* 1994; 1998; Faulkes *et al.* 1997a; Lacey & Sherman 1997). It has recently been extensively reviewed by Jarvis *et al.* (1994) and Lacey and Sherman (1997). In short the AFDH maintains that various trends associated with aridity hold the answers to an understanding of the evolution and causes of sociality in the bathyergids. In particular, mole-rat coloniality appears to have evolved in response to (1) the energetic costs of burrowing and (2) the distribution of crucial food resources in arid environments. An overview of the AFDH is outlined below, and a schematic summary is presented in Figures 1.1 and 1.2.

When dry, the soils in arid regions may be either very hard or very soft. Jarvis *et al.* (1994) note that both soil types are difficult to work. Whilst excavating hard soils, a mole-rat's incisors are rapidly worn down (Jarvis *et al.* 1994). Burrows formed in loose soil readily collapse, and furthermore, excavated soil cannot be efficiently compacted and ejected from the burrow system (Lovegrove & Painting 1987; Jarvis *et al.* 1994). Consequently, mole-rats tend to dig their foraging burrows after rain when the damp soil is more readily worked (Brett 1986; 1991; Lovegrove & Painting 1987; Jarvis & Bennett 1991; Jarvis et al 1994; 1997) and the high energetic costs associated with burrowing (Vleck 1979; 1981; Lovegrove 1989) are at a minimum. The low, sporadic rainfall and high evaporation rates in arid regions mean that mole-rats are restricted to short periods during which burrowing, and hence foraging, conditions are optimal (Bennett 1988; Jarvis & Bennett 1991; Jarvis *et al.* 1994). During these periods mole-rats will be forced to dig as much as possible to provide access to sufficient resources to last them through the subsequent dry periods. Even when digging conditions are optimal, however, there are limits to the absolute distance a lone mole-rat can dig each day. These are associated with the energetic costs of burrowing (Vleck 1979; 1981; see Chapter 3), the maximal rate of incisor growth (Jarvis & Bennett 1991), and the risk of overheating (McNab 1966; 1979; Lovegrove 1989; see Chapter 2). The social mole-

rats are all geophyte[3]-specialists, consuming the underground storage organs of a range of plant species (Beviss-Challinor 1980; Broll 1981; Lovegrove & Wissel 1988). Foraging mole-rats apparently search blindly for geophytes as no obvious sensory cues appear to be used in food location (Heth *et al.* 1989; Lovegrove & Knight-Eloff 1988; Brett 1991; Jarvis *et al.* 1998). Although similar mean amounts of energy are available in mesic and arid environments, the food resources (geophytes) in arid areas tend to occur at low densities, and are often widely and patchily distributed (Brett 1986; 1991; Lovegrove & Knight-Eloff 1988; Jarvis *et al.* 1994; 1998). The AFDH therefore maintains that bathyergid sociality represents an evolutionarily stable adaptation to the high energetic costs and low probability involved in locating widely dispersed geophytes by blind burrowing in arid areas, where rainfall is unpredictable and prolonged droughts are common (Lovegrove & Painting 1987). Consequently, whilst those mole-rats predisposed to sociality are able to invade and efficiently exploit arid environments, solitary species are effectively excluded from these areas (Jarvis & Bennett 1991; Jarvis *et al.* 1994; Lacey & Sherman 1997) (Figure 1.2).

Other factors that have been suggested as important in the evolution of bathyergid sociality include body size, metabolic considerations, reproductive biology (Burda 1990; Lovegrove 1991), and predation (Alexander 1991; Alexander *et al.* 1991). The first three factors are expected to influence social behaviour primarily by altering the costs of burrow excavation and foraging and consequently their effects are subsumed by the AFDH (Lacey & Sherman 1997). By contrast, predation does not directly influence constraints on foraging and is unlikely to be important in the evolution of mole-rat sociality because: (1) no obvious differences exist in the types or abundance of predators on sympatric solitary versus social species (Jarvis *et al.* 1994); and (2) the subterranean ecotope is buffered against extensive predation (Nevo 1982; Jarvis & Bennett 1990).

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[3] Geophytes are a group of cryptophytes whose buds or shoot-apices are borne on subterranean shoots (Raunkiaer 1934). These subterranean shoots may be corms, tubers, rhizomes or bulbs and represent the plant's underground storage organ.

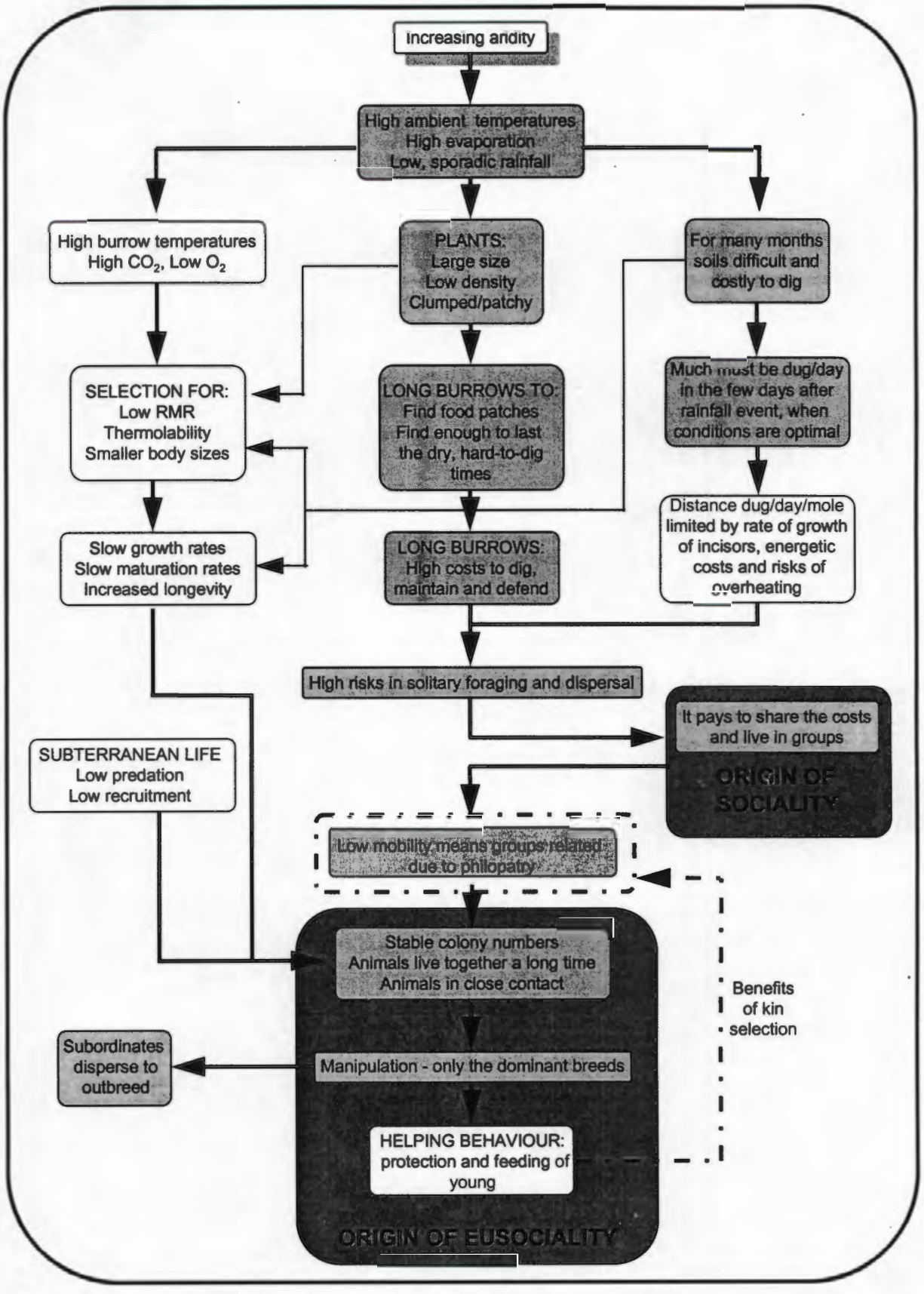

Figure 1.1: Schematic summary of the Aridity Food-Distribution hypothesis, showing the inter-relationship of factors which have contributed to the evolution of sociality in the Bathyergidae. The shaded boxes indicate those areas addressed in this thesis (modified from J.U.M. Jarvis unpublished diagram).

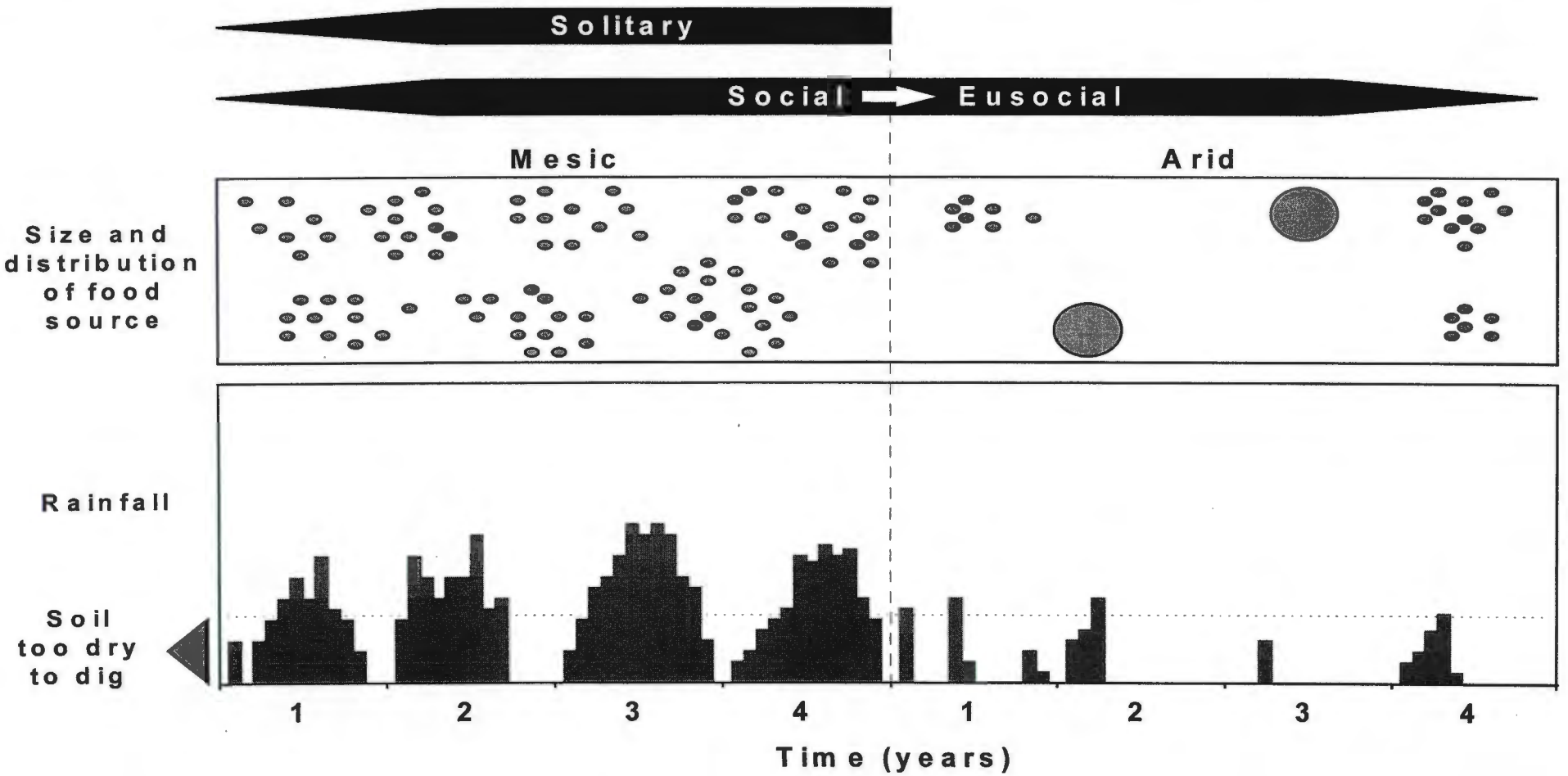

Figure 1.2: A graphical illustration of ecological factors thought to influence the evolution of sociality in the Bathyergidae. In arid regions, the few opportunities to extend foraging tunnels due to insufficient rainfall (see dotted line), together with the widely dispersed food, preclude the survival of solitary species (modified with permission from Jarvis *et al.* 1994).

Once sociality has evolved, the subsequent elaboration of social organisation would lead to: (1) an overlap of generations; (2) a reproductive division of labour; and (3) cooperative care of the young (Jarvis & Bennett 1991). Accordingly, bathyergid eusociality (*sensu* Michener 1969; Wilson 1971), as exemplified by *H. glaber* and *C. damarensis*, would develop (Jarvis 1981; Brett 1986; Jarvis & Bennett 1991; 1993).

The Sociality-Risk Hypothesis

Lovegrove and Wissel (1988) formulated aspects of the AFDH into a mathematical model, which they termed the Sociality-Risk Hypothesis (SRH). Briefly, this model proposed that increased group size greatly reduces the risks faced by solitary foragers when burrowing for widely dispersed geophytes. Risk in this situation was defined as the probability distribution of the distance that would have to be burrowed before a geophyte was encountered (Lovegrove & Knight-Eloff 1988; Lovegrove & Wissel 1988). Subsequently, Lovegrove (1991) expanded the SRH to incorporate energetic considerations. The model revealed that cooperative foraging reduces the risks of unproductive foraging, and represents a more stable long-term behaviour in arid habitats where the energetic costs of foraging are high and resources are widely dispersed (Lovegrove & Knight-Eloff 1988). The AFDH and SRH are intimately linked, the basic assumptions of the SRH being derived from the AFDH, and its predictions being fully compatible and complementary to those of the AFDH. Consequently, in this thesis the SRH will be subsumed within the broader theoretical framework of the AFDH, and as such will not be considered on its own.

SCOPE AND OBJECTIVES OF THIS THESIS

Despite the conceptual allure and general acceptance of the AFDH as an explanation for bathyergid social evolution, corroborative empirical data are largely lacking. Several single population studies have been undertaken (Brett 1986; Lovegrove & Painting 1987; Lovegrove

& Knight-Eloff 1988; Braude 1991; Jarvis & Bennett 1993; Jarvis *et al.* 1998) but, while these have contributed to the theoretical refinement of the AFDH, they have not provided rigorous tests of the theory. Bennett's (1988) pioneering comparative interspecific investigation of social elaboration within the Cape mole-rat, *Georychus capensis*, the common mole-rat, *C. h. hottentotus*, and the Damaraland mole-rat, *C. damarensis*, provided relevant information and initiated the first really rigorous evaluation of the AFDH. However, the predictive value of his results was limited because of an inability to separate species idiosyncrasies from ecological determinants. More recently Faulkes *et al.* (1997a), using comparative analysis by independent contrasts, were able to show that ecological variables were significantly correlated with group size (as an index of social development) in the 15 bathyergid species they examined. Whilst this is an elegant elaboration of the AFDH, it cannot be viewed as a critical test of the theory.

It should be patently evident from the preceding paragraph that, in order to critically evaluate the validity of the AFDH, there is an urgent need for an intraspecific study in which the differential social status of one species along a gradient of environmental severity is investigated. Krebs and Davies (1993) note that such comparative studies hold the key to relating specific differences in behaviour to differences in ecology. To address this need, a comparative investigation of the social development evident in two populations of the common mole-rat, *C. h. hottentotus* (Lesson 1826), one inhabiting an arid environment, and the other a mesic environment, was initiated. Specifically, aspects relating to ecological constraints, foraging behaviour, population demography, reproductive biology and aggressive behaviour were compared to assess how inter-habitat divergence in ecological attributes has influenced social elaboration within the two populations. In addition to facilitating the first comprehensive evaluation of the AFDH, this thesis also contributes substantially to our impoverished knowledge of the basic biology of the common mole-rat.

THE STUDY ANIMAL

Explanations for the causes and evolution of sociality in the bathyergids, initially focused attention on the naked mole-rat (*Heterocephalus glaber*) (Jarvis 1978; Jarvis 1985; Brett 1986). However, Jarvis (1985) noted that studies on the other mole-rat genera (*Cryptomys, Bathyergus, Georychus* and *Heliophobius*) were crucial to explain why *H. glaber* was so highly social. Consequently, recent investigations have emphasised the other social bathyergid genus *Cryptomys*, particularly the Damaraland and common mole-rats. Several workers have suggested that *C. damarensis* is a key species in establishing the factors promoting sociality in the bathyergids (Lovegrove 1986; 1988; Lovegrove & Painting 1987; Bennett & Jarvis 1988a; Lovegrove & Knight-Eloff 1988; Allard & Honeycutt 1992). However, Jarvis & Bennett's (1993) elevation of *C. damarensis* to eusocial status has necessarily focused attention on the other cryptomids. The common mole-rat is an ideal model for assessing the ecological determinants of bathyergid sociality, for the following reasons: (1) other than *C. damarensis*, it is the best studied social cryptomid (Davies & Jarvis 1986; Lovegrove & Jarvis 1986; Bennett 1988; 1989; 1992; Reichman & Jarvis 1989; Rosenthal *et al.* 1992; Spinks *et al.* 1997); (2) it occurs over the widest range of habitats for the bathyergids, from mesic to arid (Skinner & Smithers 1990); and (3) its colony size is significantly smaller than either of the eusocial species, and its colony structure less rigid, suggesting an intermediate position between them and the solitary species.

The common mole-rat

The common mole-rat, *Cryptomys hottentotus hottentotus* (Plate 1.1), is a cooperative breeder living in colonies of two to fourteen individuals (Bennett 1989). It is widely distributed throughout southern Africa, and occurs in both mesic and arid areas (Figure 1.3; De Graaff 1981). Like all mole-rats, *C. h. hottentotus* permanently inhabits an elaborate and dynamic network of burrows, which it uses to access food resources (Jarvis & Bennett 1990;

Plate 1.1: The common mole-rat, *Cryptomys hottentotus hottentotus*; (a) an aggressive individual, and (b) a colony close-up (Photographs© by Neville Eden and Tim Jackson respectively).

1991). It is herbivorous and feeds almost exclusively upon geophytes which it harvests as it extends its burrow system (De Graaff 1964; Beviss-Challinor 1980; Lovegrove & Jarvis 1986; Bennett 1988).

Common mole-rats are group-living and behaviourally monogamous. Monogamy is rare amongst mammals (Kleiman 1977) and the combination of monogamy and group living is even less frequent (McNutt 1996). *Cryptomys h. hottentotus* colonies consist of familial groups, comprising the parents and at least two litters (Bennett 1989; 1992). Like the other cryptomids (Jarvis & Bennett 1993; Burda 1995; Rickard & Bennett 1997), the common mole-rat appears to be an obligate outbreeder, since subordinate colony members avoid incest and only reproduce when ecological conditions favour dispersal and outbreeding (Jarvis *et al.* 1994; this thesis). Colonies exhibit a reproductive division of labour superficially similar to that found in the naked (*Heterocephalus glaber*) and Damaraland (*C. damarensis*) mole-rats. Reproduction is typically restricted to the largest male and female in a colony, while the remaining colony members are reproductively quiescent (Bennett, 1989; 1992; Rosenthal *et al.*, 1992; Spinks *et al.*, 1997).

Figure 1.3: South Africa, showing the distribution of the common mole-rat (De Graaff 1981; J.U.M Jarvis, N.C. Bennett, C.G. Faulkes & G.H. Aguilar unpublished data)

The common mole-rat is apparently unique among the social bathyergids in exhibiting seasonal reproduction (Bennett *et al.* 1991; Jarvis & Bennett 1991; Spinks *et al.* 1997). The birth of offspring in this species is typically restricted to the southern hemisphere summer period (late November to January in the study populations), during which time usually one and a maximum of two litters may be reared (Skinner & Smithers 1990; Jarvis &

Bennett 1991; this thesis). As a consequence of this reproductive periodicity and the small litter sizes of only two to four pups (Bennett 1989; this thesis), *C. h. hottentotus* exhibits the slowest rate of colony recruitment amongst the social bathyergids studied to date, and this may account for their relatively small group sizes.

The genus *Cryptomys* has been problematic for systematists, primarily because extreme variation in external and cranial morphology makes it difficult to determine whether named forms are species, subspecies or local variants (Honeycutt *et al.* 1991a). Hence, the classification of this group has been characterised by both extreme lumping (Ellerman *et al.* 1953; De Graaff 1964, 1971) and extreme splitting (Ellerman 1940, Roberts 1951). For example, De Graaff (1971) recognised three species of *Cryptomys*, including eleven subspecies, while Ellerman (1940) recognised forty-nine species, which included only six subspecies. As a consequence nomenclatural usage for this genus has been fraught with inconsistency, and most notable for this thesis, at least six different species have been referred to as the common mole-rat, *C hottentotus*. Modern molecular techniques have gone a long way to resolve this confusion (Allard & Honeycutt 1992; Faulkes *et al.* 1997a), and the most up-to-date bathyergid phylogeny is presented in Figure 1.4. The common mole-rat referred to in this study is *C. h. hottentotus* (Lesson 1826). This species is distinct from: (1) De Graaff's (1962) *C. hottentotus,* which is in fact the Damaraland mole-rat, *C. damarensis*; (2) Genelly's (1965) "common mole-rat", which is the Mashona mole-rat, *C. darlingi*; (3) Hickman's (1978; 1979b; 1980; 1982) *C. hottentotus*, which is in fact the Natal common mole-rat, *C. h. natalensis*; (4) Haim and Fairall's (1986) "common mole-rat", and Poduschka's (1978a; 1978b) *Cryptomys hottentotus*, which is in fact a new species from Pretoria, referred to as *C. h. "pretoria"* in Figure 1.4; and (5) Burda's (1989; 1990; 1995) and Marhold and Nagel's (1995) "common mole-rat" which is the Lusaka mole-rat, *C. amatus*.

Morphological, karyotypic and genetic data indicate that the two populations selected for this investigation (*i.e.* Sir Lowry's Pass and Steinkopf, see Chapter 2) show little systematic divergence. Morphological attributes do not differ significantly between the populations and

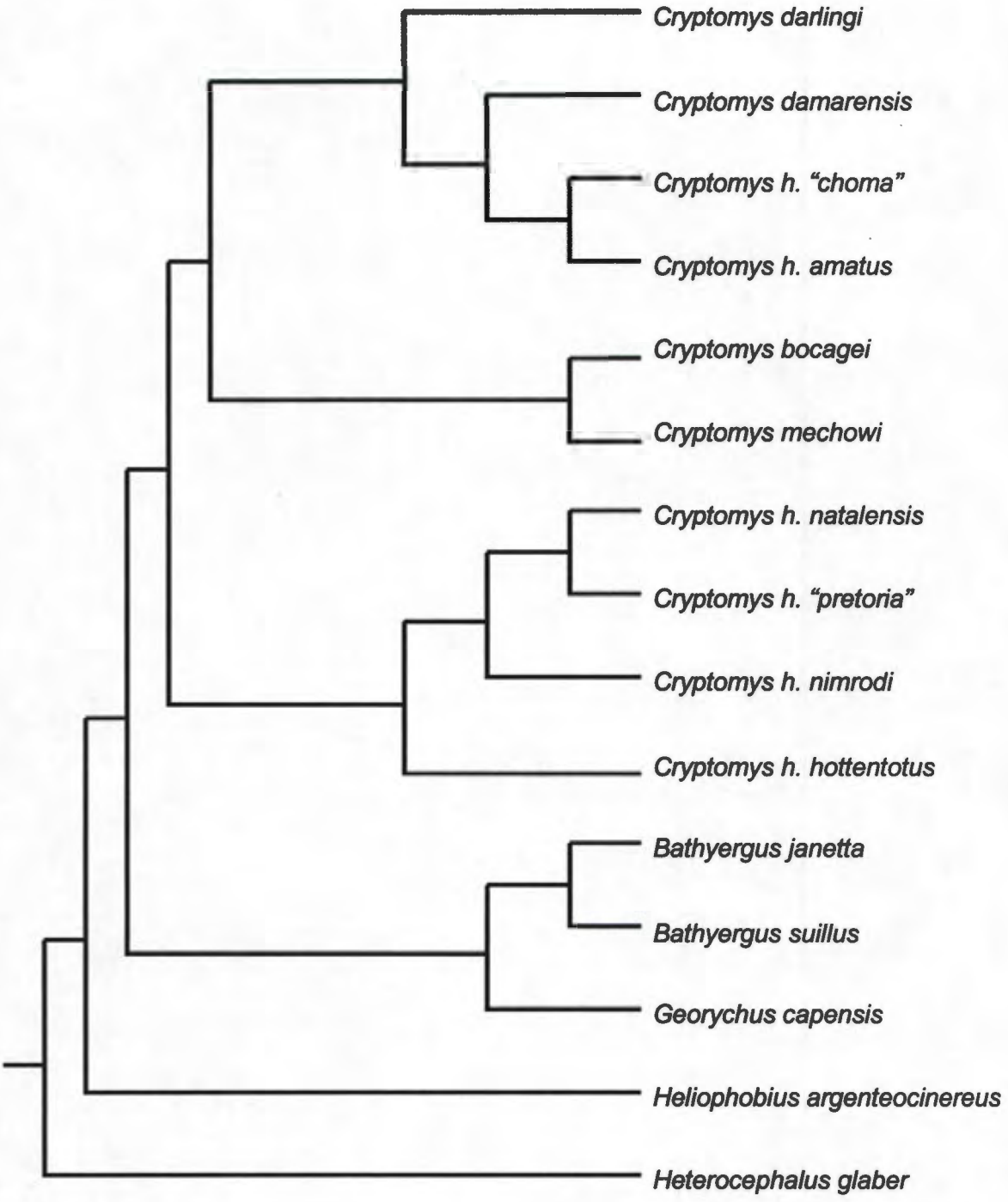

Figure 1.4: Phylogenetic relationships of 15 mole-rat haplotypes based on a strict consensus tree following parsimony analysis of 12S rRNA sequences (modified from Faulkes *et al.* 1997a).

both exhibit a diploid chromosome number of 2n = 54 (G.H. Aguilar unpublished data). Moreover, sequence variation between the two populations for 1140 sequenced basepairs of the cytochrome b gene was 2.4% (C.G. Faulkes unpublished data). This compares with an intraspecific sequence variation of: 5.4% in *C. mechowi* (C.G. Faulkes unpublished data); 5.8% in *H. glaber* (Faulkes *et al.* 1997b) and 1.5% in *C. damarensis* (C.G. Faulkes unpublished data). Consequently, it can be safely assumed that the two study populations represent the same species.

ORGANISATION OF THIS THESIS

Excluding the general introduction (Chapter 1) and synopsis (Chapter 10), this thesis consists of eight chapters. The thesis falls logically into two subsections, each with four chapters. The first subsection, Chapters 2 to 5, evaluates the AFDH prediction that sociality evolves due to the foraging and dispersal restrictions imposed by energetic constraints and resource distribution patterns in arid environments. Chapter 2 contrasts the basic floristic, edaphic and climatic features for the two study sites. Chapter 3 provides a qualitative and quantitative description of basic foraging behaviour in the common mole-rat, and relates this to optimal foraging theory. Chapter 4 compares and contrasts the differential foraging behaviour of the study populations, highlighting how those ecological constraints relevant to the AFDH impinge on foraging and dispersal decisions in the two populations. Chapter 5 uses information from Chapters 2, 3 and 4, and other sources, to generate a computer model to simulate foraging and the concomitant effects of ecological constraints.

The second subsection (Chapters 6 to 9) contrasts the relative degrees of social elaboration/degeneration evident in the two populations, given the ecological constraints discussed in Chapters 2 to 5. Based on the assumption that differences in reproductive biology reflect differences in social cohesion and elaboration, Chapter 6 investigates the reproductive characteristics of the study populations. Chapters 7 and 8 investigate the

demographic features of the study populations to assess inter-populational differences in colony composition and colony cohesion. Chapter 9 addresses the conflict that outbred mole-rats, like *C. h. hottentotus*, face between maintaining colony integrity to enhance foraging success and hence survival and dispersal to maximise individual lifetime reproductive success. This is based on the expectation that the relative response of the two populations will reflect differences in social elaboration.

Although each chapter has been written in a manner which effectively allows it to be read in isolation, frequent reference is made to relevant sections from other chapters. This, together with the fact that many chapters build on previous chapters and each chapter addresses only a circumscribed portion of the AFDH, means that this thesis needs to be read in its entirety for a full understanding of the issues covered. The approach has forced some repetition of aspects relating to specific predictions of the AFDH and the general biology of the common mole-rat, but only where it was deemed necessary to enable the reader to obtain a better understanding of the hypotheses being tested. In addition, although discussion in this thesis is largely confined to those facets pertinent only to the AFDH, other aspects are discussed where they are either considered to contribute to the knowledge of common mole-rat biology, or to help elucidate the intrinsic (non-ecological) forces moulding the evolutionary responses of this species.

SECTION I

Chapter 2

The study sites: general vegetation, geology and climatology

ABSTRACT

The location and key ecological features of the two study sites used in the thesis are described in this chapter. Steinkopf, the arid locality, is situated in the Northern Cape and is characterised by Bushmanland Nama Karoo vegetation, and loose sandy soils. Rainfall is low and sporadic, and evaporation levels are high. The mesic locality, Sir Lowry's Pass, exhibits highly disturbed vegetation (dominated by invasive plant species) and compacted clay soils. Rainfall is high and predictable, and evaporation levels are low. Air and soil temperatures are far more moderate at the mesic site. Both areas show identical patterns of winter rainfall, with a concurrent rise in precipitation, drop in evaporation and drop in minimum and maximum temperatures over the winter period from May to August. The edaphic and climatic properties of Steinkopf will have a serious impact on foraging mole-rats, greatly reducing the opportunities for foraging and hence ultimately for dispersal. By contrast the corresponding mesic site characteristics will not significantly curtail foraging. These marked inter-habitat differences in edaphic and climatic properties provide a unique opportunity to evaluate the Aridity-Food Hypothesis as an explanation for social evolution within the African mole-rats.

INTRODUCTION

The Aridity-Food Distribution Hypothesis (AFDH) asserts that the ecological constraints concomitant with aridity have induced the social elaboration evident within the African mole-rats (Jarvis 1978; Lovegrove & Painting 1987; Bennett 1988; Lovegrove & Wissel 1988; Lovegrove 1991; Jarvis & Bennett 1991; Jarvis *et al.* 1994; Lacey & Sherman 1997; Chapter 1). Thus ecological differences between arid and mesic habitats should be reflected in the differential social status of bathyergids occurring there. As outlined in Chapter 1, in this thesis the AFDH is critically evaluated by comparing the social development evident in two populations of the common mole-rat, one inhabiting an arid environment, and the other a

mesic environment. However, a prior knowledge of the predominant ecological characteristics (especially climate) of the study areas is fundamental to any understanding of inter-habitat differences in the biology of these study populations.

In this chapter the location and key ecological features of the two study sites are described. Inter-habitat divergence in ecological attributes is emphasised to elucidate the differences in environmental constraints acting upon the respective mole-rat populations. Due to the aforementioned importance of climatic variables (Chapter 1), this chapter focuses on the comparative climatology of the study sites. However, the basic vegetation and pedology are also described in some detail. The resource characteristics are considered in Chapters 3 and 4.

MATERIALS AND METHODS

All the data used were obtained from existing databases or the appropriate literature. Logistic constraints precluded the physical measurement of these variables at the study localities.

Climatological variables were obtained from the Computing Centre for Water Research at the University of Natal, Pietermaritzburg. Variables included rainfall, evaporation, air temperature and soil temperature. It was not always possible to obtain climatic data from the immediate vicinity of the study sites, as the availability of regional data was dependant upon the location of weather stations collecting the appropriate data. Consequently, data from stations in close proximity to the study sites, were used. Table 2.1 summarises the positions of these stations, the type of data retrieved from each (*i.e.* rainfall, evaporation, air temperature or soil temperature), and the number of years for which data were available. Most of the consulted stations were very close to the study localities.

Table 2.1: Summary of data sources for precipitation, evaporation, air temperature and soil temperature used in this chapter. All data were obtained from the Computing Centre for Water Research, University of Natal, Pietermaritzburg.

Habitat Type	Data Source			Data Type†	Data Years
	Name	Latitude	Longitude		
Mesic	Bizweni	34° 05'	18° 51'	Ta	105/21
Mesic	Elsenberg	33° 51'	18° 50'	Ts	8
Mesic	Nooitgedacht	34° 02'	18° 51'	Ev	10
Mesic	Somerset West	34° 05'	18° 51'	Rf	113
Arid	Springbok	29° 40'	17° 53'	Ev/Ta	1/6
Arid	Steinkopf	29° 15'	17° 44'	Rf	109
Arid	Upington	28° 25'	21° 16'	Ts	13

†For data type: Rf = rainfall; Ev = evaporation; Ta = air temperature; Ts = soil temperature.

Statistical analysis

Only the climatic data were analysed statistically, as no numerical data are presented for the vegetation and soils of the two localities. Differences between the study sites in the average annual rainfall, the average monthly rainfall and the average monthly minimum and maximum temperatures were tested using Students t-tests (Zar 1984). Significant differences in the levels of evaporation could not be examined, due to the small sample size for the arid area (n = 1). Variability in climatic features was expressed using the co-efficient of variation (V) *i.e.* the standard deviation expressed as a percentage of the mean (Zar 1984). Differences in the co-efficient of variation of mean annual rainfall for the study sites was tested using the variance ratio test on log transformed data (Zar 1984). For the co-efficients of variation for the monthly rainfall data, differences were not tested for each month, but over the entire year using the Students t-test (Zar 1984). The remaining data presented in this chapter were not analysed statistically, as the graphical patterns were considered unambiguous.

RESULTS

The study sites

Two localities, both within South Africa, were selected as study sites: Steinkopf (16°50'E, 29°20'S) in the Northern Cape and Sir Lowry's Pass (18°55'E, 34°07'S) in the Western Cape (Figure 2.1; Plates 2.1 & 2.2). The study sites were selected mainly due to the marked climatic differences between the two areas (discussed below) and the likely effects of these on the mole-rat populations occurring there. The two study sites lie at the distributional extremes for the common mole-rat (see Chapter 1). Dispersal southwards is prevented by the Indian Ocean, and northwards by the Orange River Valley and its accompanying low rainfall.

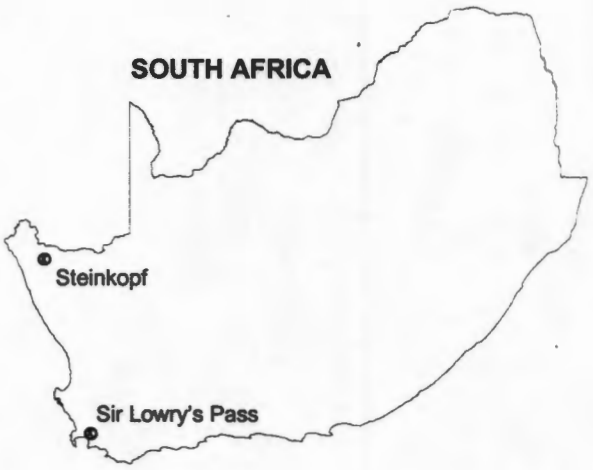

Figure 2.1: South Africa, showing the relative locations of the two study sites.

Vegetation

The vegetation in the Steinkopf area is described as Bushmanland Nama Karoo by Low and Rebelo (1996), and as Arid Karoo/False Succulent Karoo by Acocks (1988). It is dominated by annuals and non-succulent shrubs. In addition, a broad diversity of geophytes occur there and together with the annuals comprise some 50% of the floristic diversity (Low & Rebelo 1996).

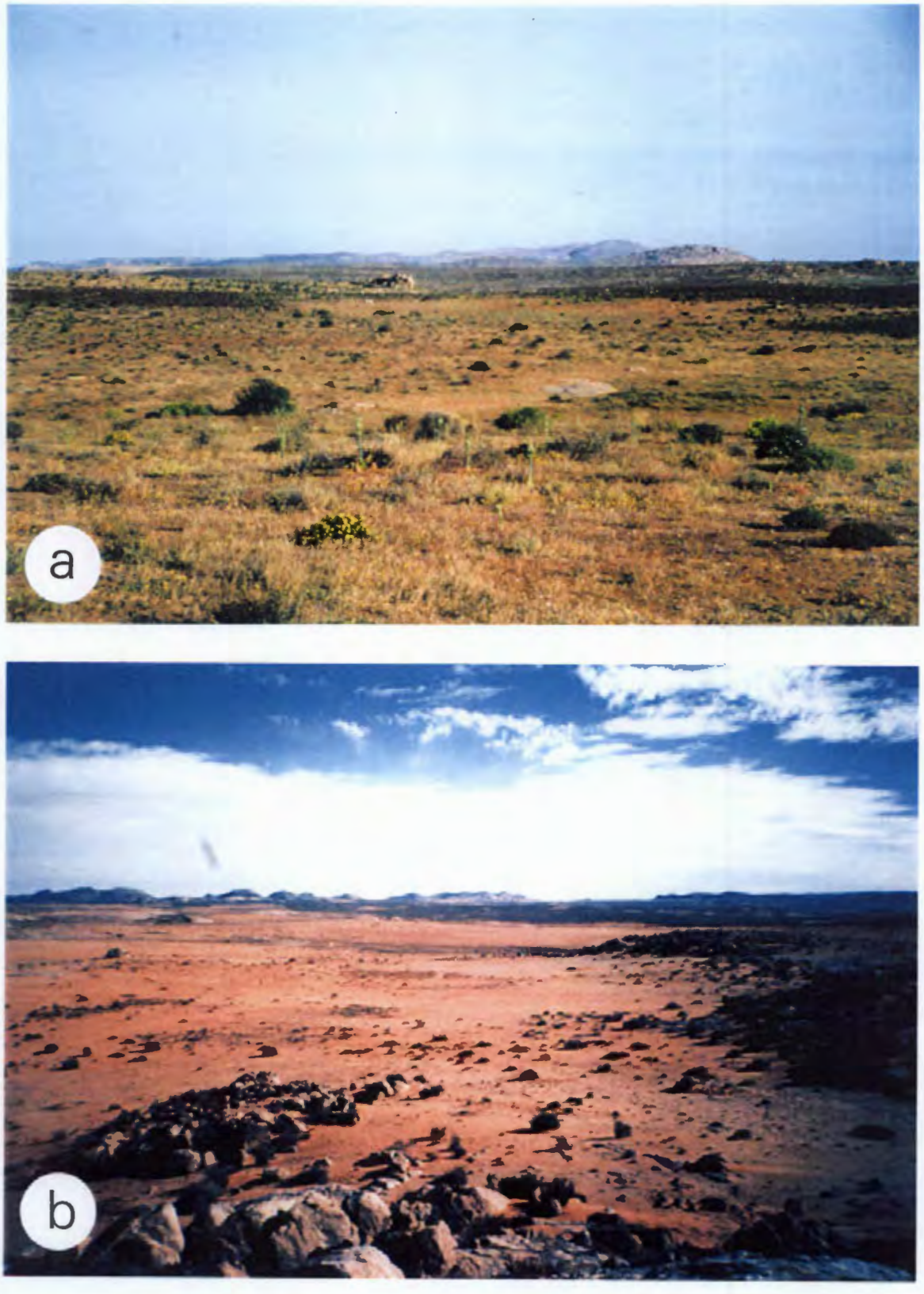

Plate 2.1: Photographs to show the vegetation and relief of the arid study site at Steinkopf in the northern Cape; (a) taken in September 1993 after a spell of good rain had stimulated the growth of annuals and geophytes, and (b) taken in March 1995 at the end of summer (Photographs© by Andrew Spinks).

Plate 2.2: Photographs to show the vegetation and relief of the mesic study site at Sir Lowry's Pass in the western Cape; (a) taken in June 1994 at the start of winter, and (b) taken in February 1994 towards the end of summer (Photographs© by Andrew Spinks).

The vegetation within which Sir Lowry's Pass occurs was historically West Coast Renosterveld (Low & Rebelo 1996) or Coastal Renosterveld (Acocks 1988). However, Low & Rebelo (1996) note that 97% of this habitat type has been transformed. Consequently, very few indigenous elements are found at the Sir Lowry's Pass study site and the area is dominated by alien species (*Acacia*, *Eucalyptus*, pines and several grass species, pers. obs.). The disturbed nature of the vegetation is exemplified by the fact that the most common food plants utilised by the mole-rats, *Oxalis* spp (Chapter 4), are typical pioneer species.

Geology and soils

In the Bushmanland Nama Karoo, Quaternary sands and Karoo Sequence shales give rise to weak and structureless clay and sandy soils (Werger 1978; Low & Rebelo 1996). Von M. Harmse (1978) characterised the soils of this arid area as weakly developed shallow calcareous sands and loams, mainly overlying calcrete. The soils at Steinkopf are all very coarse sandy soils, and in many areas they are very poorly developed, forming only a thin layer over the underlying rock (Low & Rebelo 1996; pers. obs.). Areas where the bedrock is exposed or covered by a very shallow soil layer may represent potent barriers to dispersal in subterranean organisms.

The West Coast Renosterveld soils are derived largely from Malmesbury Group shales, Cape Granite Suite and Klipheuwel Formation shales, which give rise to heavy clays and loamy soils (Low & Rebelo 1996). Von M. Harmse (1978) described the soils of this area as mainly red fersiallitic clays. At Sir Lowry's Pass, the soils are generally deeply developed, heavily consolidated clays.

Climate

The Bushmanland Nama Karoo biome occurs in one of the most arid parts of South Africa, with a rainfall ranging between 50 and 200 mm *per annum* (Acocks 1988; Low & Rebelo 1996). The low, unpredictable rainfall is highly patchy and is the major determinant of the ecosystem dynamics of this biome (Acocks 1988; Low & Rebelo 1996; Cowling & Hilton-Taylor in press). By contrast, the West Coast Renosterveld is a mesic system with heavy, predictable rains of between 300 and 600 mm *per annum* (Low & Rebelo 1996). The climate is typically Mediterranean with most rain falling during winter (Low & Rebelo 1996).

This prelude provides a general overview of the climatic patterns affecting the biomes within which the study sites occur. However, to better understand the differential climatic environmental constraints operating on the two mole-rat populations, it is essential to consider the specific climatic data for the two study localities in some detail.

Rainfall and evaporation

The mean annual rainfall for the mesic locality is significantly higher than for the arid locality (Mesic = 652 ± 17 mm; Arid = 145 ± 9 mm; Students t-test: $t_{(213)} = 26.01$, $p < 0.00001$). In addition the arid region exhibits a substantially higher co-efficient of variation in mean annual rainfall (Arid = 63%; Mesic = 27%; Variance ratio test: $F_{(108:105)} = 3.65$, $p < 0.0001$). A similar pattern is evident from the mean monthly rainfall results (Figures 2.2 & 2.3). For each month, the mean rainfall is substantially greater at the mesic than the arid site (Figure 2.2; Students t-test: $p < 0.00001$ for all months except February where $p < 0.0001$). Furthermore the co-efficients of variation for monthly rainfall are significantly lower in the mesic area (Figure 2.3; Students t-test: $t_{(22)} = -4.78$, $p < 0.00001$). These findings suggest, that apart from the obvious difference in the magnitude of rainfall at the two sites, the intrinsic variability in rainfall at Steinkopf is significantly greater than at Sir Lowry's Pass.

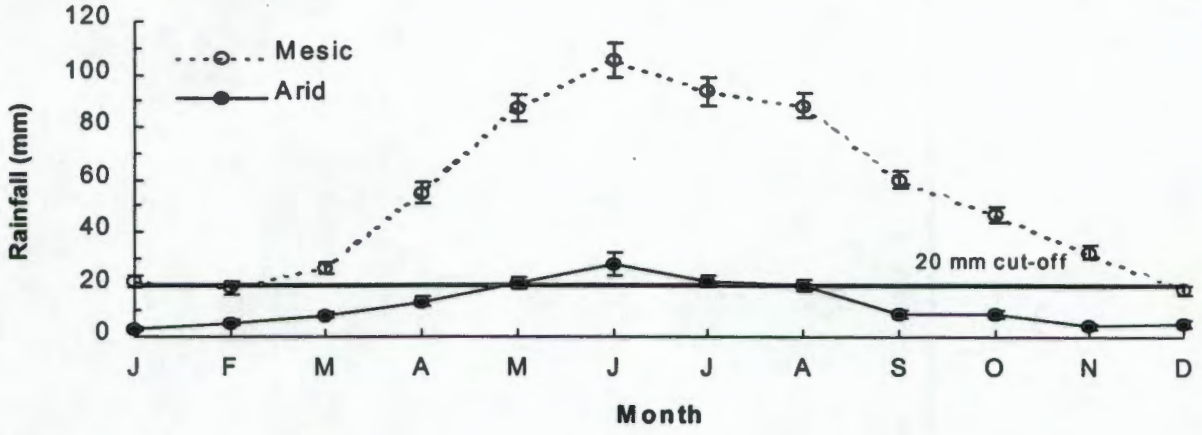

Figure 2.2: The mean monthly rainfall for the mesic and arid study areas. Error bars indicate SE's for each month at each locality. The 20 mm cut-off line (broad, black, horizontal line) represents the minimum monthly rainfall required to stimulate a substantial increase in burrowing activity.

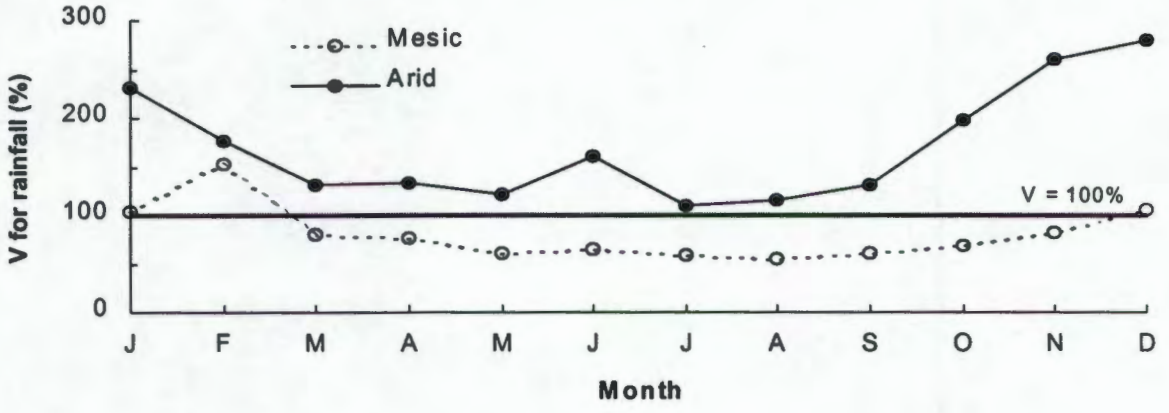

Figure 2.3: The monthly co-efficients of variation (V) in rainfall for the mesic and arid study areas.

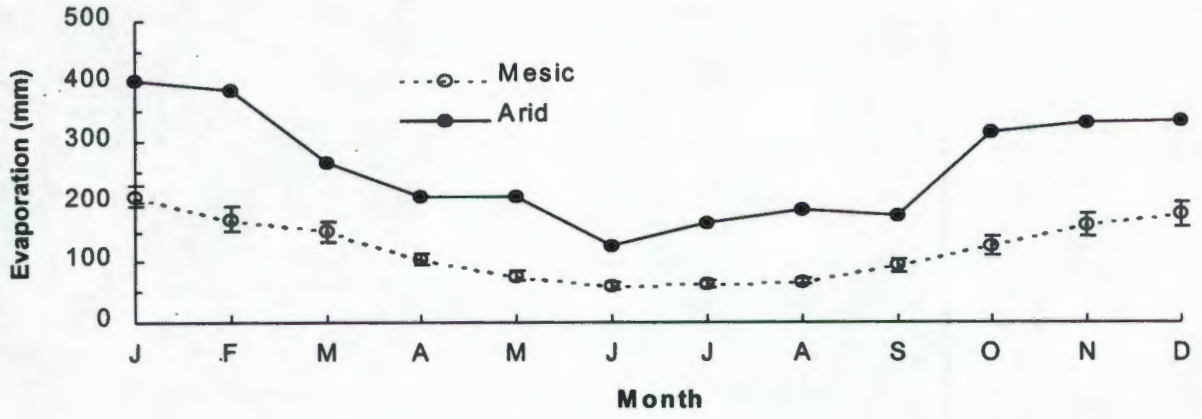

Figure 2.4: The mean monthly evaporation for the mesic and arid study areas. Error bars indicate SE's for each month at the mesic locality. Sample sizes were too small to calculate SE's for the arid site.

Average annual evaporation is markedly higher in the arid area (Arid = 3111 mm; Mesic = 1493 ± 142 mm). This pattern holds true for each month (Figure 2.4), with monthly evaporation levels being much lower at the mesic locality than at the arid locality.

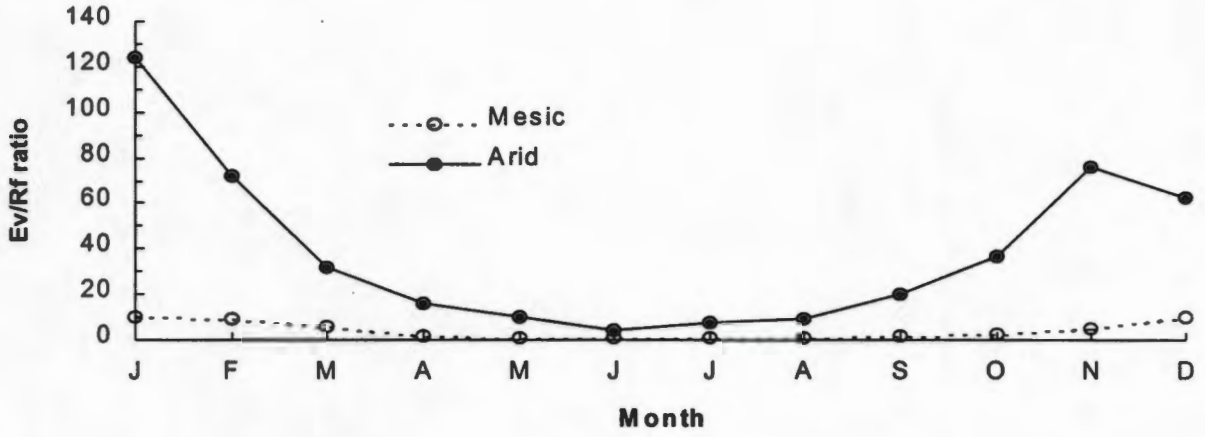

Figure 2.5: The ratio of evaporation to rainfall (Ev/Rf ratio) for each month in the mesic and arid study areas. Ratio calculated by dividing evaporation for each month by the rainfall for that month.

Figure 2.5 shows the ratio of evaporation to rainfall (Ev/Rf ratio) for each month at each study site. This ratio represents an attempt to illustrate how the differences in evaporation levels and incoming rainfall affect water retention by the different habitats. The ratio approaches a minimum (close to one) where levels of evaporation and rainfall are equitable. At the outset It must be appreciated that, unlike rainfall, evaporation is not measured directly but is determined using experimental pans, and consequently the resultant values represent maximum potential evaporation. Actual evaporation levels are unlikely to be this high. Nevertheless, substantial insight may be gained by speculation on the significance of inter-habitat differences in evaporation and the Ev/Rf ratio. In the mesic area the Ev/Rf ratio is close to or below one for most of the year, reaching a maximum of around 10 only in summer (December to February; Figure 2.5). Consequently at this site, the evaporative demand is likely to be met by precipitational inputs and soil moisture levels should be relatively high for most of the year. In contrast, the Ev/Rf ratio for the arid region reaches a minimum of around five during May, but rises to a maximum of over 120 during

January (Figure 2.5). For most of the year the ratio is well over 10 (Figure 2.5). The incoming rainfall will be far from sufficient to meet the evaporative demands, and the consequence will be extreme desiccation of the landscape and low soil moisture levels.

Despite differences in their absolute amplitude, distinct climatic seasonality is evident from the rainfall and evaporation data for the two study areas. Both areas exhibit analogous patterns of winter rainfall, with most rain falling between May and August[1]. In addition evaporation levels in both areas peak between October and February, and are lowest between May and August.

Air and soil temperatures

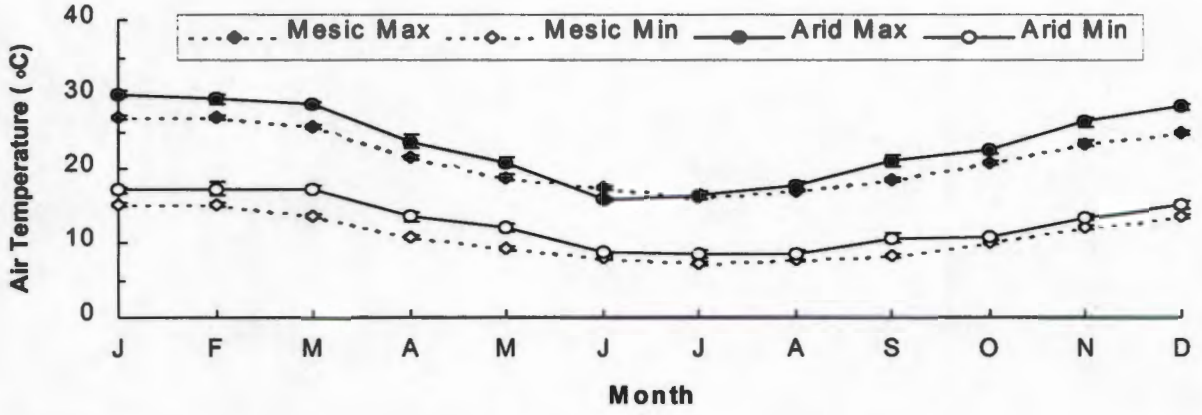

Figure 2.6: The mean monthly maximum and minimum air temperatures for the mesic and arid study areas. Error bars indicate SE's for minimum and maximum temperatures each month at each locality. Mesic = mesic area; Arid = arid area; Max = maximum temperature; Min = minimum temperature.

Average monthly maximum and minimum temperatures for the study areas are shown in Figure 2.6. Maximum temperatures are significantly higher in the arid area than in the mesic area for each month (Students t-test: January & March $p < 0.00001$; December $p < 0.0001$; February, September & November $p < 0.001$; April, May, June & October $p <$

[1] This pattern of seasonality is a little unusual for the Bushmanland Nama Karoo, which typically receives most precipitation during Autumn. However, Steinkopf does border on the Succulent Karoo Biome, a winter rainfall area, and there may be some climatic overlap. Steinkopf's other precipitational features *i.e.* low and sporadic rains, are very typical of the Bushmanland Nama Karoo.

0.01), except for the winter months of July and August (Students t-test: July $p = 0.77$; August $p = 012$). The same pattern is true for minimum temperatures, the arid area exhibiting significantly higher temperatures for each month (Students t-test: May $p < 0.00001$; March, April & September $p < 0.0001$; January $p < 0.001$; February, July, November & December $p < 0.01$) except the winter months of June and August and the autumn month of October (Students t-test: June $p = 0.07$; August $p = 0.11$; October $p = 0.24$).

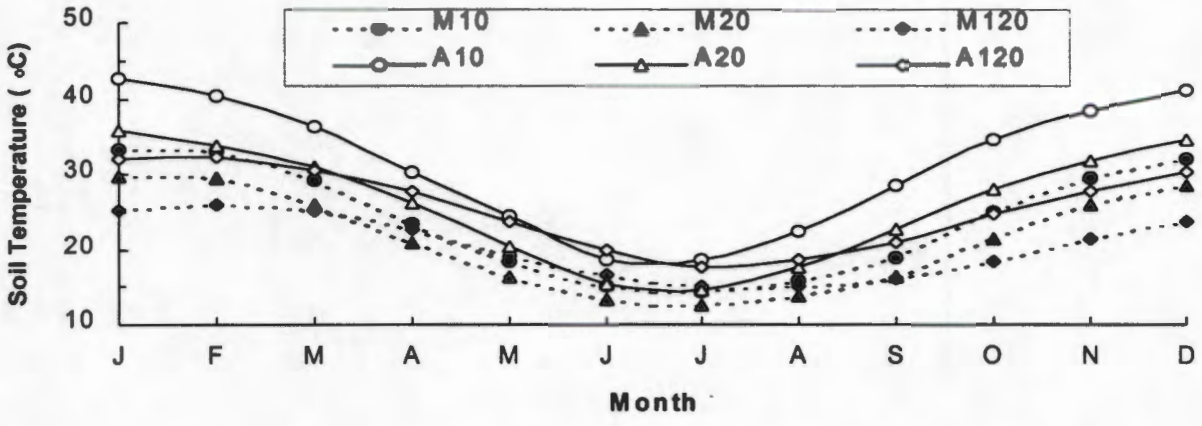

Figure 2.7: The mean monthly soil temperatures at three depths for the mesic and arid study areas. Error bars are not show, but SE ranges are comparable to those for air temperature. M = mesic area; A = arid area; 10 = at depth of 10 cm; 20 = at depth of 20 cm; 120 = at depth of 120 cm.

The differences in air temperature have a marked impact on the soil temperatures for the two localities (Figure 2.7). For all three depths presented, soil temperatures are substantially higher in the arid area, with temperatures in excess of 40 °C (10 cm below ground) during the summer months. By contrast soil temperatures in the mesic area did not rise above 35 °C. Another important pattern is also evident from the soil temperature data. In both localities soil temperature decreased with increased depth from 10 cm to 120 cm, and is far less variable (Figure 2.8).

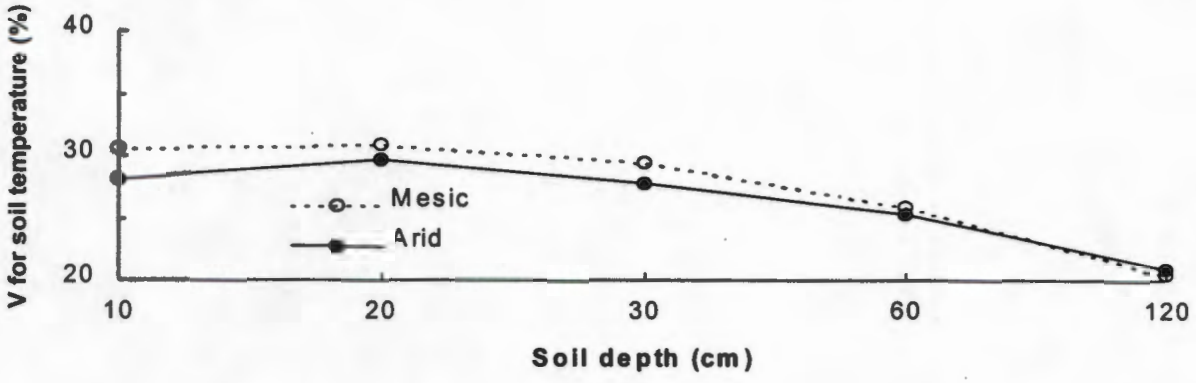

Figure 2.8: The annual co-efficients of variation (V) in soil temperature at five depths (*i.e.* 10, 20, 30, 60 & 120 cm) for the mesic and arid study areas.

The same pattern of seasonality evident in the rainfall and evaporation data, is also visible in the temperature data. Air and soil temperatures for both localities drop to a minimum during winter from May to August. Significantly, seasonal fluctuations in the deeper soil temperatures are relatively small.

DISCUSSION

Some confusion exists over the exact definition of arid environments, such as deserts (Louw & Seely 1982; Lovegrove 1993). Several, often contradictory, and to date fruitless, attempts have been made to combine climatic variables *e.g.* temperature, rainfall and evaporation into an appropriate definition (Louw & Seely 1982). Noy-Meir (1973) suggested that in light of the critical role played by water in controlling the productivity of desert ecosystems, the classification proposed by McGinnes *et al.* (1968) based solely on rainfall, is the most practical. McGinnes *et al.* (1968) classified arid regions into three broad types: (1) extremely arid (less than 60-100 mm mean annual precipitation); (2) arid (from 60-100 mm to 150-250 mm); and (3) semi-arid (from 150-250 mm to 250-500 mm). In addition, Noy-Meir (1973) identified three important characteristics of arid ecosystems: (1) low rainfall makes water the major constraint on most biological processes; (2) rainfall is extremely variable and occurs

as infrequent and discrete events; and (3) variation in rainfall has a significant unpredictable component.

Steinkopf, with its low annual rainfall of less than 150 mm, can be recognised as an arid environment, according to McGinnes *et al.*'s (1968) classification. Furthermore, the high intrinsic variability of the rainfall will translate into low predictability, concordant with Noy-Meir's (1973) predictions for arid ecosystems. Variability in rainfall at Steinkopf, falls within the upper range recorded for arid areas within southern Africa (Leistner 1979; Lovegrove 1993). The aridity at Steinkopf will be enhanced by high evaporation rates, which will promote the loss of any water which may be present and further desiccate the ecosystem. These precipitation and evaporation patterns contrast markedly with the pattern of high and relatively predictable rainfall and low evaporation evident at Sir Lowry's Pass.

In addition to the divergence in rainfall and evaporation, the study sites exhibit markedly different soils, Steinkopf being characterised by loose sandy soils, and Sir Lowry's Pass by compact clays. The combination of these edaphic features and the climatic properties outlined above will have substantial implications for foraging by mole-rats at the two localities. When dry, the clay soils at Sir Lowry's Pass may be extremely hard, while the top 25-30 cm of the sandy soils at Steinkopf may become extremely soft. As outlined in Chapter 1, both soil types are difficult to work, and consequently mole-rats will tend to concentrate burrow excavation in post rainfall periods to minimise energetic costs. However, Jarvis *et al.* (1994; 1998) observe that at least 15-25 mm of rain has to fall, within a relatively short period, for the soil to become damp enough to work at the depths of the mole-rat's foraging burrow's (15-25 cm; 1 mm rain for every 1 cm penetrated). Burrow depths for common mole-rats at both sites were about 20 cm (Chapters 3 & 4) and consequently at least 20 mm of rain would need to fall in a relatively short time, to provide optimal digging conditions. This so called "20 mm cut-off" has been included in Figure 2.2. At Steinkopf, rains of appropriate magnitude will only fall over a relatively short interval during winter from May to August (Figure 2.2). During this period mole-rats will be forced to dig as much as

possible to provide access to sufficient resources to last them through the subsequent dry periods. The unpredictable and sporadic nature of precipitation at Steinkopf will further aggravate foraging constraints and colonies will need to be able to respond rapidly to appropriate foraging conditions when they arise. In contrast, at Sir Lowry's Pass rainfall levels are always above the 20 mm cut-off, even during the dry mid-summer months (December to February; Figure 2.2). The high, predictable rainfall at this mesic locality will readily reduce soil compaction, and translate into optimal burrowing opportunities for most, if not all of the year. The AFDH would predict that these differences should be reflected in the differential social elaboration of *C. h. hottentotus* at the two sites.

The patterns of rainfall may have other effects on foraging unrelated to burrow excavation. As alluded to, water is probably the critical determinant of ecosystem productivity in arid environments (Noy-Meir 1973; Louw & Seely 1982; Werger 1986; Lovegrove 1993). The patterns of low and sporadic rainfall characteristic of arid areas like Steinkopf, will consequently have important implications for the structure of the vegetation occurring there (Schulze & McGee 1978; Werger 1978; 1986). The absolute abundance of individual plants will be expected to decrease relative to more mesic environments, as a consequence of a reduction in environmental carrying capacity (Lovegrove & Wissel 1988; Lovegrove 1991). Furthermore, although clumping of plants in many environments may be expected as a simple consequence of dispersal patterns and competition, in arid environments this clumping may be exaggerated by the low density of individuals, and heightened competition for limited resources (Werger 1986; Jarvis *et al.* 1994). This low density and highly clumped nature of food resources in arid environments, including Steinkopf, must restrict encounters of resources by foraging mole-rats (Jarvis *et al.* 1994; Brett 1986; 1991). Conversely, the more predictable and higher levels of precipitation at Sir Lowry's Pass should translate into higher densities of resources and more ready access to these resources by foraging animals. Again, the AFDH would expect these differences to be

reflected in the mole-rat populations from the two areas. The resource characteristics are discussed in Chapters 3 and 4.

Air and soil temperatures exhibited distinct differences between the two study sites. The differences in soil temperature in particular, may be of considerable importance to foraging mole-rats (Lovegrove 1986). McNab (1966; 1979) and MacMillen and Lee (1970) maintain that the combination of a low resting metabolic rate, high conductance and low body temperature in subterranean mammals represent an adaptation to minimise the risk of overheating in closed burrow systems, where evaporative and convective cooling are greatly reduced. Overheating is most likely to occur when subterranean mammals are digging burrows, as the high energetic costs of digging (Vleck 1979; 1981) translate into substantial metabolic heat production (McNab 1979; Lovegrove 1989; Marhold & Nagel 1995). In addition, soil and burrow temperatures will also influence the risk of overheating through their effect on the relative rates of heat gain and heat loss (McNab 1979). To avoid this potentially lethal heat stress, burrowing animals should either burrow during the cooler periods of the day, or restrict activity bouts and off-load accumulated heat (Lovegrove 1989). For example, Lovegrove (1989) demonstrated that Damaraland mole-rats foraging in the Kalahari, southern Africa, during summer (burrow temperature $\geq$ 33.5 °C) face a substantial risk of overheating. Animals thus restricted foraging bouts to *ca.* 60 min (32 min of which was spent actually digging) and then returned to the cooler nest areas and the bolt-hole to off-load stored body heat via conduction (Lovegrove 1988; 1989). The high summer soil temperatures at Steinkopf will restrict any burrowing which may occur, as, due to the risks of overheating, foraging animals will be forced to curtail their digging and retreat to the deeper, cooler, less thermally labile areas of the burrow system. The more moderate thermal characteristics at Sir Lowry's Pass should minimise this type of foraging restriction. Furthermore, the heavy and reliable rainfall should reduce burrowing costs and the concomitant risk of overheating.

Mole-rats are extremely poor thermoregulators (McNab 1966; Jarvis & Bennett 1991) and several workers have shown that mole-rats typically retreat into deeper sections of their burrow to avoid temperature extremes (Brett 1986; 1991; Bennett *et al.* 1988; Lovegrove & Knight-Eloff 1988). In the hottest parts of summer, mole-rats at Steinkopf may be forced to abandon foraging during the hottest periods of the day, to avoid the potentially lethal temperatures (> 40 °C) in the shallower foraging burrows. During winter, animals from both localities, but particularly Sir Lowry's Pass, may also have to forgo foraging and retreat to the warmer burrow depths to avoid thermally extreme periods. This enforced behavioural thermoregulation must ultimately impact on foraging efficiency.

A crucial feature of the climatic data is the high congruence between the study localities in climatic seasonality. Both areas show identical patterns of winter rainfall, with a concurrent rise in precipitation, drop in evaporation and drop in minimum and maximum temperatures over the winter period, from May to August. This is important as it ensures synchronous periodicity for any of the physiological processes which may be seasonal (*e.g.* reproduction - Chapter 6) in the study populations. It effectively provides an intrinsic control, guaranteeing that biological data collected from both environments are fully compatible, as long as they are collected at similar times.

In conclusion, Steinkopf and Sir Lowry's Pass exhibit marked differences in their basic environmental characteristics. The arid ↔ mesic differences correspond closely to those predicted by the AFDH as central to determining the occurrence of mole-rat sociality. Consequently, these two study sites provide an opportunity for an intraspecific investigation, such as the study undertaken in this thesis, to critically evaluate the AFDH as an explanation for social elaboration within the Bathyergidae.

Chapter 3

General foraging behaviour of wild and captive colonies from the arid locality.

ABSTRACT

The general foraging behaviour of wild and captive colonies of the common mole-rat was investigated using field and laboratory studies. Field studies were undertaken at Steinkopf. Food resources (geophytes) occurred at relatively low densities, and exhibited a clumped distribution. However, as geophytes tended to be large, the biomass of food resources and the total available energy were amongst the highest recorded for any area occupied by mole-rats. We postulate that the low probability of encountering these widely dispersed geophytes by "blind" burrowing should restrict dispersal and promote cooperative foraging in common mole-rats. The pattern of burrowing did not differ notably from that previously documented for common mole-rats, and bathyergids in general, and apparently served to minimise energetic costs and maximise the probability of encountering resources. The burrowing patterns are assessed within the context of energetic constraints. Harvested bulbs were typically stored in central food caches, and both field and laboratory data indicated size-based selectivity in their storage and consumption. Laboratory studies revealed that bulb handling and consumption times were dependent upon both animal size and bulb size. An alternative foraging strategy, termed "*in situ* harvesting" was also identified in the field, in which bulbs which were to large to be carried to the food store were left *in situ*, and served as a renewable resource. The patterns of resource utilisation are discussed in the context of optimal foraging theory in general, and central placed foraging theory in particular. The most striking aspect of foraging behaviour was its inherent flexibility; common mole-rats, and mole-rats in general, exhibit a remarkable plasticity in their response to the foraging constraints dictated by their environment. Sociality may be a key component facilitating this foraging pliability.

INTRODUCTION

Studies investigating the evolution and maintenance of sociality within the African mole-rats have consistently highlighted the pivotal importance of resource characteristics (Jarvis 1978; 1985; Brett 1986; 1991; Bennett 1988; Lovegrove & Knight-Eloff 1988; Lovegrove & Wissel 1988; Jarvis & Bennett 1990; 1991; Jarvis *et al.* 1994; 1998). As

outlined in Chapter 1, the Aridity Food-Distribution Hypothesis (AFDH) predicts that foraging is constrained in arid environments by the distribution of critical food resources. Increased group size and cooperative foraging in mole-rats reduces the risks of unproductive foraging and therefore represents an evolutionary stable adaptation to foraging in arid habitats (Lovegrove & Wissel 1988; Lovegrove 1991; Jarvis *et al.* 1994; Lacey & Sherman 1997). Consequently, in evaluating the AFDH as an explanation for the evolution of bathyergid sociality, two principal questions must be addressed: (1) do resource characteristics differ markedly between arid and mesic localities? and (2) how do any differences in resource characteristics impinge on mole-rat foraging abilities in arid and mesic environments? The answers to these questions may challenge the very basis of the AFDH.

Due to the magnitude of study encompassed by these particular aspects of the AFDH, the examination of resource characteristics and foraging behaviour is spread over two chapters (Chapter 3 & 4). A detailed arid/mesic comparison of differential resource characteristics and foraging abilities is undertaken in Chapter 4. In this chapter I attempt to lay the foundation and establish baseline foraging behaviour in the common mole-rat. The general foraging behaviour of an arid-occurring population of *C. h. hottentotus* is investigated. Field studies were used to examine food resource characteristics (abundance, quality and spatial distribution), burrow system architecture and the patterns of resource exploitation by foraging mole-rats. Laboratory studies were undertaken to address two important questions: (1) is there any size-based selectivity in the storage and consumption of geophytes? and (2) how do food size and animal size influence energy acquisition during feeding? The findings from this investigation are evaluated within the framework of optimal foraging theory.

MATERIALS AND METHODS

Field Studies

Field work was undertaken at the Steinkopf study site. The floristic, edaphic and climatic features of this site are outlined in Chapter 2.

Resource characteristics for the study site were assessed using 100 randomly placed 25×25 cm quadrats[1], dug to a depth of 20 cm (none of the geophytes consumed by the mole-rats at Steinkopf occur below this depth). Estimates of the density and biomass of geophytes in the study site were obtained from the quadrat samples. A standardised Morisita Index of Dispersion was used to assess resource distribution, as it has the advantage that it is independent of population density and sample size (Krebs 1989). The index ranges from -1.0 (perfectly uniform) to +1.0 (clumped), with 95% confidence limits at -0.5 and +0.5. Perfectly random patterns give an index of zero.

Five complete colonies of *C. h. hottentotus* were captured using modified Hickman live-traps (Hickman 1979a), after which the entire burrow systems of four colonies were excavated. Characteristics of these colonies (B3, E1, R1 and T1) are summarised in Table 3.1. Burrow depth and diameter were measured at regular intervals. The position and depth of any food stores were recorded, and their contents collected for analysis. After excavation, each system was mapped on graph paper using a grid system. The soil surrounding each system was sampled for geophytes by excavating and sieving 20 quadrats (30×30 cm), dug to a depth of 20 cm. The quadrats were placed at random points along the burrow systems,

[1] A preliminary investigation revealed that measures of density and dispersion obtained from quadrats of 25x25 cm, 50x50 cm and 1x1 m did not differ significantly, and consequently quadrats of 25x25 cm were considered sufficiently representative and logistically sensible.

Table 3.1: Characteristics of the *C. h. hottentotus* colonies used in this study; their burrow systems, resources around the burrow systems and foraging strategies. Colonies T1 and T3 were used in the laboratory-based studies. The burrow system of T1 was not excavated.

Variable		Colony				
		B3	E1	R1	T3	T1
Colony information	Colony size	2	2	8	9	10
	Sex ratio (f:m)	1:1	1:1	3:5	4:5	2:3
	Mean mass (g)	75	78	34 ± 4	50 ± 6	39 ± 5
	Mass range (g)	55 & 94	72 & 83	29-60	32-74	20-73
	Total mass (g)	149	155	301	452	392
Burrow system	Length (m)	290	150	510	300	-
	Biomass per metre of burrow ($g.m^{-1}$)	0.5	1.0	0.6	1.5	-
Burrow depth	Mean (cm)	17.9 ± 0.3^{a}	19.3 ± 0.8^{a}	13.1 ± 0.4^{b}	13.6 ± 0.3^{b}	-
	Range (cm)	11.1 - 22.5	11.5 - 26.5	6.2 - 20.6	8 - 21	-
Burrow diameter	Mean (cm)	5.8 ± 0.1^{a}	6.4 ± 0.1^{b}	4.8 ± 0.1^{c}	5.3 ± 0.1^{d}	-
	Range (cm)	4.2 - 7.9	5.1 - 8.7	2.9 - 6.2	3.6 - 7	-
Geophyte characteristics	Mean mass (g)	12.8 ± 2.2	6.2 ±1.3	2.0 ± 1.3	3.9 ± 2.8	-
	Biomass ($g.m^{-2}$)	590.9 ± 100.9	707.8 ± 141.4	154.2 ± 101.2	80.7 ±56.5	-
	Density ($no.m^{-2}$)	46.3 ± 17.0	113.9 ± 18.4	75.6 ± 29.2	20.6 ±7.4	-
Foraging strategy	Geophyte storing	yes	no	yes	no	-
	in situ harvesting	yes	yes	no	no	-

values presented as means ± SE; a,b,c,d - significantly different groups (Tukey multiple range test), $p < 0.00001$ (ANOVA)

but within 10 cm of a burrow. In the laboratory, the weight (to 0.01g), the diameter[2] (to 0.01mm) and identity were determined for all geophytes collected from the food stores and quadrats. The water content (as a % of wet mass) for the most abundant geophyte species was determined by drying pre-weighed samples (at 60 °C) to a constant weight. Geophyte energy content ($kJ.g^{-1}$) was determined by bomb calorimetry (Bennett & Jarvis 1995). Total available energy ($kJ.m^{-2}$) for each geophyte species was calculated as follows:

total available energy = biomass x [1 - (water content/100)] x energy content

where biomass was measured in $g.m^{-2}$, water content as a percentage of wet mass and energy content in $kJ.g^{-1}$.

The chi-square goodness-of-fit test (Zar 1984) was used to determine whether common mole-rats selectively store a specific size category of geophyte. Expected frequencies were obtained by dividing all the geophytes gathered from quadrats around each burrow system into four size classes, each containing a similar number of geophytes. Observed frequencies were calculated from the food stores by determining the total number of geophytes within each size class. This was done separately for burrow system B3 and R1 (no food stores were located for systems E1 and T3). Food store N1 was located by chance, without burrow excavation. Expected frequencies for N1 were consequently based on random quadrats placed near this food store.

Inter-colony differences in mean burrow depth, mean burrow diameter and mean mass of stored geophytes were analysed statistically using one-way Analysis of Variance (ANOVA; Zar 1984). Comparisons of individual means were made *post hoc* using Tukey's multiple range test as Zar (1984) suggests that this is the most robust and most widely accepted multiple comparison test. Regression analysis was used to examine the

[2] Bulb diameter was significantly correlated with bulb mass ($r_{(801)} = 0.97$, $p < 0.00001$), and consequently for the purposes of this investigation only the data for bulb mass are presented.

relationship between the mean body mass of mole-rats in a colony and the mean depth and diameter of their burrow system (Zar 1984).

Laboratory studies

Foraging behaviour

Two of the colonies (T1 & T3, Table 3.1) captured at Steinkopf were taken back to the laboratory. Each animal was weighed, sexed and toe-clipped for permanent identification. For easy identification during the behavioural study, mole-rats were marked on their dorsal surface with non-toxic dyes (gentian violet, orange G and mercurochrome) in distinctive patterns. The room temperature during the study was maintained between 24°C and 26°C. The room received a natural photoperiod and in addition, during the period of study or when their housing was cleaned, fluorescent lights were used. The mole-rats were initially fed on sweet potatoes, gem squash and carrots. Once the experimental trials had started, they were fed only *Ornithogalum secundum*. These geophytes were collected at the study site, and form a substantial part of the animal's natural diet.

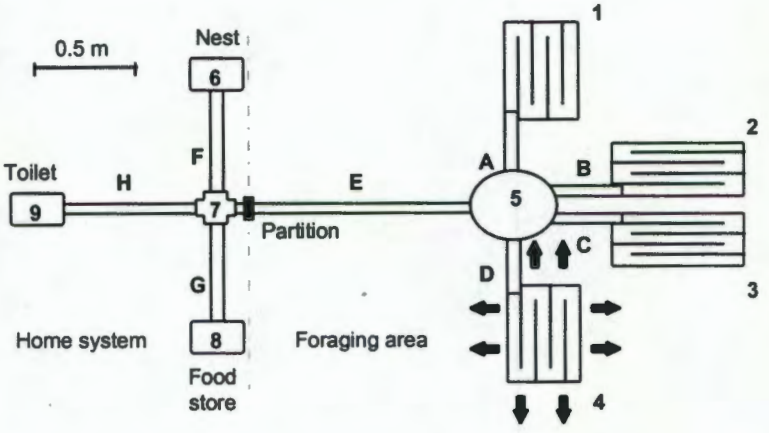

Figure 3.1: Experimental apparatus used for laboratory foraging trials. Numbers one to nine indicate the different chambers, and letters A-H the different tunnels making up the experimental system. Arrows from tray 4 indicate where sand could be ejected from the digging trays by the mole-rats, and was the same for all digging trays.

The experimental system consisted of a "home system" and a "foraging area" (Figure 3.1). The home system comprised the nest, food store and toilet, all linked by acrylic plastic burrows. The foraging area consisted of four digging trays (partitioned trays containing 3m of potential "burrow") linked to the home system by

acrylic plastic burrows. Sheets of glass on top of all containers and digging trays eased observation. Wood shavings were provided as nesting material. Animals were housed in the experimental apparatus for the duration of the study, but were confined to the home system between observation periods, by a partition (Figure 3.1). At the start of observation, this partition was removed, giving the animals access to the foraging area. Digging trays were filled with damp sand, and contained different treatments of *O. secundum* bulbs (Table 3.2).

Table 3.2: Bulb treatments in the four digging trays attached to the experimental system.

Tray number	No. of bulbs	Bulb size class	Range in bulb mass (g)	Mean total mass of bulbs (g)
1	12	small	0.1 - 2.0	13
2†	0	-	-	0
3	12	medium	2.1 - 5.0	40
4	12	large	5.1 - 28.0	104

bulbs were evenly spaced in all trays;† = control tray

The colonies were given an initial period of two days to adjust to the experimental set-up before data collection started. Each colony was observed for two hours a day for 10 consecutive days (excluding preliminary trials). Behaviour was recorded using both scan-samples and focal-samples (Altmann 1974). Scans were conducted by noting the behaviour and position of each animal at 10-minute intervals throughout each two-hour observation period. In focals, a particular individual was observed, and the details of each behaviour were recorded (see Rosenthal *et al.* 1992 for ethogram). Focal individuals were pre-selected before the day's observation started; if these animals were inactive, the active animal with the least focal time recorded was observed. Some animals were very inactive and only a few focals were recorded, but every animal was observed on at least three days, for a minimum of four bouts of activity. Only the least active animal in each colony was observed for less than 75 minutes in total. Results from the scans and focals were

used to examine any size-based selectivity in the storage and consumption of geophytes by the members of both colonies.

Geophyte consumption rates

To assess how food size and animal size influence energy acquisition during feeding, experiments were conducted to compare the time taken by the different individuals within each colony, to handle and consume geophytes of different sizes. Individuals were placed in separate metabolic chambers and given a single *O. secundum* bulb to consume, either small, medium or large in size. Food deprivation is known to affect feeding rates (Curio 1976; Benkman 1987; Croy & Hughes 1991), and accordingly, all mole-rats were deprived of food for one hour prior to the experiment, to standardise their motivational states. Preparation time (time taken to dehusk the bulb, *i.e.* remove the outer husk before eating), eating time, and total consumption time (preparation time plus eating time) were determined. These experiments were repeated twice for each bulb size, making a total of six trials for each mole-rat in each colony. Regression analysis was used to examine the relationship between body mass and preparation, eating and total consumption times of different sized bulbs.

RESULTS

Field studies

Resource characteristics

The mean density of geophytes at Steinkopf was 75.84 ± 8.14 bulbs.m^{-2} and the biomass was 329.20 ± 57.91 g. m^{-2} (Table 3.3). The standardised Morisita index of dispersion for the study site was 0.54, indicating that the distribution of geophytes at Steinkopf is significantly clumped (95% confidence limits at - 0.5 and + 0.5). Food store analysis and anecdotal observation indicate that *C. h. hottentotus* at Steinkopf consume a wide range of food plants,

Table 3.3: The mean mass, water content, energy content, density, biomass and total available energy for geophytes collected from 100 random quadrats at Steinkopf.

Species	Mass (g)	Water content (%)	Energy content ($kJ.g^{-1}$)	Density ($No.m^{-2}$)	Biomass ($g.m^{-2}$)	Total available energy ($kJ.m^{-2}$)
Albuca cooperi	3.69†	-	-	0.32 ± 0.23	1.18 ± 0.85	4.46‡
Herrea blanda	2.29 ± 1.38	89.41 ± 0.69	14.51 ± 0.25	0.64 ± 0.32	1.10 ± 0.83	1.69
Homeria schleretchi	1.99 ± 0.95	-	-	0.48 ± 0.27	0.96 ± 0.66	3.63‡
Lachenalia klinghardtiana	0.34 ± 0.11	70.01 ± 1.46	15.32 ± 0.10	1.28 ± 0.59	0.43 ± 0.25	1.98
Oxalis sp.	0.27 ± 0.05	-	-	3.36 ± 2.33	0.89 ± 0.61	3.36‡
Ornithogalum secundum	17.76 ± 3.12	66.55 ± 1.25	15.30 ±0.28	15.36 ± 3.35	269.98 ± 57.52	1381.72
Trachyandra revoluta	1.06 ± 0.14	66.14 ± 0.85	10.85 ± 0.46	50.24 ± 7.21	53.12 ± 10.90	195.15
Other	0.38 ± 0.26	-	-	4.16 ± 1.50	1.54 ± 1.1	5.82‡
Overall		71.33 ± 1.49	14.33 ± 0.31	75.84 ± 8.14	329.20 ± 57.91	1597.81

values presented as means ± SE (n); † sample size too small to calculate SE ; ‡ available energy estimated using average water and energy content for other geophyte species

including at least nine different geophyte species. In addition to those listed in Table 3.3, *Hessea pilosula, Homeria miniata* and *O. xanthochlorum* also occurred in the diet.

The most abundant food plants at Steinkopf were *O. secundum* and *Trachyandra revoluta*. (Table 3.3). Although *T. revoluta* was the most abundant geophyte at the study site, it was only stored by R1, and even then comprised just 5% of the food store by numbers (Table 3.3). By contrast, although *O. secundum* was markedly less abundant than *T. revoluta*, its large bulbs accounted for 82% of the total geophyte biomass available at Steinkopf (Table 3.3), and dominated the food stores (Table 3.4)[3]. The remaining geophyte species consumed by *C. h. hottentotus*, at Steinkopf, constituted a negligible proportion of the available food, in terms of both numbers and biomass (Table 3.3). *Lachenalia klinghardtiana* was the only other species that was frequently stored (Table 3.4).

The average water content of geophyte species at Steinkopf was 71.33 ± 1.49% and ranged from 66.14 ± 0.85% for *T. revoluta* to 89.41 ± 0.69% for *Herrea blanda* (Table 3.3). Energetic contents averaged 14.83 ± 0.31 $kJ.g^{-1}$, ranging from 10.85 ± 0.46 $kJ.g^{-1}$ for *T. revoluta*, to 15.32 ± 0.10 $kJ.g^{-1}$ for *L. klinghartiana*. The total energy in geophytes at Steinkopf was 1597.81 $kJ.m^{-2}$ (Table 3.3). Bennett and Jarvis (1995) estimate coefficients of digestibility of between 95 - 97% for *C. h. hottentotus* and *C. damarensis*, feeding on a range of geophytes. Thus, the total digestible energy available to foraging animals at Steinkopf ranged between 1517.92 - 1549.86 $kJ.m^{-2}$.

Burrow excavations

Excavated burrow systems had contained colonies with two to nine individuals (Table 3.1). The smallest colonies (E1 and B3) each comprised a breeding pair, whereas the larger colonies included a reproductive pair plus several generations of offspring. A plan of the B3

[3] The high storage quantities, and large available biomass of *O. secundum* at Steinkopf was considered sufficient justification for using this species in the laboratory trials.

burrow system (Figure 3.2) shows its extent and pattern. In general, burrow systems consisted of deeper primary burrows, which formed the main artery of the burrow system and were the straightest and longest section of the system. Branching off at right angles from the primary burrows were a series of secondary burrows, which ramified into a succession of shallower foraging burrows. Overall burrow system length (including primary, secondary and foraging burrows) ranged from 150 m to 510 m for the four excavated systems (Table 3.1). The biomass of mole-rats per metre of burrow ranged from 0.5 to 1.5 $g.m^{-1}$ (Table 3.1). The mean mass of mole-rats in the colonies was positively correlated with both the mean burrow depth ($r_{(4)} = 0.97$, $p < 0.025$) and mean burrow diameter ($r_{(4)} = 0.95$, $p < 0.05$). The burrows of the pairs were significantly deeper than those of the larger colonies (Table 3.1; ANOVA, $F_{(3, 222)} = 55.23$, $p < 0.0001$). The burrows for all colonies had significantly different diameters (Table 3.1; ANOVA, $F_{(3, 229)} = 41.45$, $p < 0.0001$), with the burrows of the pairs being markedly wider in diameter than those of the larger colonies

Analysis of food stores

Table 3.4: Analysis of food stores collected from three *C. h. hottentotus* colonies at Steinkopf.

	Burrow system		
Variable	B3	R1	N1
Number of food stores	2	2	1
Food store depth (cm)	46 & 50	15 & 18	-
Total bulbs stored	283	168	156
Total mass (g)	1200.02	294.66	778.77
Mean mass (g)	4.24 ± 0.19^{a}	1.78 ± 0.18^{c}	5.09 ± 0.29^{b}
Mode (g)	1.65	0.65	2.4
Range (g)	0.55 - 24.78	0.17 - 19.32	0.34 - 21.46
Number of species	5	8	2
Dominant species	OS (>90%)	LK (>60%)	OS (>90%)

values presented as means ± SE; OS - *Ornithogalum secundum*; LK - *Lachenalia klinghartiana;* a,b,c - significantly different groups, (Tukey multiple range test), $p < 0.00001$ (ANOVA).

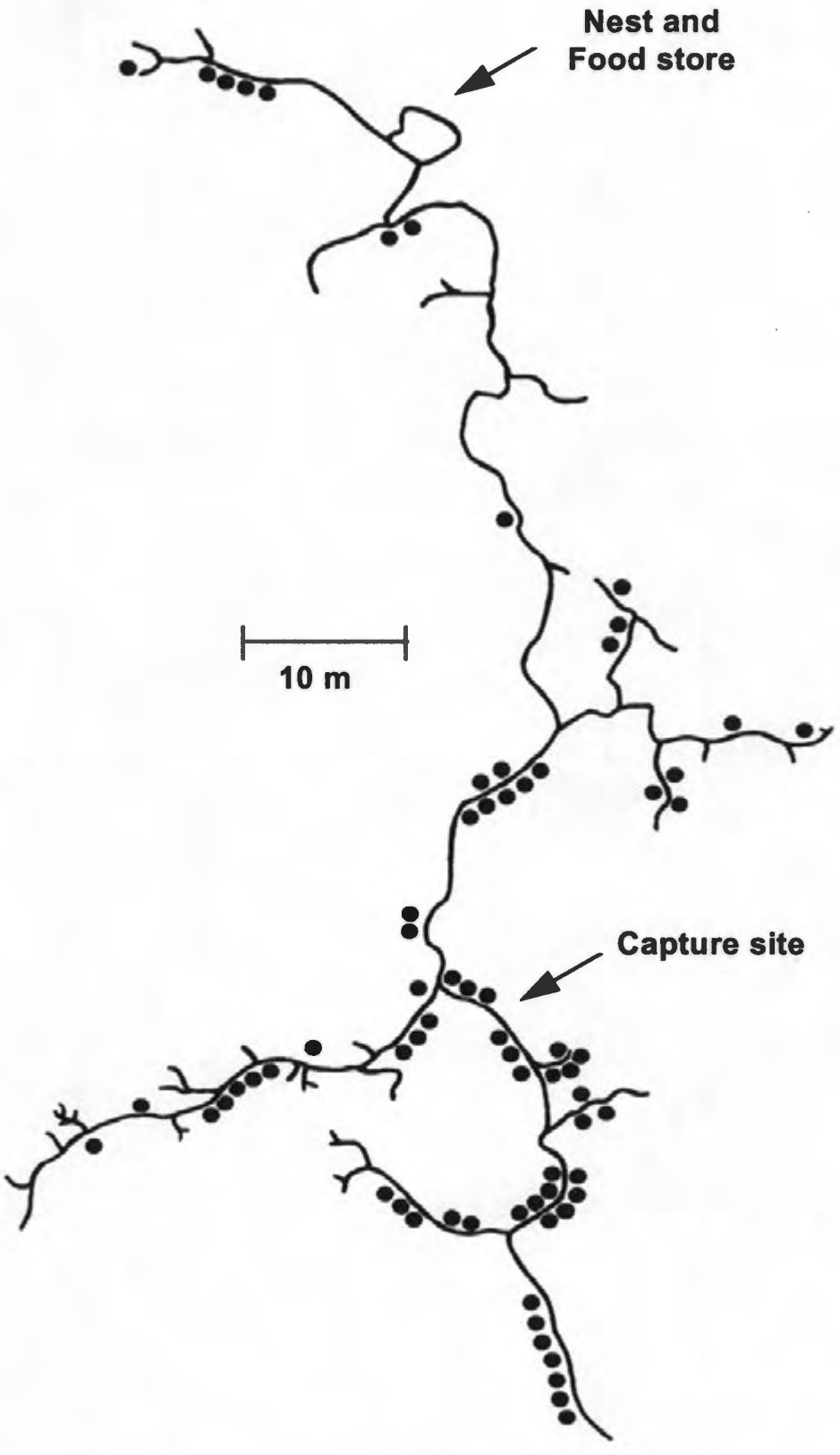

Figure 3.2: Plan diagram of a representative *C. h. hottentotus* burrow system excavated at Steinkopf (Colony B3), to indicate the general burrowing pattern. The solid circles indicate the position of large *O. secundum* bulbs which were left *in situ* by the foraging animals. Each circle represents two bulbs.

The excavated burrow systems of B3 and R1 each contained two food stores, situated close to each other and near to the nest (e.g. Figure 3.2). In addition, a food store from another, unexcavated, system (N1) was located by chance. Each food store was tightly packed into a sand-filled chamber and contained several geophyte species (Table 3.4). The total biomass of geophytes stored in each system differed substantially; B3 contained just over 1 200 g, while R1 contained less than 300 g. These differences were due to differences in both the total number of bulbs stored and their average mass (Table 3.4). Colony B3 had stored almost twice as many bulbs as the other colonies. The mean mass of the stored geophytes differed significantly between the three systems (Table 3.4, ANOVA, $F_{(2, 598)} = 51.16$, $p < 0.0001$), with B3 and N1 containing bulbs of substantially larger mean mass than R1. Differences in the mean mass of bulbs in the food stores were related to differences in the dominant species of bulbs stored. The food stores for B3 and N1 were composed almost entirely of *O. secundum* (> 90%), while those in R1 contained a substantial proportion (> 60%) of *L. klinghartiana*. *Ornithogalum secundum* is a relatively large geophyte with an average mass of 17.76 ± 3.12g, while *L. klinghartiana* is much smaller, weighing 0.34 ± 0.11g (Table 3.3).

In all three systems examined, the size frequencies of geophytes in the food stores differed significantly from random quadrats around the same burrow systems (Figure 3.3, Table 3.5). The food stores contained fewer geophytes in the smaller size categories and more geophytes in the larger size categories (Table 3.5).

In two colonies (B3 and E1) an alternative foraging strategy to geophyte storage was evident. Both of these systems went through patches of *O. secundum* bulbs (Figure 3.2) with diameters greater than 6 cm. Once located these geophytes were left untouched, or were partially consumed, before the foraging burrow was re-filled with loose sand, leaving the bulbs *in situ*. This foraging strategy was termed "*in situ* harvesting". While E1 exhibited only *in situ* harvesting, B3 displayed geophyte storage and *in situ* harvesting, and R1

exhibited only geophyte storage (Table 3.1). It is noteworthy that neither foraging strategy was evident from the burrow system of T3 (Table 3.1). The area around this burrow was characterised by small bulbs similar in size to those around the R1 system (Table 3.1). However, the estimated bulb density around T3 (20.6 ± 7.4 bulbs.m^{-2}) was only 27% of the mean density for the study site as a whole, and the biomass estimate (80.7 ± 56.3 g.m^{-2}) just 24% of that for the study site as a whole (Table 3.1).

Table 3.5: Comparative proportion of various size classes of geophytes collected from food stores and from random samples around the burrow system, for three *C. h. hottentotus* colonies at Steinkopf. Size classes were obtained by dividing the random samples into four groups with approximately equal frequencies

		Bulbs/size class			
Colony	Size class (g)	Expected	Observed	$\chi^2_{(3)}$	Sig. level
B3	0 - 0.25	83	0		
	0.26 - 0.50	66	0		
	0.51 - 1.80	65	47		
	>1.80	69	236	558.17	p<0.00001
N1	0 - 1.10	41	5		
	1.11 - 2.40	36	36		
	2.41 - 4.70	38	41		
	>4.70	38	71	60.51	p<0.00001
R1	0 - 0.20	44	1		
	0.21 - 0.30	36	1		
	0.31 - 0.50	50	8		
	>0.50	35	155	522.56	p<0.00001

Laboratory studies

Foraging behaviour

The mole-rats of both experimental colonies exhibited distinct size-based selectivity in their response to the bulbs they encountered during foraging (Figure 3.4). Depending on their

size, bulbs were either ignored and left *in situ*, carried to the central food store, or consumed. Results revealed that in both T1 and T3, small bulbs were preferentially eaten, and large bulbs preferentially stored or ignored (Figure 3.4). The response to medium bulbs was equivocal, but a relatively larger proportion were stored or ignored, and a relatively smaller proportion consumed (Figure 3.4). The frequency with which geophytes were stored increased as a function of geophyte mass, while the reverse trend was apparent for geophyte consumption (Figure 3.4).

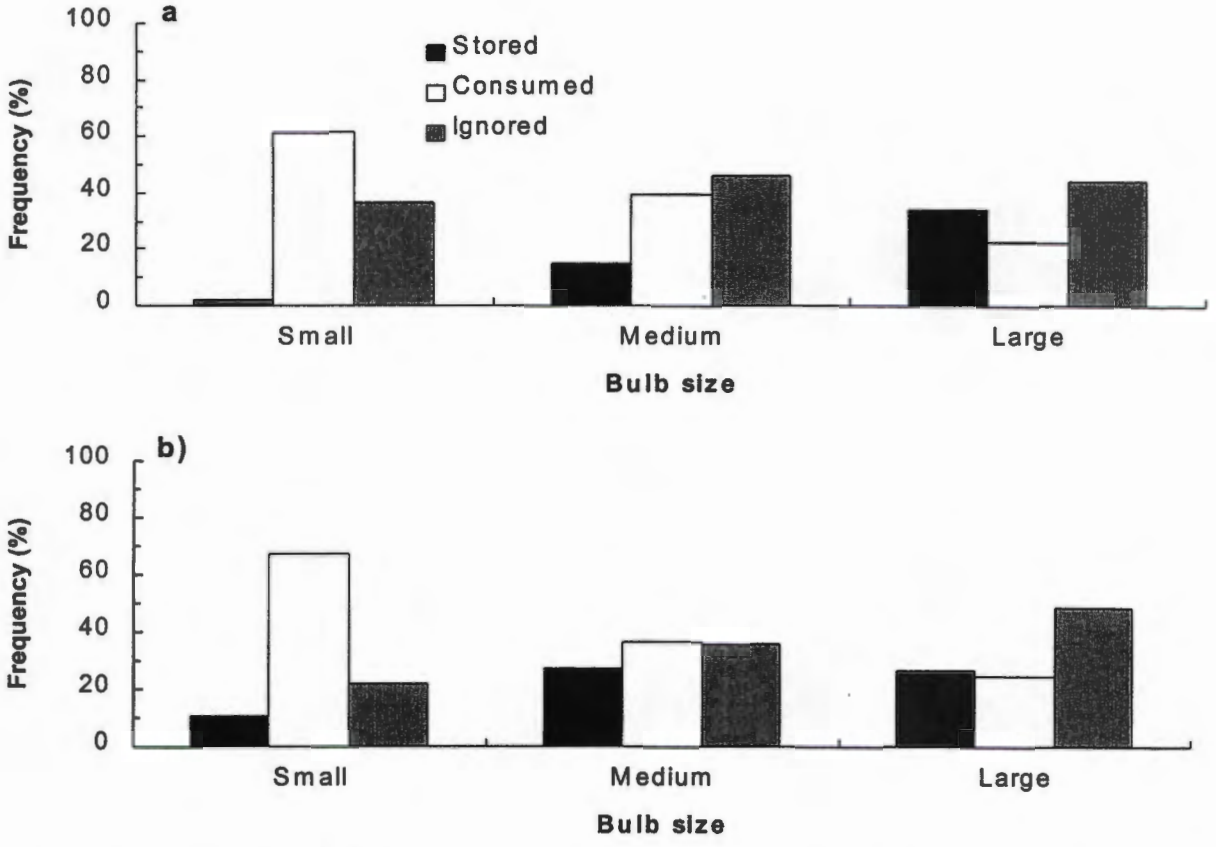

Figure 3.4: Reaction of *C. h. hottentotus* mole-rats from (a) T1 and (b) T3, to bulbs of different sizes encountered in the experimental apparatus. Bulbs were either carried to the food store (stored), eaten (consumed) or left (ignored).

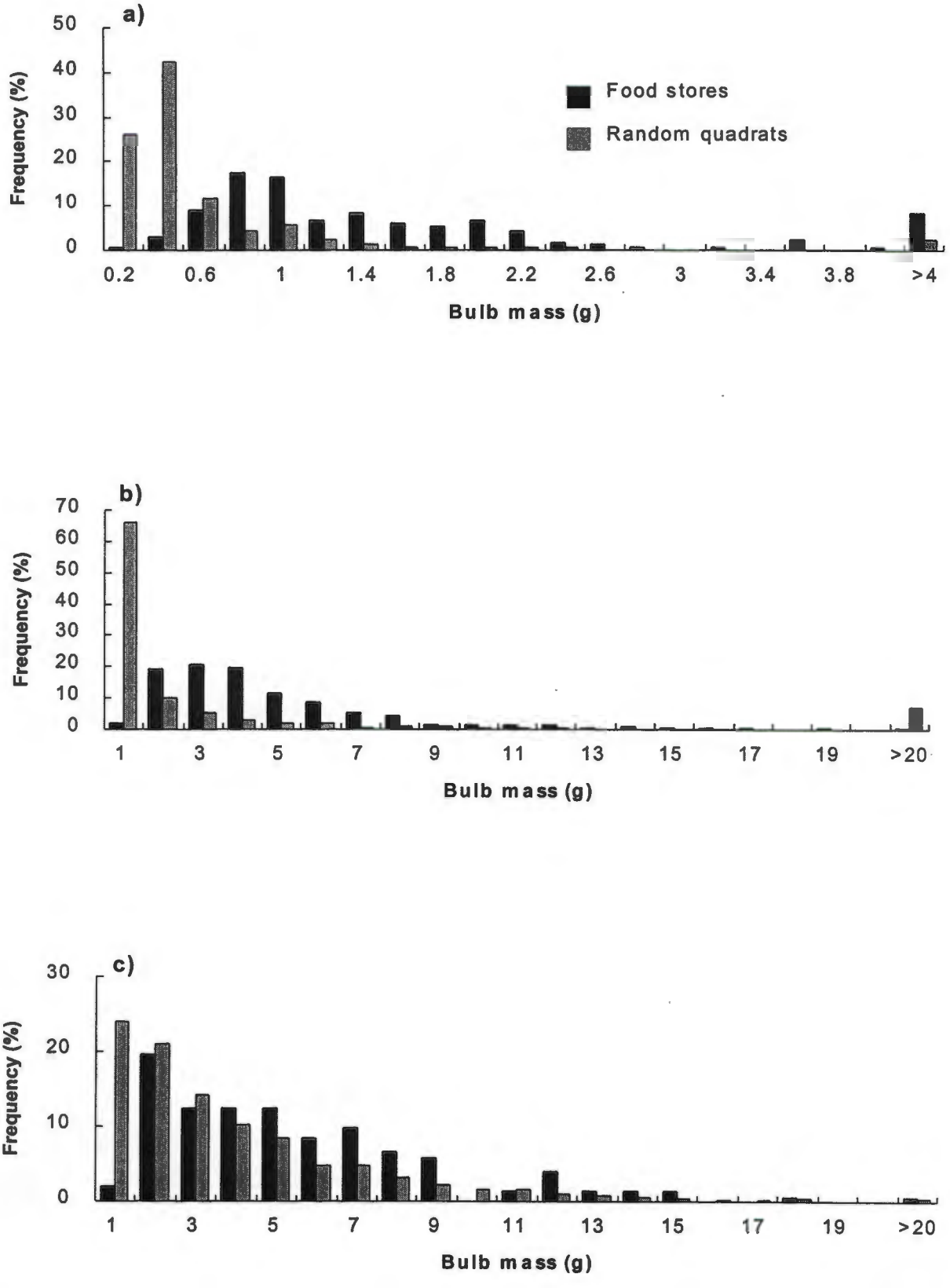

Figure 3.3: Comparison of size-frequency distributions of geophytes collect from *C. h. hottentotus* food stores and those collected in random quadrates surrounding the burrow system. Results are given for three systems (a) R1, (b) B3 and (c) N1.

Geophyte consumption rates

Common mole-rat feeding behaviour was rather stereotyped, and similar to that previously documented for *C. h. hottentotus* (Davies & Jarvis 1986) and *C. damarensis* (Barnett 1994). External husks were completely removed from most of the geophytes before eating began, although very large bulbs were often only partially dehusked. This was particularly apparent for smaller animals, who failed to completely remove the husks from a large proportion of the geophytes presented to them, when compared to larger animals. The smallest mole-rats completely dehusked only 21% of the large bulbs, 69% of the medium bulbs and 86% of the small bulbs (Table 3.6). In contrast, the largest mole-rats completely dehusked 89% of the large bulbs, 93% of the medium bulbs and 98% of the small bulbs (Table 3.6).

Table 3.6: Percentage of geophytes of various sizes, completely dehusked by different sized *C. h. hottentotus* individuals, in the feeding experiments. Animals were weighed before the trials.

	Bulb size class		
Mole-rat size class	Small	Medium	Large
<40g	86%	69%	21%
40-55g	91%	78%	62%
>55g	98%	93%	89%

The rate at which geophytes were consumed was dependent on both animal size and geophyte size. There was a significant negative correlation between preparation time, eating time and total consumption time, and body mass for all three size classes of bulb ($p < 0.005$ for all, Table 3.7). For all bulb sizes, consumption time (preparation, eating and total time) decreased proportionally with an increase in animal size. In addition, smaller bulbs were consumed more rapidly than larger ones (Table 3.7).

Table 3.7: Regression statistics for the processing of small, medium and large geophytes by *C. h. hottentotus* individuals. For all regressions n = 19.

Bulb size	Variable	Regression equation	r	Sig. level
Small	Preparation	y = -1.97x + 187.14	-0.89	p < 0.0005
	Eating	y = -2.69x + 241.45	-0.87	p < 0.0005
	Total	y = -4.66x + 428.59	-0.92	p < 0.0005
Medium	Preparation	y = -2.50x + 252.49	-0.81	p < 0.0005
	Eating	y = -2.56x + 326.85	-0.80	p < 0.0005
	Total	y = -5.06x + 579.34	-0.89	p < 0.0005
Large	Preparation	y = -2.10x + 328.40	-0.71	p < 0.0005
	Eating	y = -3.55x + 602.29	-0.70	p < 0.0005
	Total	y = -5.66x + 930.68	-0.77	p < 0.0005

DISCUSSION

As previously suggested, food resource characteristics may be a pivotal determinant of the foraging constraints ultimately shaping mole-rat foraging behaviour and group-living (Jarvis 1978; Lovegrove & Painting 1987; Lovegrove & Wissel 1988; Lovegrove 1991; Jarvis *et al.* 1994). The significance of the resource characteristics detailed in this study are possibly best understood by contrasting them with the patterns described for other *C. h. hottentotus* populations, and other mole-rat species in general (Table 3.8). In absolute terms, energy does not appear to be a limiting resource for mole-rats at Steinkopf. The geophyte biomass, and associated available energy levels, are amongst the highest reported for any site occupied by bathyergids, marginally higher than for *H. glaber* in Kenya (Table 3.8), but within the range reported for *C. damarensis* in Namibia (Table 3.8). However, as outlined in Chapter 1, Jarvis *et al.* (1994) note that both solitary and social bathyergids generally occur in habitats with similar mean amounts of energy available to them. They suggest it is in fact the pattern of resource distribution and density, not total available energy, which ultimately constrains foraging efficiency and promotes group-living. The geophyte density at Steinkopf

Table 3.8: Comparison of resource characteristics for *C. h. hottentotus* at Steinkopf with those reported for other bathyergid species.

Species	Social structure	Site	Bulb size (g)	Density (no.m^{-2})	Biomass (g.m^{-2})	Available energy (kJ.m^{-2})	Distribution pattern
Bathyergus janetta [a,b]	solitary	Namibia	<10	-	-	84.6	clumped
Georychus capensis [a,c,d]	solitary	western Cape[†]	0.5-2	100-500	-	536.2	clumped?
C. h. hottentotus [a,c,d]	social	western Cape[†]	0.5-2	100-500	-	536.2	clumped
C. h. hottentotus [a]	social	northern Cape[†]	1-4	-	-	181.4	clumped
C. h. hottentotus [e]	social	northern Cape[†]	0.3-17.8	75.8	329.2	1597.8	clumped
C. damarensis [f,g]	eusocial	Nossob, Kalahari[†]	0.4-5.2	39.9-117.9	55.4-118.0	195.3-416.1	random?
C. damarensis [g]	eusocial	Dune, Kalahari[†]	670	0.19-0.41	-	-	random
C. damarensis [h]	eusocial	TWR, Kalahari[†]	409	0.03-0.6	12.7-257.7	36.4-733.4	clumped
C. damarensis [h]	eusocial	Namibia	5.6	4-160	0.7-431	2.5-1519.7	clumped
Heterocephalus glaber [i,j]	eusocial	Kenya	2-30 000	0.06	313	1170	clumped/ random

[†] all localities within South Africa

[a] Bennett 1988; [b] J.U.M. Jarvis & N.C. Bennett unpublished data; [c] Du Toit *et al.* 1985; [d] J.U.M. Jarvis & B.G. Lovegrove unpublished data; [e] this study (shaded grey); [f] Lovegrove 1988; [g] Lovegrove & Knight-Eloff 1988; [h] Jarvis *et al.* 1998; [i] Brett 1986; [j] Brett 1991

was roughly intermediate between those reported for solitary and social species in other studies (Table 3.8), and geophyte distribution was clumped. Jarvis *et al.* (1998) estimated that, in Namibia, where geophyte densities may be as high as 160 bulbs.m^{-2}, an average sized Damaraland mole-rat would still have to burrow over 10 m each day to satisfy its daily energy requirements. Thus the more modest resource densities at Steinkopf should impact significantly on foraging. The low probability of locating clumped and widely dispersed geophytes by blind burrowing should markedly constrain foraging success, restricting dispersal and promoting cooperative foraging in common mole-rats from Steinkopf.

Common mole-rats foraging at Steinkopf consumed a broad diversity of geophytes, including all of the species with subterranean storage organs commonly occurring in the study site. Optimal foraging theory argues that foraging animals should select from the set of potential food items encountered, a smaller subset which maximises energetic returns relative to cost (Kaufman & Collier 1981). The lack of selectivity in common mole-rats may reflect the low variation in mass specific energetic content of the geophytes at Steinkopf (Table 3.3). This is unlikely, however, as there was considerable variation in bulb size, which would impinge directly on handling costs, and ultimately energetic returns. Alternatively, the catholic tastes of *C. h. hottentotus* may reflect dietary generalism. Heth *et al.* (1989) showed that due to the large search costs and variability in food resources experienced by subterranean foragers, the optimal foraging strategy is dietary generalism, where animals collect all of the relevant food that they encounter. Damaraland mole-rats in Namibia and common mole-rats from Darling in South Africa also feed on a wide range of species of geophyte (Jarvis *et al.* 1998; J.U.M. Jarvis & B.G. Lovegrove unpublished data), further supporting this contention of dietary generalism in subterranean foragers.

The burrow system structure of *C. h. hottentotus* at Steinkopf is similar to that previously reported for other mole-rat species (De Graaff 1972; Hickman 1979b; Davies & Jarvis 1986; Lovegrove & Painting 1987; Lovegrove & Knight-Eloff 1988), and simply reflects the typical pattern of resource exploitation in which burrows tend to be linear, with

greater branching when patches of food are encountered. Brett (1991) suggests that this pattern of foraging is an example of area-restricted searching (*sensu* Krebs 1978), and as such represents an optimal foraging strategy. Foraging in this manner will ensure economy of effort, as only areas that are likely to render substantial energetic rewards are extensively exploited (Jarvis & Sale 1971; Jarvis *et al.* 1997). Maximum burrow system length (510 m) was comparable to the 464 m recorded for *C h. hottentotus* by Davies and Jarvis (1986). The biomass of mole-rats per metre of burrow (0.5–1.5 $g.m^{-1}$) was also similar to that documented by Davies and Jarvis (1986) (0.8–1.1 $g.m^{-1}$), and remains the lowest recorded for any subterranean mammal (Davies & Jarvis 1986; Heth 1989; Jarvis & Bennett 1991). In general, social mole-rats exhibit much lower biomass per metre of burrow than solitary species. It is not clear why this should be so, but may be due to: (1) their diet, these geophyte-specialists consume little above-ground vegetation (Lovegrove & Wissel 1988), and consequently must excavate extensive burrow systems to locate sufficient subterranean resources; (2) the enhanced ability of colonies to protect and maintain extensive burrow systems; or (3) the need for access to sustainable resources within the colony territory, as the colony may be resident within a given area for an extended period (Jarvis & Bennett 1991; Jarvis *et al.* 1998; J.U.M. Jarvis & B.G. Lovegrove unpublished data; A.C. Spinks unpublished data).

Burrowing is an energetically costly mode of locomotion, and depending on edaphic characteristics may be 360–3400 times as expensive as above-ground travel (Vleck 1979). Digging metabolic rate may be five times that of resting metabolic rate (Lovegrove 1989). Vleck (1981) notes that natural selection should favour adaptations in subterranean foragers that optimise the benefits of foraging relative to costs. Consequently, mole-rats exhibit both physiological and behavioural adaptations to conserve energy (summarised in Lovegrove 1986; Jarvis *et al.* 1994; see also Arieli 1991). The inter-colony differences in burrow depth and diameter revealed in this investigation may also reflect the curtailment of energetic expenditure during burrow construction. The energetic cost of burrowing is

directly proportional to the mass of soil removed, and hence to burrow diameter (Vleck 1981). Accordingly, mole-rats should attempt to minimise burrow diameter and thus it is not surprising that burrow diameters correspond closely to the sizes of colony members within them. Clearly, the lower limit to burrow diameter would be dictated by the size of the digging animal. In the larger colonies most of the digging will be done by the smaller colony members. The average burrow diameter of these systems would thus be smaller than those of the pairs, where the large reproductive animals are forced to do all the digging. The cost of burrowing also increases with depth (Vleck 1981), and so mole-rat burrows should be as close to the surface as possible. However, because foraging tunnels serve to provide access to food, these burrows must correspond to those depths at which geophytes are most abundant. Consequently, the depth of the foraging burrows probably represents a compromise between energetic constraints and the depth at which most bulbs will be found. The greater overall depth of the burrow systems containing pairs may be related to the fact that, due to the inevitably larger diameter of these burrows, they would be more susceptible to collapse at shallower depths (Lovegrove and Painting 1987).

Food caching is a widespread phenomenon amongst the bathyergids (Genelly 1965; Du Toit et al. 1985; Davies & Jarvis 1986; Lovegrove & Jarvis 1986; Bennett 1988; Jarvis et al 1997; this thesis). Nevertheless, mole-rats comprise part of a suprisingly small group of mammals that store food (Sherry 1985). The location and physical structure of the food stores at Steinkopf were similar to that already documented for other bathyergids (Jarvis & Bennett 1990; Jarvis *et al.* 1998; J.U.M. Jarvis & B.G. Lovegrove unpublished data) as well as for eastern chipmunks, *Tamias striatus*, feeding on seeds and nuts (Elliott 1978), and for red squirrels, *Tamiasciurus hudsonicus*, feeding on conifer cones (Hurly & Lourie 1997). An obvious reason why mole-rats might hoard food is that they depend on these stored resources at times of the year when foraging in uneconomical or not possible. However, this seems unlikely as the food stores of *C. h. hottentotus* were relatively small, both in terms of number of geophytes stored and total biomass. They probably only served as a food source

for juveniles and for the breeding female when she had pups to feed (Jarvis *et al.* 1998), or as a temporary "energy relief" if the colony encounters a particularly resource deficient patch. Roberts (1979) and Sherry (1985) suggest that food caching may increase the association among kin, resulting in nepotism and cooperative breeding. However, the Cape mole-rat, *Georychus capensis*, one of the most compulsive food storers, is also solitary (Lovegrove & Jarvis 1986), negating the generality of this suggestion.

Optimal foraging theory assumes that animals will forage in ways that maximise their Darwinian fitness (Pyke *et al.* 1977; Hassell & Southwood 1978; Pyke 1981; 1984). The predictions of optimality may thus be confounded in social species, like the bathyergids, which forage cooperatively. However, although common mole-rats cooperate in the sense of provisioning a communal, central food store, each individual essentially forages on its own. Consequently, foraging mole-rats face exactly the same constraints and decisions faced by solitary foragers, and optimal foraging predictions should be pertinent.

Optimal foraging theory predicts that due to their behaviour of provisioning a central food store, mole-rats should act as central place foragers (CPFs; Charnov 1976; Orians & Pearson 1979). Mole-rats differ from typical aboveground CPFs in two ways; Firstly, in contrast to aboveground foragers, where energy expenditure in searching for prey is negligible compared to pursuit and handling costs (Schoener 1971; Heth *et al.* 1989), the searching costs of subterranean foragers may represent a substantial portion of the overall energy intake (Heth *et al.* 1989). Secondly mole-rats are single-prey loaders in which the mouth is also the "capture" apparatus, and this will have direct implications on the rate of provisioning of the central place (Orians & Pearson 1979). Having said this, do mole-rats exploit their food resources according to the principles of optimality? Results from this investigation suggest they do. The field data show that larger geophytes are present in *C. h. hottentotus* food stores in a greater proportion than would be expected from the frequency distribution of bulb sizes around the burrow systems, suggesting that mole-rats at Steinkopf are selectively storing the larger bulb size-classes. This notion is supported by the

laboratory data, which indicate that foraging animals selectively consume small bulbs and store large bulbs. This pattern of consumption/storage appears to be common to bathyergids in general (Davies & Jarvis 1986; Lovegrove & Jarvis 1986; Bennett 1988; Jarvis et al 1997; B.G. Lovegrove & J.U.M. Jarvis unpublished data; S.R. Telford, M. Barnett, J.U.M. Jarvis & N.C. Bennett unpublished data), and supports CPF predictions (Orians & Pearson 1979). In single-prey loaders, like mole-rats, CPF theory predicts that the load-size effect may select for the transportation of large prey to the store and consumption of small prey at the capture site, if the distance from the capture site to the nest is above a certain limit (Orians & Pearson 1979; Schoener 1979; Korpimäki *et al.* 1994). The extensive nature of the burrow systems excavated in this study, and indeed bathyergid systems in general, suggest that travelling distances back to the food store may be considerable (in excess of 60m; Lovegrove & Jarvis 1986). This is exacerbated by the high costs associated with the initial location of food. Given these costs, the rate at which energy is delivered to the central cache may be maximised by storing only larger geophytes. Foraging mole-rats must satisfy their own energetic requirements, in addition to provisioning the central food store, and hence optimal foraging efficiency might be attained by consuming a modest amount of food at the beginning of most foraging bouts, rather than filling the gut completely during a smaller number of trips (Orians & Pearson 1979). This may best be achieved by consuming small bulbs whenever they're encountered and storing the larger ones. Interestingly, the complete absence of food cache by colony T3 may reflect the low biomass, low density and small size of bulbs around the burrow system; all bulbs may have been consumed as they are encountered.

Further insight into the pattern of geophyte storage is obtained by considering the response of individual mole-rats to a food item. Foraging efficiency is optimised by maximising the ratio between the energetic yield and handling cost of food items (Pyke *et al.* 1977). In mole-rats the handling costs comprise three elements: (1) searching time *i.e.* the time taken to find a geophyte; (2) preparation time *i.e.* the time taken to prepare the

geophyte for consumption; and (3) eating time *i.e.* the time taken to consume the geophyte [(2) and (3) combined represent total consumption time]. Searching time is independent of bulb size (Heth *et al.* 1989). However, this study indicates that preparation, eating and total consumption times are dependent on both the geophyte size and animal size. Thus, for small bulbs handling costs are low, but the associated energetic returns are also poor. Storage of these smaller bulbs would simply elevate handling costs, significantly reducing the energetic yield-to-cost ratio. It makes more sense energetically to consume these bulbs when they are encountered. For large bulbs the ratio is less affected by the additional costs of storage. It is essential to remember that foraging responses will be individual-specific depending on the size and nutritional state of the mole-rat, and the size of the encountered food item.

Cryptomys h. hottentotus actively stores not only those species of geophyte that have large-sized bulbs, but for any given species it stores the subset of larger bulbs. Thus, although energetic considerations may be important, this suggests that there are other factors, unrelated to optimal foraging *per se*, that favour the preferential storage of larger bulbs. Mass sprouting of the geophytes held in the food store is unfavourable as the quality of the stored food rapidly decreases. Bathyergids curtail sprouting by nipping off the fresh shoots as soon as they appear (Dreyer 1910; De Graaff 1981; Bennett 1988; Nanni 1988; J.U.M. Jarvis & B.G. Lovegrove unpublished data). Similar bud-nipping behaviour has been observed in Israeli mole-rats (Galil 1967), and eastern chipmunks (Elliott 1978). A few large bulbs require less maintenance to prevent such sprouting in the food store than do numerous small bulbs. It has also been suggested that larger bulbs may have a longer shelf-life, better palatability, more favourable protein, fat and carbohydrate compositions, or be less susceptible to desiccation due to their favourable surface-area-to-volume ratios (Bennett 1988; B.G. Lovegrove & J.U.M Jarvis pers comm.). The contention that mole-rats selectively store bulbs on the basis of their storage qualities is supported by the fact that colonies tended to hoard a restricted subset of the species of geophytes available to them.

For example *T. revoluta* was notably absent from the food stores, probably because of its small size, fleshy structure, making it very susceptible to desiccation, and also its low mass specific energetic content (Table 3.3).

Common mole-rat colonies studied in this investigation also exhibited an alternative foraging strategy to geophyte storage, termed "*in situ* harvesting", representing a novel variation on traditional CPF. Large bulbs, with a diameter greater than the burrow diameter, and hence too large to be carried back to the food store, were left *in situ*. These were untouched or only partially consumed before the partly hollowed-out bulb and the burrow leading to the bulb were filled with soil. A similar strategy has been documented for *C. damarensis* (Lovegrove & Painting 1987; Jarvis et al 1997), and for *H. glaber* (Jarvis & Sale 1971; Brett 1986; 1991). The bulb left *in situ* can subsequently regenerate and will thus constitute a renewable resource for the mole-rats, with substantial energetic yields and minimal handling costs (Jarvis 1978; Brett 1986; 1991; Jarvis & Bennett 1990). Jarvis and Sale (1971) also suggest that *in situ* harvesting in *H. glaber* might circumvent the problems of desiccation and rotting that may occur in food stores. *In situ* harvesting may in fact improve the energetic yield of the resource, as many plant species show compensatory increases in root growth following mechanical root pruning (Andersen 1987a). Furthermore, the loss of a substantial portion of the root system may have no discernible impact on the functioning of the plant (Andersen 1987a) and consequently these geophytes might constitute a continually replenished supply of food. This may be important, as field studies show that mole-rat colonies typically remain resident within a given area for a considerable period of time (Jarvis *et al.* 1998; A.C. Spinks unpublished data).

In conclusion, common mole-rats from Steinkopf exhibit a complex foraging behaviour, which is compatible with optimal foraging theory generally, and central place foraging theory specifically. Figure 3.6 is a schematic summary of the foraging behaviour of *C. h. hottentotus* at Steinkopf, revealed in this investigation. The energetic considerations are summarised in block (a), and the foraging consequences of these considerations in

block (b). Storage costs for small bulbs and medium sized bulbs should be comparatively low, and virtually independent of size. These costs are purely related to excavation costs and the distance to the food store. As bulbs increase in size beyond this the costs will increase substantially with bulb size, due to the increased handling costs. The energetic yield is obviously directly proportional to bulb size. Thus the energetic yield-to-cost ratio increases with an increase in bulb size up to the larger of the medium sized bulbs, as storage costs are relatively constant, but energetic yield is increasing. Beyond this point, the greatly increased storage costs will diminish the yield-to-cost ratio, and hence the energetic returns. These, and other considerations, will affect the foraging response of *C. h. hottentotus* to the resources they encounter (Figure 3.6b). Small bulbs should be selectively consumed for the reasons outlined previously. Above a certain size, for all bulb size-classes, there should be an equal likelihood of bulb consumption, depending on the nutritional status of the foraging animal. There is a high probability that the very small bulb size-classes will go unnoticed by the foraging mole-rats (Ignoring in Figure 3.6b). There was evidence of this from the laboratory foraging trials. It is unlikely for any bulbs to be intentionally ignored, due to the intensive searching costs (Heth *et al.* 1989). Again the results from this study reveal that above a certain size, bulbs are more likely to be stored and this likelihood should increase with increased bulb size. However, beyond a certain size bulbs are too large to carried to the store and must be left *in situ*. This will signify a switch from geophyte storing to *in situ* harvesting. Colonies may exhibit either one or both of these foraging strategies, depending on the distribution of different bulb size-classes around the foraging burrows. This diagram obviously represents a very simplistic summary of foraging behaviour in the common mole-rat. These relationships only hold true for a given travelling distance to the food store, if travelling costs change the exact quantitative nature of the relationships will shift accordingly.

The most striking feature of the foraging behaviour of *C. h. hottentotus* is its inherent flexibility; common mole-rats, indeed mole-rats in general, exhibit a remarkable ability to

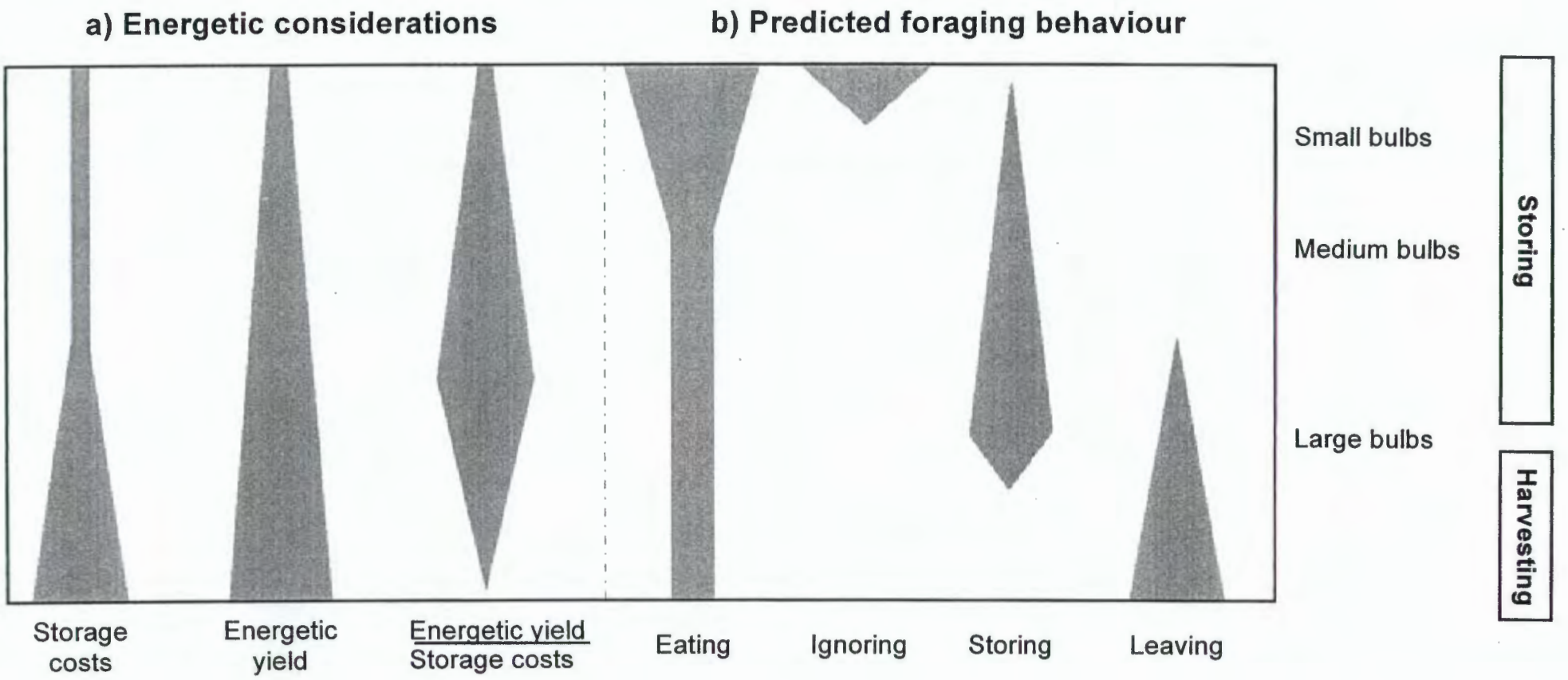

Figure 3.6: Schematic representation summarising the foraging behaviour of *C. h. hottentotus* from Steinkopf. The energetic considerations are summarised in block (a), and the foraging consequences of these considerations in block (b). For the energetic considerations, the size of the polygon indicates the relative costs/yields represented by different sized bulbs; for the foraging behaviour the polygon size reflects the frequency with which that behaviour is expect, given a particular bulb size. Ignoring occurs when bulbs are accidentally missed during foraging, and leaving occurs when bulbs are intentionally left *in situ*.

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respond to the differential foraging constraints dictated by their environment. Such flexibility is not unique to the bathyergids, predator functional responses in general tend to be very plastic (Abrams 1982; Gordon 1991), but mole-rats show an unusual refinement of this plasticity. Sociality may be one of the key components facilitating such foraging pliability in the Bathyergidae, and will be considered in some detail in the next chapter (Chapter 4).

Chapter 4

Comparative patterns of foraging in wild populations from an arid and a mesic locality

ABSTRACT

The comparative foraging patterns of wild colonies of the common mole-rat from Steinkopf and Sir Lowry's Pass was investigated to address the following questions: (1) how do resource characteristics differ between arid and mesic localities? and (2) how do any resource differences impinge on foraging by mole-rats in these environments? The biomass of resources and total available energy was comparable for both sites. Although both localities exhibited a clumped distribution of geophytes, the density of geophytes was lower, and the distance between resource clumps concomitantly greater at Steinkopf relative to Sir Lowry's Pass. Geophytes from Steinkopf were on average significantly larger than those from Sir Lowry's Pass. It is suggested that this larger size compensates for the reduced geophyte density at Steinkopf and enables colonies to meet their collective energy requirements, thus assuring long-term group stability. Inter-habitat differences in resource characteristics influenced the pattern of foraging. In response to the low geophyte density and associated longer foraging distances, burrow systems were notably longer at Steinkopf. Burrow systems at Steinkopf were linear whilst those from Sir Lowry's Pass were reticulate. These differences relate to differences in geophyte densities and the pattern of post rainfall burrow excavation in arid areas. Food storage and *in situ* harvesting are essential aspects of cooperative foraging in the common mole-rat as they minimise the risks of starvation, particularly in arid habitats. The inter-habitat differences in resource characteristics and foraging patterns revealed in this study justify the underlying premise of the Aridity Food-Distribution Hypothesis that mole-rat coloniality and cooperative foraging have evolved in response to: (1) the energetic costs of foraging; and (2) the distribution of food resources in arid environments.

INTRODUCTION

As outlined in Chapter 3, to evaluate the Aridity Food-Distribution Hypothesis (AFDH) as an explanation for the evolution of bathyergid sociality, two principal questions must be addressed: (1) how do resource characteristics differ between arid and mesic localities; and (2) how do any differences in resource characteristics impinge on the foraging

abilities of mole-rats in arid and mesic environments? Although Chapter 3 touched upon these issues, it did not deal with them in substantial detail nor adequately resolve them. Its intention was to provide a grounding by outlining the basic foraging behaviour of the common mole-rat within the context of established foraging theory. In this chapter the resource characteristics and foraging behaviour of arid and mesic populations of common mole-rats are compared and contrasted in an attempt to comprehensively address these questions. Ultimately, if it cannot be demonstrated that ecological disparities between arid and mesic environments have driven divergence in resource characteristics which impinge directly on foraging success, then it would seem spurious to suggest that constraints on foraging have promoted social elaboration within the Bathyergidae.

MATERIALS AND METHODS

The fieldwork for this investigation was conducted at Steinkopf and Sir Lowry's Pass. The floristic, edaphic and climatic features for these study localities are outlined in Chapter 2. Although the results for Steinkopf have already been presented in Chapter 3, summaries of pertinent information from Chapter 3 are included here to facilitate ready inter-site comparisons.

Mole-rats at both study sites consume a wide diversity of geophytes, at least nine species at Steinkopf and at least seven species at Sir Lowry's Pass (Table 4.1). Many of these plant species are difficult to identify unless in bloom. Moreover, the pattern of dietary generalism suggested in Chapter 3 makes it likely that the mole-rats will utilise all geophytes which they encounter. Consequently, in this chapter, all these geophytes are lumped together.

As at Steinkopf (Chapter 3), resource characteristics for Sir Lowry's Pass were assessed using 25×25 cm quadrats, randomly placed throughout the study site and dug to a depth of 20 cm. None of the geophytes consumed by mole-rats occur below this depth.

After excavation, each quadrat was sieved and any geophytes were collected. Estimates of the geophyte mass (to 0.01g), density (No.m^{-2}) and standing biomass (product of density and mean bulb mass) in the study area were obtained from the quadrat samples. The water content and energy content for the most abundant geophyte species were determined using the same techniques outlined in Chapter 3. Both water content and energy content were averaged for all geophyte species to provide mean water and mean energy contents for the study locality. Total available energy (kJ.m^{-2}) for Sir Lowry's Pass was calculated as follows:

total available energy = biomass x [1 - (mean water content/100)] x mean energy content

where biomass was measured in g.m^{-2}, water content as a percentage of wet mass and energy content in kJ.g^{-1}. As for Steinkopf (Chapter 3), a standardised Morisita Index of Dispersion was used to assess the pattern of resource distribution in the study area (Krebs 1989).

Three colonies of *C. h. hottentotus* were captured at Sir Lowry's Pass, using modified Hickman live-traps (Hickman 1979a), after which their entire burrow systems were excavated. Characteristics of these colonies (KO, 14000's, NCC) are summarised in Table 4.2. Burrow depth and diameter was measured at regular intervals. The position and depth of any food stores were recorded, and their contents collected for analysis. After excavation, each system was mapped on graph paper using a grid system. In the laboratory, the weight (to 0.01g), the diameter[1] (to 0.01mm) and species were determined for all geophytes collected from the food stores.

For one colony, colony NCC from Sir Lowry's Pass, the chi-square goodness-of-fit test (Zar 1984) was used to determine whether the resident mole-rats selectively stored certain sizes of geophyte. Expected frequencies were obtained by dividing all the geophytes

[1] Bulb diameter is significantly correlated with bulb mass (Chapter 3), and consequently only the data for bulb mass are presented in this chapter.

(n = 1851) gathered from the quadrats around the study site into four size classes, each containing a similar number of geophytes (class 1 = 0.01–0.06g; class 2 = 0.07–0.13g; class 3 = 0.14–0.26g; class 4 = >0.26g). Expected frequencies were corrected relative to the number of bulbs in the food store using the formula;

$$expt_{fs} = (obs_{rs} \times total\ bulbs_{fs})/Total\ bulbs_{rs}$$

where expt = expected frequency; obs = observed frequency; $_{fs}$ = food store; $_{rs}$ = random samples. Observed frequencies were calculated from the food stores by determining the total number of geophytes within each size class.

Inter-site differences, between Steinkopf and Sir Lowry's Pass, in the mean geophyte mass, geophyte density and mean mass of stored geophytes were analysed statistically using the Mann Whitney U-test (Zar 1984). Regression analysis was used to examine the relationship between colony size and burrow system length and between the mean body mass of mole-rats within a colony and the mean diameter of their burrow system (Zar 1984).

RESULTS

Resource characteristics

The comparative resource characteristics for the two study sites are summarised in Table 4.1. Mean geophyte mass was significantly greater at Steinkopf than at Sir Lowry's Pass (Mann-Whitney U-test, $Z = -21.35$, $n = 2320$, $p < 0.00001$), bulbs from Steinkopf being 22 times heavier than those from Sir Lowry's Pass (Table 4.1). Inter-site differences in the range of masses of geophytes exhibited a similar pattern to mean geophyte mass, with bulbs at Sir Lowry's Pass only reaching a maximum of 5.72 g, whilst those from Steinkopf peaked at 129.2 g (Table 4.1).

Table 4.1: The general resource characteristics for the two study localities at Sir Lowry's Pass and Steinkopf. The data for Steinkopf are summarised from Chapter 3 (Table 3.3).

Variable	Sir Lowry's Pass	Steinkopf
Number of geophyte species‡1	7	9
Mean mass (g)	0.20 ± 0.01[a]	4.38 ± 0.71[b]
Range (g)	0.01–5.72	0.02–129.17
Mean water content (%)‡2	47.54 ± 5.57	71.33 ± 1.49
Mean energy content ($kJ.g^{-1}$)‡2	17.29 ± 0.44	14.33 ± 0.31
Density ($No.m^{-2}$)	1424.00 ± 232.13[a]	75.84 ± 8.14[b]
Biomass ($g.m^{-2}$)	284.80‡3	329.20 ± 57.91
Total available energy ($kJ.m^{-2}$)‡4	2583.23	1597.81
Morisita index of dispersion	0.51	0.50

values presented as means ± SE; ‡1 this is a conservative estimate of the diversity of food plants consumed by mole-rats from the different sites; ‡2 average for all species; ‡3 biomass calculated as the product of mean bulb mass and bulb density; ‡4 total available energy calculated as the product of biomass, mean water content and mean energy content; a, b - significantly different groups, Mann-Whitney U-test, $p < 0.00001$ (only inter-site differences in mean geophyte mass and geophyte density were tested statistically).

The density of geophytes differed significantly between the study localities (Table 4.1; Mann-Whitney U-test, $Z = -7.3$, $n = 125$, $p < 0.00001$). Geophyte densities at Sir Lowry's Pass were more than an order of magnitude greater than those at Steinkopf (Table 4.1). Despite this, available geophyte biomass at Steinkopf was marginally higher than at Sir Lowry's Pass (Table 4.1). The standardised Morisita Indices of Dispersion were almost identical for the study sites (Table 4.1), indicating that the geophytes at both localities exhibit a significantly clumped pattern of dispersion (95% confidence limits for the standardised Morisita Index at -0.5 and +0.5).

On average water constituted a substantially greater proportion of the geophytes from Steinkopf than those from the mesic locality (Table 4.1). The mean energy content for geophytes from the mesic site was marginally higher than that for the arid site (Table 4.1).

Total available energy differed noticeably between the sites with levels at Sir Lowry's Pass being one and a half times those at Steinkopf (Table 4.1).

Burrow excavations

Excavated burrow systems had contained colonies ranging in size from a breeding pair to eight animals (Table 4.2). The colony of three included a breeding pair and a juvenile animal (too young to sex), whilst the larger colony included a reproductive pair plus several generations of offspring. Plans of all the burrow systems excavated at Sir Lowry's Pass and Steinkopf are presented in Figures 4.1 and 4.2, and show their extent and pattern. In general burrow systems at Sir Lowry's Pass exhibited a similar structure to that previously outlined for Steinkopf (see Chapter 3) with deep primary burrows (29 - 34 cm; Table 4.2) branching to give rise to secondary burrows, which in turn ramified into shallow foraging burrows (13 - 15 cm; Table 4.2). Overall burrow system length at the mesic site ranged from 50 to 200 m (Table 4.2) and in general burrow systems at Steinkopf were longer (150-510 m; Table 4.2) than those at Sir Lowry's Pass. There was no correlation between burrow length and colony size in either the mesic ($r_{(2)} = 0.92$, $p = 0.26$) or arid localities ($r_{(3)} = 0.65$, $p = 0.35$). Burrow systems at Sir Lowry's Pass typically exhibited a higher biomass of mole-rats per metre of burrow than those at Steinkopf, values ranging from 1.4 to 3.4 $g.m^{-1}$ at Sir Lowry's Pass and between 0.5 and 1.5 $g.m^{-1}$ at Steinkopf (Table 4.2).

Although mean burrow depths were comparable for Sir Lowry's Pass and Steinkopf, the "shallow" foraging burrows at Sir Lowry's Pass occurred notably deeper than those at Steinkopf (Table 4.2). Mean burrow diameter was similar for the two sites, and varied little (Table 4.2). The only exceptions were E1 and R1 at Steinkopf; E1 exhibiting a larger average burrow diameter, and R1 a markedly smaller diameter (Table 4.2). For all seven burrow systems combined, the mean mass of mole-rats in each colony was positively correlated with the mean burrow diameter ($r_{(6)} = 0.77$; $p = 0.04$).

Table 4.2: Colony and burrow system characteristics for three C. *h. hottentotus* colonies whose burrow systems were excavated at Sir Lowry's Pass.

Variable		Sir Lowry's Pass colonies			Steinkopf colonies*			
		KO	14000's	NCC	B3	E1	R1	T3
Colony information	Colony size	2	3	8	2	2	8	9
	Mean mass (g)	84	62 ± 26	64 ± 14	75	78	37 ± 4	50 ± 6
	Mass range (g)	69 & 99	20–108	20–132	55 & 94	72 & 83	29-60	32-74
	Total mass (g)	168	187	510	149	155	301	452
Burrow system	Length (m)	50	130	200	290	150	510	300
	H/B Ratio‡	1.2	5.4 (1.2)†	1.5	2.5	2.6	2.8	2.1
	Biomass per metre of burrow ($g.m^{-1}$)	3.4	1.4	2.6	0.5	1.0	0.6	1.5
Burrow depth‡4	Mean (cm)	18.7 ± 0.5	18.8 ± 0.4	21.2 ± 0.6	17.9 ± 0.3	19.3 ± 0.8	13.1 ± 0.4	13.6 ± 0.3
	Range (cm)	15–29	14–28	13–34	11.1-22.5	11.5-26.5	6.2-20.6	8-21
Burrow diameter	Mean (cm)	5.6 ± 0.1	5.9 ± 0.1	5.5 ± 0.1	5.8 ± 0.1	6.4 ± 0.1	4.8 ± 0.1	5.3 ± 0.1
	Range (cm)	4.2–7	4.9–8.5	3.7–7.5	4.2-7.9	5.1-8.7	2.9-6.2	3.6-7

values presented as means ± SE; ‡ H/B Ratio - the ratio of burrow system height to burrow system breadth; † the figure in brackets is the H/B ratio for the region of burrow outside a dense patch of kikuyu grass (see Figure 4.1b); * data summarised from Chapter 3.

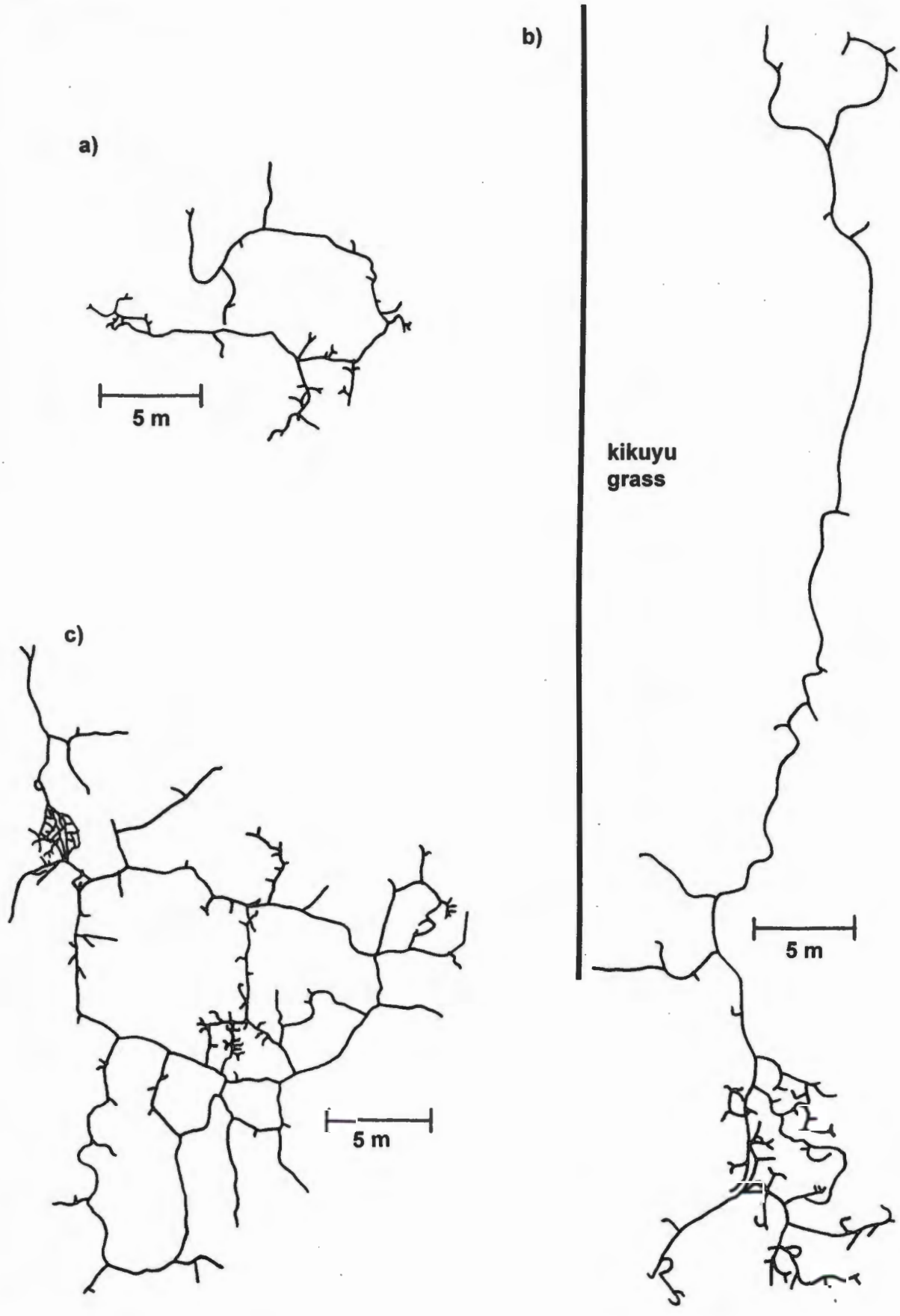

Figure 4.1: Plan diagrams of the three *C. h. hottentotus* burrow systems excavated at Sir Lowry's Pass to indicate the general foraging pattern; (a) KO, (b) 14000's and (c) NCC.

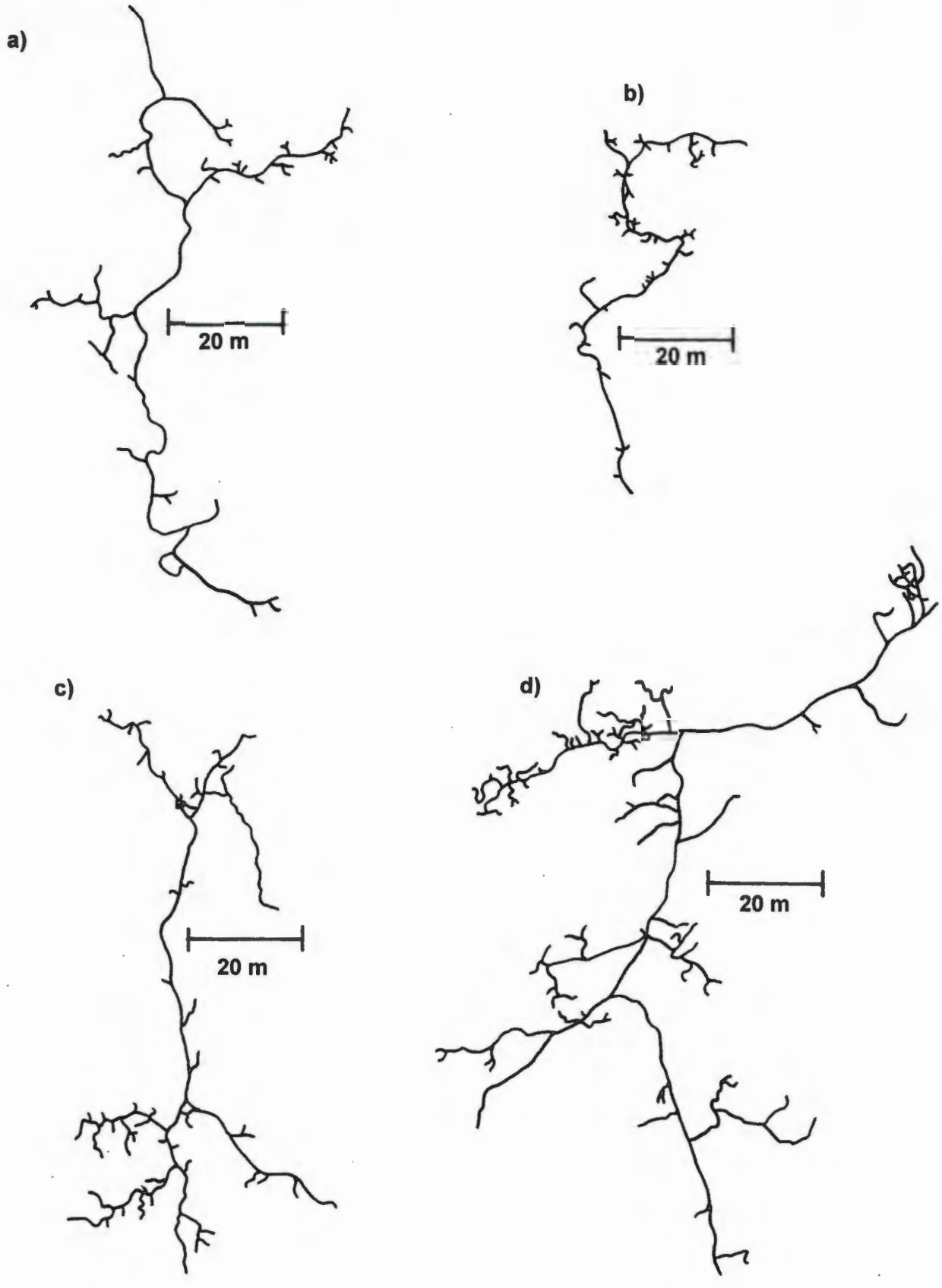

Figure 4.2: Plan diagrams of the four *C. h. hottentotus* burrow systems excavated at Steinkopf to indicate the general foraging pattern; (a) B3, (b) E1, (c) T3 and (d) R1.

As elucidated by the burrow excavations, inter-site differences in the basic pattern of burrowing existed between the arid and mesic localities (Figures 4.1 and 4.2). At Steinkopf burrow systems tended to consist of a linear main axis, with distinct regions of lateral burrow ramification (Figure 4.2). In contrast burrow systems at Sir Lowry's Pass tended to be more reticulate and interwoven with burrows diverging piecemeal throughout the burrow system area (Figure 4.1). Moreover, no clear patches of burrow ramification were evident as the entire area encompassed by the burrow system appeared to have been extensively exploited by the burrowing mole-rats. The H/B ratio [ratio of the longest axis of the burrow system *i.e.* burrow "height" (H) to burrow system breadth (B); Table 4.2] represents an attempt to quantify these inter-site differences in burrowing pattern. In calculating the H/B ratio a rectangular polygon was drawn around each burrow system diagram and the length of a perpendicular line drawn along the main axis of the burrow system, and bisecting the rectangle, was used as the burrow system "height" (H). Burrow system breadth (B) was measured as the maximum distance the burrow system deviated laterally from this perpendicular line. The H/B ratios for the burrow systems excavated at Steinkopf were generally greater than the H/B ratios for those excavated at Sir Lowry's Pass (Table 4.2), suggesting a greater linear component to foraging patterns in the arid locality. The only exception was burrow system 14 000's from Sir Lowry's Pass, which exhibited the greatest H/B ratio *i.e.* 5.4 (Table 4.2). However, as evident from Figure 4.1b, this burrow system passed into an area of dense kikuyu grass, *Pennisetum clandestinum*, in which the burrowing pattern became extremely linear. Outside this area the burrow pattern followed the characteristic reticulating mesic pattern. The H/B ratio for only the area outside the kikuyu grass was 1.2, within the typical mesic range revealed in this study (Table 4.2).

Analysis of food stores

Food stores were discovered in the excavated burrow system of colony NCC at Sir Lowry's Pass. In addition two food stores, CT and SG (Table 4.3), were located at Sir Lowry's Pass by chance, without any burrow excavation. The burrow system of NCC contained several foods stores (Table 4.3), all of which were similar, in both location and structure, to those found at Steinkopf (see Chapter 3). Each food store was situated close to the nest, was tightly packed into a sand-filled chamber and contained several geophyte species (Table 4.3). The depth at which food stores occurred varied considerably, ranging from 19 to 52 cm. Food store depths were comparable at Steinkopf (Table 4.3), and cache position is probably correlated with the depth and location of the colony nest(s).

The total biomass of geophytes stored by each colony differed substantially (Table 4.3). These inter-colony differences were due to divergence in both the total number of bulbs stored and their average mass (Table 4.3). The food stores of colony NCC (1435 bulbs) contained 15 and 35 times more bulbs than the stores collected from colonies CT and SG respectively. The burrow systems of CT and SG were, however, not excavated and it seems probable that additional food stores may have been present within them. Consequently, these small, single stores are unlikely to represent the entire food cache for these colonies. The size of the stored geophytes differed markedly between the three systems (Table 4.3), with food stores from colony CT containing bulbs of twice the average mass of those stored by colonies NCC and SG. Differences in the mean mass of bulbs in the food stores were related to differences in the dominant species of bulbs stored. The food stores of colonies NCC and SG were composed largely of *Oxalis spp.* and *Romulea sp.*, whilst that of colony CT contained mostly *Homeria sp.* bulbs (Table 4.3). *Oxalis* and *Romulea* are both relatively small geophytes with an average mass of less than 0.5 g, whilst *Homeria* bulbs are much larger, weighing in excess of 1g.

Table 4.3: Analysis of food stores collected from three *C. h. hottentotus* colonies at Sir Lowry's Pass.

Variable	Sir Lowry's Pass colonies			Steinkopf colonies*		
	NCC	CT	SG	B3	R1	N1
No. of food stores	6	1	1	2	2	1
Food store depth (cm)	19, 22, 50, 52‡	-	-	46 & 50	15 & 18	-
Total bulbs stored	1435	94	41	283	168	156
Total mass (g)	721.7	78.28	14.74	1200.02	294.66	778.77
Mean mass (g)	0.50 ± 0.01	0.90 ± 0.08	0.40 ± 0.02	4.24 ± 0.19	1.78 ± 0.18	5.09 ± 0.29
Range (g)	0.01–4.38	0.10–4.40	0.18–0.65	0.55-24.78	0.17-19.32	0.34-21.46
Number of species	4	3	1	5	8	2
Dominant species†	OX (≈ 80%)	HM (92%)	RM (100%)	OS (> 90%)	LK (> 60%)	OS (> 90%)

values presented as means ± SE; ‡ depths were not determined for two of the food stores; † figures in parenthesis indicate dominant species abundance as a percentage of the total number of bulbs stored; * data summarised from Chapter 3; OX - *Oxalis spp.*; HM - *Homeria sp.*; RM - *Romulea sp.*; OS - *Ornithogalum secundum*; LK - *Lachenalia klinghardtiana*.

These storage patterns at the mesic site differed notably from those at the arid site (Table 4.3). In general, considerably fewer bulbs were stored by the mole-rats at Steinkopf. However, the significantly greater size of the stored geophytes at Steinkopf (Table 4.3; Mann-Whitney U-test, $Z = -33.01$, $n = 2142$, $p < 0.00001$) meant that the total biomass of stored food was substantially greater here than at the mesic site. For example the largest cache at Steinkopf was almost twice the biomass of the largest cache at Sir Lowry's Pass. The diversity of stored geophytes was similar between the two sites, and at both sites food caches were dominated by single species (Table 4.3).

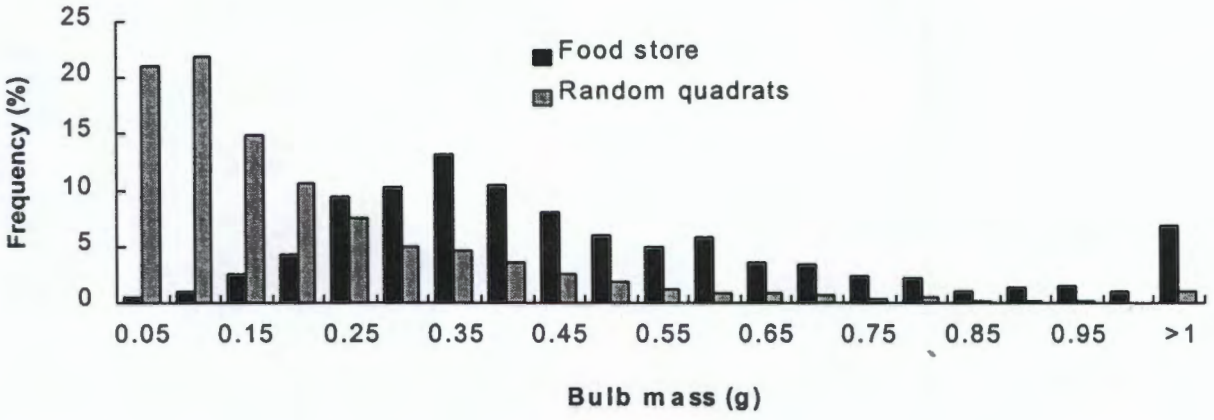

Figure 4.3: Comparison of size-frequency distributions of geophytes collect from a *C. h. hottentotus* food store and those collected in random quadrates. The food store was collected during the excavation of colony NCC at Sir Lowry's Pass.

For colony NCC the size frequency of geophytes in the food store differed significantly from random quadrats around the study site (Figure 4.3; chi-square goodness-of-fit test, $\chi^2_{(3)} = 2674.41$; $p < 0.00001$). The food stores contained fewer geophytes in the smaller size categories and more geophytes in the larger size categories, suggesting that the colony members were selectively storing the larger bulb size-classes. As noted in Chapter 3, a similar pattern was prevalent at Steinkopf (Table 3.5 & Figure 3.3).

DISCUSSION

According to the AFDH the relative foraging risks associated with habitat-related differences in resource characteristics are a principle factor determining social evolution in the bathyergids, group-living representing an optimum long term solution when these risks are high (see Chapter 1). This then raises the question; what are the inter-habitat differences, if any, in resource characteristics? Several workers have suggested that, although arid and mesic environments exhibit similar mean amounts of available energy (Bennett 1988; Jarvis et al 1994), food in arid areas tends to be larger and of poorer nutritional quality than in mesic areas, and individual food items are often widely and patchily distributed (Jarvis & Sale 1971; Jarvis 1978; Brett 1986; 1991; Lovegrove & Painting 1987; Lovegrove & Knight-Eloff 1988; Bennett 1988; Lovegrove & Wissel 1988; Jarvis & Bennett 1990; 1991; Lovegrove 1991; Jarvis *et al.* 1994; Bennett & Jarvis 1995). The results from this study generally support these predictions:

(1) Biomass and total available energy: The total available biomass was remarkably similar between the two study sites. Moreover, although total available energy levels where notably higher at Sir Lowry's Pass than Steinkopf, these differences are unlikely to be important. In absolute terms energy was extremely abundant at both sites, and total available energy levels were greater than that recorded in any other area occupied by mole-rats (Table 3.8). Consequently, energy would not appear to be a limiting resource for mole-rats in either habitat. These findings support Jarvis *et al.* (1994) and Bennett's (1988) contention that it is the pattern of resource dispersion and density, and not the total available energy, which differs between mesic and arid habitats, and which has ultimately advanced bathyergid coloniality. Du Plessis (1989; 1992) drew analogous conclusions for red-billed woodhoopoe, *Phoeniculus purpureus*, group-living and demonstrated that the dispersion of critical resources (in this case roosting sites) was the crucial determinant of group size.

(2) Geophyte density and dispersion patterns: Geophyte density was significantly and considerably greater at Sir Lowry's Pass than at Steinkopf. Lovegrove and Wissel (1988) suggest that geophyte density affects foraging efficiency via its impact on the nearest-neighbour distance of geophytes. With a decrease in geophyte density the average distance between adjacent food items will increase and foraging animals will be forced to dig for longer distances to find sufficient food. This will be exacerbated by the energetic constraints on foraging in arid environments and by the apparent lack of cues use in the location of food resources by foraging mole-rats (see Chapters 1 & 3). Lovegrove and Wissel (1988) and Lovegrove (1991) showed mathematically that coloniality and group foraging substantially reduced the risks of poor performance whilst foraging for widely dispersed geophytes. Moreover, the energetic costs are shared by the group members (Jarvis & Bennett 1991; Lovegrove 1991). Consequently, the low resource densities at Steinkopf are likely to impose considerable constraints on foraging, and constitute a powerful selective pressure for the evolution of group-living and cooperative foraging in the common mole-rats occurring there.

Geophytes exhibited a significantly clumped pattern of dispersion at both study sites. This inter-habitat congruence may seem surprising given that previous workers have suggested that resources will only tend to be patchily distributed in arid areas (see above). However, it is my contention that, although the exact scale may vary spatio-temporally, plant communities occurring in most environments (arid or mesic) should exhibit a patchy distribution. This follows from fundamental biological principles which predict clumping as a simple consequence of dispersal patterns, resource acquisition and competition (Werger 1986; see Chapter 2). In support of this notion, resources have been shown to be clumped in almost all the sites, inhabited by mole-rats which have been studied to date, be they arid or mesic (Table 3.8). This does not, however, mean that clumping is unimportant. Although both arid and mesic habitats exhibit a patchy resource distribution, the exact scale of clumping may differ. The lower geophyte densities at Steinkopf and indeed in arid areas in

general, may exaggerate clumping and result in greater mean inter-patch distances and lower resource densities within any given patch. This will have significant implications for foraging efficiency, constraining individual foraging success (Jarvis & Bennett 1991; Jarvis *et al.* 1994; 1998).

(3) Geophyte size and nutritional quality: Geophytes were on average significantly larger at Steinkopf than at Sir Lowry's Pass. In addition, the maximum size attained by geophytes at the arid site was substantially greater than at the mesic site. Mean and maximum bulb sizes at Steinkopf may in fact represent underestimates, as one rather dispersed food plant which was not present in any of the quadrats, *Ornithogalum xanthochlorum*, reaches a maximum weight of over 300 g (pers. obs.) [2]. Although the mean energy content of geophytes from Steinkopf was marginally less than those from Sir Lowry's Pass, the total energy content per geophyte at Steinkopf will be greater due to their larger average size. Alexander (cited in Gamlin 1987) suggested that one of the most important considerations in the evolution of insect eusociality was food concentration *i.e.* for sociality to be stable food must be sufficiently concentrated to support a group of individuals within a limited space. Similarly, Jarvis and Bennett (1991; 1993) note that the benefits accrued from cooperative foraging in arid environments will only pay off if sufficient food is located to satisfy the requirements of all colony members. Consequently, the size of individual food resources is of crucial importance. For foraging colonies to satisfy their energetic requirements, and hence for group-living to represent an Evolutionarily Stable Strategy (*sensu* Maynard-Smith 1972), the decrease in geophyte density in arid areas must be compensated for by an associated increase in resource item size. Thus, the larger average size of geophytes at Steinkopf will ensure that cooperatively foraging colonies of common mole-rats are likely to meet their collective energetic requirements, ensuring long term group stability. Related to these

[2] Bennett (pers com.) suggests that the larger size of bulbs at Steinkopf may represent an adaptation to achieve a more favourably surface area:volume ratio, thereby reducing the risks of desiccation.

energetic constraints, social bathyergids in general exhibit several adaptations to minimise individual, and hence colony, energy expenditure. These include reduced body-size, mass-specific metabolic rates and thermoregulatory costs, together with relatively low rates of body growth and colony recruitment (Jarvis 1978; Lovegrove & Wissel 1988; Jarvis & Bennett 1991).

Heterocephalus glaber at Mtito Andei, Kenya and *C. damarensis* at Twee Rivieren in the Kalahari Gemsbok National Park, South Africa, inhabit areas where energy resources may be concentrated into large tuberous geophytes (Bennett 1988; Brett 1986; 1991; Lovegrove & Knight-Eloff 1988; Jarvis & Bennett 1990; Jarvis *et al.* 1998). These tubers, which may weigh in excess of 30 kg (Brett 1986; 1991), are only partially eaten by the mole-rats who then fill the partly hollowed-out tuber, and the burrow leading to it, with soil. The tuber will then regenerate and represents a substantial energy cache, not only sufficient food to satisfy the immediate individual and colony requirements but enough to sustain the colony over an extended period of time. Although the largest geophytes at Steinkopf were markedly smaller than the tubers consumed by either *H. glaber* or *C. damarensis*, several common mole-rat colonies occurring in this arid site nevertheless exhibited a similar *in situ* harvesting behaviour (see Chapter 3). The *in situ* harvested geophyte's were too large to be carried to the central food store (see Chapter 3) and were consequently left, and consumed, *in situ*. The combined reserves from these geophytes may be considerable and those around a single burrow system at Steinkopf (colony B3) represented an energetic hoard in excess of 20 000 kJ, sufficient to satisfy the colony's requirements for more than two months. It seems probable that sociality may enhance the defence of these hoards against kleptoparasitic neighbours.

Jarvis and Bennett (1991) suggest that food in arid areas tends to be more fibrous and less digestible than in mesic areas. However, Bennett and Jarvis (1995) demonstrated that, for a range of geophytes from both mesic and arid areas, fibre contents were low and energy contents and coefficients of digestibility were high. The only exception was the

gemsbok cucumber, *Acanthosicyos naudinianus*, consumed by *C. damarensis* (Lovegrove & Painting 1987; Lovegrove & Knight-Eloff 1988; Jarvis *et al.* 1998), which exhibited a high fibre content and low digestibility co-efficient (Bennett & Jarvis 1995). Bennett and Jarvis (1995) note that the storage organs of geophytes are an ideal food resource, because they: (1) contain considerable quantities of nutrients stored in a relatively small volume compared to other plant growth forms; (2) are readily available for much of the year; (3) are chemically and biologically stable for much of the year; and (4) do not readily deteriorate during their dormant period. Moreover, mole-rats exhibit several dietary, anatomical and physiological modifications to optimise the efficiency of nutrient extraction from these food resources. These include: (1) coefficients of digestibility, whilst feeding on geophytes, paralleling those of granivorous rodents (Bennett & Jarvis 1995); (2) highly efficient caecal fermentation (Buffenstein & Yahav 1994), which includes having the largest caeca amongst southern African rodents [*e.g.* in *C. h. hottentotus* the caecum is 29% of hind-gut length (Perrin & Curtis 1980)]; (3) autocoprophagy enabling the utilisation of energy released by microbial action (Jarvis *et al.* 1998); and (4) an ability to consume, with apparent impunity, a range of geophyte species, many of which are toxic to livestock (Watt & Breyer-Brandwijk 1968; Kellerman *et al.* 1990) and many of which are surrounded by protective tunics and spinous coverings (Lovegrove & Jarvis 1986; Bennett 1988). Consequently, the changes in the nutritional quality of resources associated with changes in aridity are unlikely to be significant factors in bathyergid sociality. Rather, the high costs of searching for and locating these resources (Heth *et al.* 1989), related to inter-habitat differences in their abundance, is likely to be pivotal to the evolution of coloniality.

The answer to the second question raised in the introduction to this chapter lies in looking at the different patterns of burrow construction evident at the two study sites. Although burrow system excavations represent snapshots, revealing a single, static geometry of what is essentially a continuously dynamic system, the geometries of the burrow

systems excavated in this study seem to reflect sufficient differences to warrant speculation on the adaptive significance of inter-habitat divergence in the pattern of foraging.

It is well established that food resources play a central role in determining the pattern of burrowing by subterranean foragers (Andersen 1982; 1987b; 1988; Reichman *et al.* 1982; Sparks & Andersen 1988; Heth 1989; Davis & Kalisz 1992). For example in the fossorial pocket gopher, *Thomomys bottae*, the placement and geometry of individual burrow systems may directly influence the efficiency of resource exploitation (Reichman *et al.* 1982). Proponents of optimal foraging theory presume that the movements of foraging animals are a consequence of natural selection favouring phenotypes which display behavioural traits that minimise the costs relative to the benefits of their movements (Pyke 1984). Covich (1976) and Andersen (1988) note that because the cost of excavating burrows is extremely high (Vleck 1979) the pattern of burrowing should optimise access to food resources. Therefore, subterranean foragers might be expect to modify their exact burrow architecture in different habitats, coincident with any resource idiosyncrasies. The differences between resource characteristics in Steinkopf and Sir Lowry's Pass had a marked effect on the foraging patterns of the common mole-rats occurring there. Burrow systems were notably longer at Steinkopf than Sir Lowry's Pass, and the average biomass of mole-rats per metre of burrow was concomitantly smaller (0.9 $g.m^{-1}$ versus 2.5 $g.m^{-1}$). Jarvis and Bennett (1990; 1991) and Jarvis *et al.* (1994) note that burrow length appears to be correlated with the availability of food, and they suggest that with increasing aridity mole-rats must dig longer burrow systems to gain access to sufficient quantities of the widely dispersed and clumped food in these arid habitats. The pocket gopher also exhibits longer burrow system lengths in areas of depressed food availability (Reichman *et al.* 1982). Consequently, common mole-rats foraging at Steinkopf have apparently been compelled to increase the length of their burrow systems, relative to those in mesic areas, in response to the low geophyte density and associated longer foraging distances. Obviously, by foraging cooperatively, individual

burrowing costs within these larger burrow systems can be substantially curtailed (Lovegrove & Wissel 1988; Jarvis & Bennett 1991).

In addition to inter-habitat differences in burrow system length, the architecture of burrow systems also differed notably between Steinkopf and Sir Lowry's Pass. As evident from the burrow diagrams and H/B ratios, burrow systems in the arid site were distinctly linear in construction, whilst those from Sir Lowry's Pass were more reticulate. As outlined in Chapter 3, although bathyergids forage blindly, the pattern of burrowing represents an example of area restricted searching (Brett 1991). Mole-rats typically dig long, straight relatively unbranched burrows until they encounter a geophyte or geophyte clump, whereupon turning or lateral ramification may occur, thereby optimising resource exploitation. Andersen (1988) suggests that linear foraging patterns with lateral branching are consistent with the search path predicted for a "harvesting animal" (Pyke 1978) from optimal foraging theory, and serve to minimise burrowing costs. At Steinkopf the long linear burrow sections reflect the low geophyte densities and concomitant large distances between individual geophytes or geophyte clumps. Areas of burrow ramification indicate where patches have been thoroughly excavated. At Sir Lowry's Pass geophytes (individual or patches) are encountered frequently due to their high density, and reticulate foraging patterns result. The foraging pattern of colony 14 000's from the mesic site provides support for these contentions. The burrow system of colony 14 000's contained an atypically linear section (Figure 4.1b). This section of the burrow system entered a dense patch of kikuyu grass, which competitively excluded any other plant species, including geophytes, from the area. Consequently, resource availability was severely depressed in this kikuyu patch, and the linear foraging pattern and lack of branching of the burrow system in this area probably reflects the low rate of resource encounters, mimicking the pattern for the arid site.

To circumvent the exorbitant energetic costs of burrowing (Vleck 1979; 1981; Lovegrove 1989), mole-rats concentrate foraging in post-rainfall periods, when the soils are more readily worked (Brett 1986; 1991; Lovegrove & Painting 1987; Jarvis *et al.* 1998; see

Chapter 3). However, the low and sporadic rainfall characteristic of arid areas like Steinkopf (see Chapter 2) will significantly curtail favourable digging spells. During these favourable periods the mole-rats will be compelled to ensure access to sufficient food to last them through the subsequent dry times. Although most bathyergids hoard food, these stores typically represent small energy caches (see Chapter 3) and, unless continually replenished, they will be insufficient to last through the dry periods. For example the largest food store at Steinkopf (colony B3, Table 4.3) only represents sufficient food to last the colony a maximum of 6 - 10 days[3]. However, the basic pattern of foraging itself may facilitate ready access to resources, even during dry periods, negating the need for capacious food stores. Field observations of *C. h. hottentotus* at Steinkopf (pers. obs.), and *C. damarensis* in Namibia (Jarvis *et al.* 1998), reveal that following a suitable rainfall event, intense burrowing occurs, the entire colony work force being mobilised to dig long relatively unbranched tunnels. During this initial phase the mole-rats focus on expanding their burrow system and hence their foraging territory, and little harvesting of food items occurs. As the soil dries out, these extensive exploratory tunnels are revisited by the mole-rats and the geophytes harvested by digging lateral forays from the main tunnel. When the soil is very dry and no mounds can be thrown onto the surface, the mole-rats resort to shunting the excavated soil into unused portions of the burrow system, thereby minimising the burrowing costs. Thus, by digging long exploratory tunnels when burrowing conditions are optimal, and minor lateral excursions when the soils are dry, not only do mole-rat colonies in arid areas minimise burrowing costs, but they also ensure long-term access to food resources. The result of this foraging pattern in arid areas will be the linear burrow systems described for *C. h. hottentotus* from Steinkopf. In mesic areas like Sir Lowry's Pass burrowing conditions are optimal for a substantial part of the year (see Chapter 2) and animals can simply forage from one resource encounter to the next, producing the characteristic reticulate burrow system structure. It is important to

[3] Based on the energy requirements for inactive mole-rats *i.e.* 0.75 - 1.41 $kJ.g^{-1}$ body mass per day (Bennett & Jarvis 1995). Obviously the energetic demands of active animals will be substantially higher [five times (Lovegrove 1989)], and the food store exhausted more rapidly.

appreciate that in arid areas a large work force is essential to facilitate a rapid response to suitable rains and to maximise the expansion and defence of the colony territory and associated access to food resources. Consequently, there will be potent selection for the evolution of group-living and cooperative foraging in arid environments.

According to Clark and Mangel (1986) a common misconception in investigations of group foraging is based on the assumption that individual fitness should be optimised by group behaviour. They suggest that this assumption overlooks the fact that intra-group competition may be as important as cooperation in determining group behaviour. Indeed, selfish behaviours are commonplace within all social mole-rat colonies (*e.g.* Schieffelin & Sherman 1995; O'Riain 1996), yet in trying to understand the evolution of bathyergid coloniality and group foraging it is an understanding of the cooperative behaviours which may facilitate critical insight. Here cooperation refers to situations where the behaviour of one animal enhances resource availability or access for another individual (Holekamp & Smale 1995). For the benefits of cooperative foraging envisaged by the AFDH to accrue, the intra-colony exchange of located resources is essential. Indeed Lovegrove and Wissel (1988) remark that for cooperative foraging to operate successfully, the supposition that individuals share their resource acquisitions with the colony must hold. Here the food caches (both food stores and farmed geophytes) may be of crucial importance. After satiating themselves, foraging animals carry all portable surplus food items to the central food store or, if they are too large, leave them *in situ*. Consequently, any unsuccessful foragers are guaranteed access to the colony's food cache and are assured of meeting their daily energy requirements. Although at any one time the food hoards may not be considerable, they are continually replenished ensuring a continued supply of food to the colony members. Therefore, albeit that individuals do not directly sustain each other[4], the combined efforts of foraging and provisioning a central store dramatically reduces the risks

[4] Judd and Sherman (1995) suggest that naked mole-rats follow each other's odour trails to food, and consequently individuals can recruit colony mates to food sources. This is an intriguing example of bathyergid cooperation.

of starvation in arid environments where resources are widely and patchily dispersed (Lovegrove & Wissel 1988). Several factors mitigate against significant individual fitness costs related to food-sharing: (1) food storage is subject to the selfish precedent of satiation (see Chapter 3); (2) stored food can later be accessed by the storer; (3) the inclusive fitness benefits of provisioning kin (Hamilton 1964a; 1964b), since colonies are family groups; and (4) the potential benefits of reciprocal altruism (Axelrod & Hamilton 1981). Moreover, individual foraging costs are minimised as individuals apparently forage in accordance with the predictions of optimal foraging theory (see Chapter 3). For example at both sites mole-rats selectively consumed small bulbs and stored large bulbs, coincident with central place foraging predictions (Orians & Pearson 1979).

In conclusion, the study sites examined in this thesis exhibit distinct differences in their resource characteristics. Results from this investigation reveal that, together with the climatic restrictions on burrowing in arid areas (see Chapter 2), resource characteristics may have a marked impact on the pattern of foraging, imposing foraging constraints on the mole-rats occurring there and ultimately shaping their foraging responses. This justifies the underlying premise of the AFDH that mole-rat coloniality and cooperative foraging have evolved in response to: (1) the energetic costs of foraging; and (2) the distribution of critical resources in arid environments (see Chapter 1).

Chapter 5

Habitat constraints and sociality in the common mole-rat: a foraging simulation model.

ABSTRACT

The energetics of the foraging behaviour of the common mole-rat were investigated using a simulation model based on empirical data collected from Steinkopf and Sir Lowry's Pass. The model is used to explore to what extent differences in resource characteristics and rainfall patterns between the arid and mesic study sites affect foraging success and hence to what extent the Aridity Food-Distribution Hypothesis (AFDH) explains the evolution of sociality within the common mole-rat. Model results suggest that the energetic rewards gained from foraging at the mesic locality, characterised by a relatively even spread of food resources, are almost three times greater than that of an animal foraging at the arid locality, where resources are more patchy. Absolute food availability was less important in determining mole-rat foraging success than the spatial pattern of food distribution. The food distribution pattern was also found to influence burrow system architecture, with systems changing from a long and dominantly linear pattern to a shorter, more reticulated pattern as resources become more dense and evenly distributed. Furthermore, model results indicated that there was no simple energetic benefit to be gained from increasing colony size; rather, a group existence may be enforced in an arid environment because of the necessity to reduce the risk of unproductive foraging. The model was most sensitive to parameters which affect the speed and distance that a mole-rat burrows per day to increase its access to food resources. In conclusion the results indicate that the spatial dispersion of food resources and sporadic rainfall in arid areas interact to elevate foraging costs and reduce energetic returns, ultimately constraining foraging efficiency in the common mole-rat. The model suggests that increased group size and cooperative foraging dilutes foraging costs and reduces the risks of unproductive foraging, and as such represents an evolutionarily stable adaptation to foraging and survival in arid areas. These findings therefore support the underlying premise of the AFDH.

INTRODUCTION

Progress in understanding and evaluating the effects of foraging constraints on mole-rat sociality, and thus in assessing the validity of the Aridity Food-Distribution Hypothesis (AFDH), has been constrained in part by: (1) the difficulties faced in executing manipulative

field experiments, which typically require repeated, lengthy and labour intensive excavations of burrow systems; and (2) an inability to quantify the fitness consequences of differences in habitat variables and alternative foraging strategies. Here we address these questions using a spatially explicit simulation model that links ecological and energetic constraints to the location of food resources by foraging mole-rat(s). The aims of this chapter were to: (1) assess the influence of habitat variables (rainfall and food resource characteristics) on foraging success and energetic returns of mole-rats; and (2) assess the importance of group size in influencing foraging success. The findings of this investigation should provide keen insights into the validity of the AFDH as an explanation for the evolution of bathyergid sociality.

METHODS

Table 5.1: Resource characteristics, burrow system lengths and mean colony size for the study populations at Sir Lowry's Pass and Steinkopf. Data summarised from Chapters 4 and 6.

Variable	Sir Lowry's Pass	Steinkopf
Mean mass (g)	0.20 ± 0.01	4.38 ± 0.71
Range (g)	0.01–5.72	0.02–129.17
Mean water content (%)	47.54 ± 5.57	71.33 ± 1.49
Mean energy content ($kJ.g^{-1}$)	17.29 ± 0.44	14.33 ± 0.31
Density ($No.m^{-2}$)	1424.00 ± 232.13	75.84 ± 8.14
Biomass ($g.m^{-2}$)	284.80	329.20 ± 57.91
Total available energy ($kJ.m^{-2}$)	2583.23	1597.81
Burrow length (m)	50-200	150-510
Mean colony size	5.1 ± 0.2	5.1 ± 0.2

Model description

A simulation model was constructed to compare aspects of the foraging ecology of *C. h. hottentotus* at Sir Lowry's Pass and Steinkopf, using empirical data on resource

Table 5.2: Definitions of variables and parameters used in the foraging model.

Model variables/ parameters	Definition	Units
Variables		
s	soil condition (moist or dry)	-
n	number of mole-rats in a colony	-
t_{tot}	total daily time available for burrowing activities	$hr.d^{-1}$
t_{cell}	time taken for a mole-rat to dig through one model cell	hr
b	length of the main axis of a burrow system	m
$\bar{x}$	mean number of bulbs in each model cell	-
k	overdispersion parameter	-
E_{net}	daily net energetic returns	$kJ.mole\text{-}rat^{-1}.d^{-1}$
E_{gain}	daily energetic gain	$kJ.mole\text{-}rat^{-1}.d^{-1}$
E_{loss}	daily energetic expenditure	$kJ.mole\text{-}rat^{-1}.d^{-1}$
wt	total mass of bulbs consumed (or stored) per colony per day	g
t_B	total time per colony per day spent at rest	hr
t_A	total time per colony per day spent in activities such as running and handling food	hr
t_D	total time per colony per day spent digging	hr
Parameters		
d_{max}	maximum daily extension of burrow system	$m.d^{-1}$
t_{max}	maximum number of hours of active behaviour per day	$hr.d^{-1}$
d_{rate}	observed distance dug per hour	$m.hr^{-1}$
ε	mean energy content per bulb	$kJ.g^{-1}$
v_B	resting metabolic cost	$kJ.g^{-1}.\ hr^{-1}$
v_A	metabolic cost of activities such as running and handling food	$kJ.g^{-1}.\ hr^{-1}$
v_D	digging metabolic cost	$kJ.g^{-1}.\ hr^{-1}$
$\bar{m}$	average mass of a mole-rat	g

characteristics for the two localities (Table 5.1). In each instance a 200m x 200m model area was divided into 160 000 cells each measuring 0.25m x 0.25m. The model was run over a three month period using a time step of one day. To assess the effects of cooperative foraging on foraging efficiency, the mole-rat group size present in the model area was varied from one to 12. Summaries of model parameter and variable definitions, and base-case parameter values are presented in Tables 5.2 and 5.3 respectively (the simulation model is presented in detail in Appendix I).

Table 5.3: Base-case values for parameters used in the foraging model.

Model parameter	Base-case value	Source
d_{max} ($m.d^{-1}$)	2	S. Telford, M. Barnett, J.U.M. Jarvis & N.C. Bennett (unpublished data)
t_{max} ($hr.d^{-1}$)	6	Jarvis & Bennett (unpublished data)
d_{rate} ($m.h^{-1}$)	0.3	S. Telford, M. Barnett, J.U.M. Jarvis & N.C. Bennett (unpublished data)
ε ($kJ.g^{-1}$)	17.29 (SLP)‡ 14.33 (ST)‡	This thesis
v_B ($cm^3O_2.g^{-1}.hr^{-1}$)	0.68	Haim & Fairall (1986)
v_A ($cm^3O_2.g^{-1}.hr^{-1}$)	2 x v_B = 1.36	N.C. Bennett (pers. comm.)
v_D ($cm^3O_2.g^{-1}.hr^{-1}$)	moist soil = 5.02 x v_B = 3.41 dry soil = 4.53 x v_B = 3.08	Lovegrove (1989)
$\overline{m}$ (g)	65	This thesis

‡ SLP = Sir Lowry's Pass; ST = Steinkopf

Empirical data for *C. h. hottentotus* was used wherever possible. However, when unavailable, data from the Damaraland mole-rat was used.

Input data

As outlined in Chapter 1, mole-rats concentrate their foraging efforts in post-rainfall periods when the damp soils are more readily worked, and the high energetic costs associated with burrowing are at a minimum (Vleck 1979; 1981; Lovegrove & Painting 1987; Brett 1991; Lovegrove 1989; Jarvis & Bennett 1991; Jarvis *et al.* 1994;1998). For each of the two areas, a three-month series of daily rainfall (obtained from the Computing Centre for Water Research, University of Natal, Pietermaritzburg 3200, South Africa) was used to compile a time-series of soil condition in each area (Figure 5.1). Jarvis *et al.* (1998) have observed that 15-25 mm of rain needs to fall, in a relatively short period, for the soil to become damp enough to work at the depth of the mole-rat foraging burrows (15-25 cm). Consequently, a day was categorised as moist (coded as 1) if ≥ 20 mm of rain had fallen in the preceding seven days and as dry (coded as 0) if < 20 mm had fallen in the preceding week.

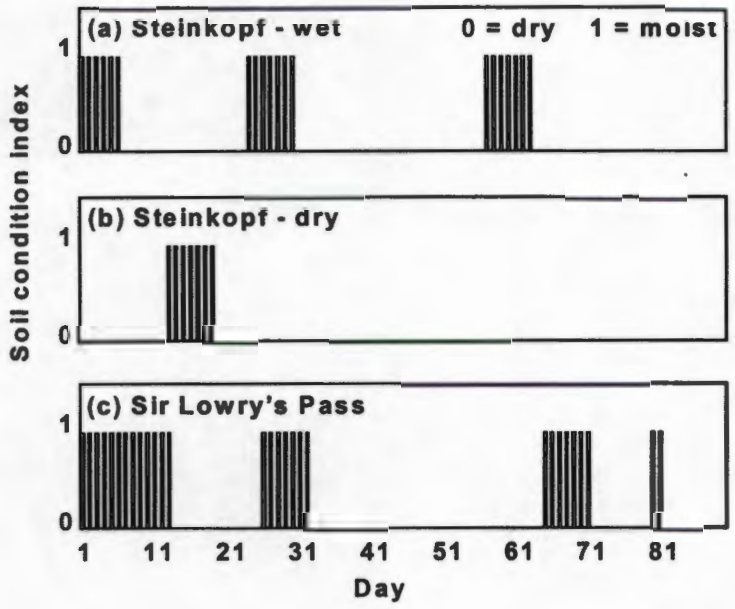

Figure 5.1: A time series of daily soil condition for a three month period at the two study sites; (a) a wet series from Steinkopf (1994), (b) a dry series from Steinkopf (1995) and (c) a series from Sir Lowry's Pass (1994).

Given the importance of rainfall in determining mole-rat foraging behaviour, and the sporadic nature of precipitation in arid environments, two three-month rainfall data series were used for Steinkopf: a "wet" series (based on data for 1994; Figure 5.1a) and a "dry" series (based on data for 1995; Figure 5.1b). Due to the more predictable nature of rainfall

at Sir Lowry's Pass, a single rainfall data series was considered sufficient (based on data for 1994; Figure 5.1c).

Burrowing

Maximum daily burrowing effort was constrained by two parameters: the maximum daily extension of a burrow system d_{max} assumed feasible for one mole-rat (set at 2 $m.d^{-1}$; S. Telford, M. Barnett, J.U.M. Jarvis & N.C. Bennett unpublished data)[1] and the maximum number of hours of active behaviour per day t_{max} (set at 6 $hr.d^{-1}$; J.U.M. Jarvis & N.C. Bennett unpublished data)[2]. Simulations revealed that daily burrow extensions were almost always limited by t_{max}. The total daily time available for burrowing activities t_{tot} was calculated as:

$$t_{tot} = t_{\max} \times n \qquad (5.1)$$

where n = the number of mole-rats.

The rate of extension to the burrow system was modelled as a function of the soil condition index s as follows:

$$t_{cell} = \begin{cases} \frac{1}{4 \cdot d_{rate}} & s = 1 \\ \frac{1}{d_{rate}} & s = 0 \end{cases} \qquad (5.2)$$

where t_{cell} = the time (in hrs) for one mole-rat to dig through one model cell, and d_{rate} = the observed distance (in m) dug per hour. An estimate of d_{rate} (set at 0.3 $m.h^{-1}$) was obtained from S. Telford, M. Barnett, J.U.M. Jarvis and N.C. Bennett (unpublished data)[1]. Following

[1] parameter based on results from laboratory based foraging trials for *C. damarensis*
[2] parameter based on data from field based radiotelemetry study of *C. damarensis*

Lovegrove (1989), digging rates are assumed to be four times slower under dry soil conditions.

The mole-rat "nest" was assumed to be situated in the centre of the model area. As mole-rats typically forage blindly *i.e.* without the use of sensory cues (Brett 1991; Jarvis *et al.* 1998), their movements through the model area were simulated using a simple random walk approach; each time a mole-rat moved through a model cell, the probability of it continuing in a forward direction was set at 0.8, with equal probabilities of 0.1 of continuing to either its left or right. Burrow systems in the model comprised a main branch (constructed in a randomly determined direction), primary branches and secondary branches. Additional burrowing constraints, based on plots of burrow excavations presented in Chapters 3 and 4, dictated that no branching off the main branch occurred within 6 m of the nest and that there was a 74% probability of a secondary branch being formed off a primary branch. These constraints ensured a secondary/primary branch ratio of 0.74, as has been observed in the field. The branch endpoint at which a mole-rat began its burrowing activity each day was randomly determined.

To obtain a rough indication of burrow system size, the length of the main axis of each burrow system was used as a measure of burrow system length *b*.

Resource Distribution

The negative binomial distribution was used to describe the pattern of resource distribution at the two sites. The shape of the distribution at each site depends on two parameters: $\bar{x}$, the mean number of bulbs in each model cell and *k*, the "overdispersion"

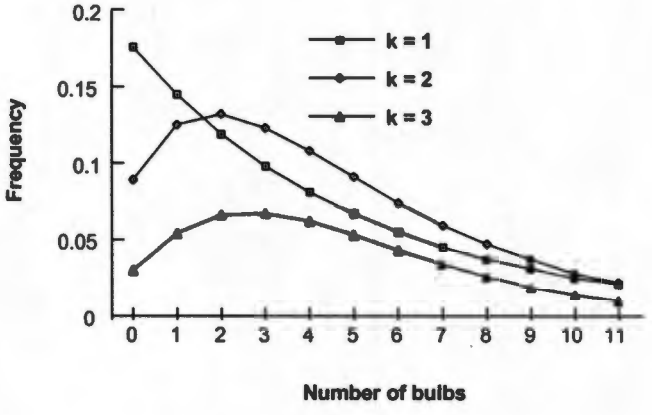

Figure 5.2: The effect of changing the overdispersion parameter (*k*), in the negative binomial distribution, on the frequency distribution of bulbs.

parameter. Because the effect of increasing k is to change the distribution from a clumped to a more even distribution (Figure 5.2), a smaller value of k (k = 1) was assumed for Steinkopf than for Sir Lowry's Pass (k = 2). The parameter $\bar{x}$ was calculated from the values presented in Table 5.1. The effects on mole-rat foraging success of a change in the underlying resource density and distribution were respectively investigated by successively increasing $\bar{x}$ and k.

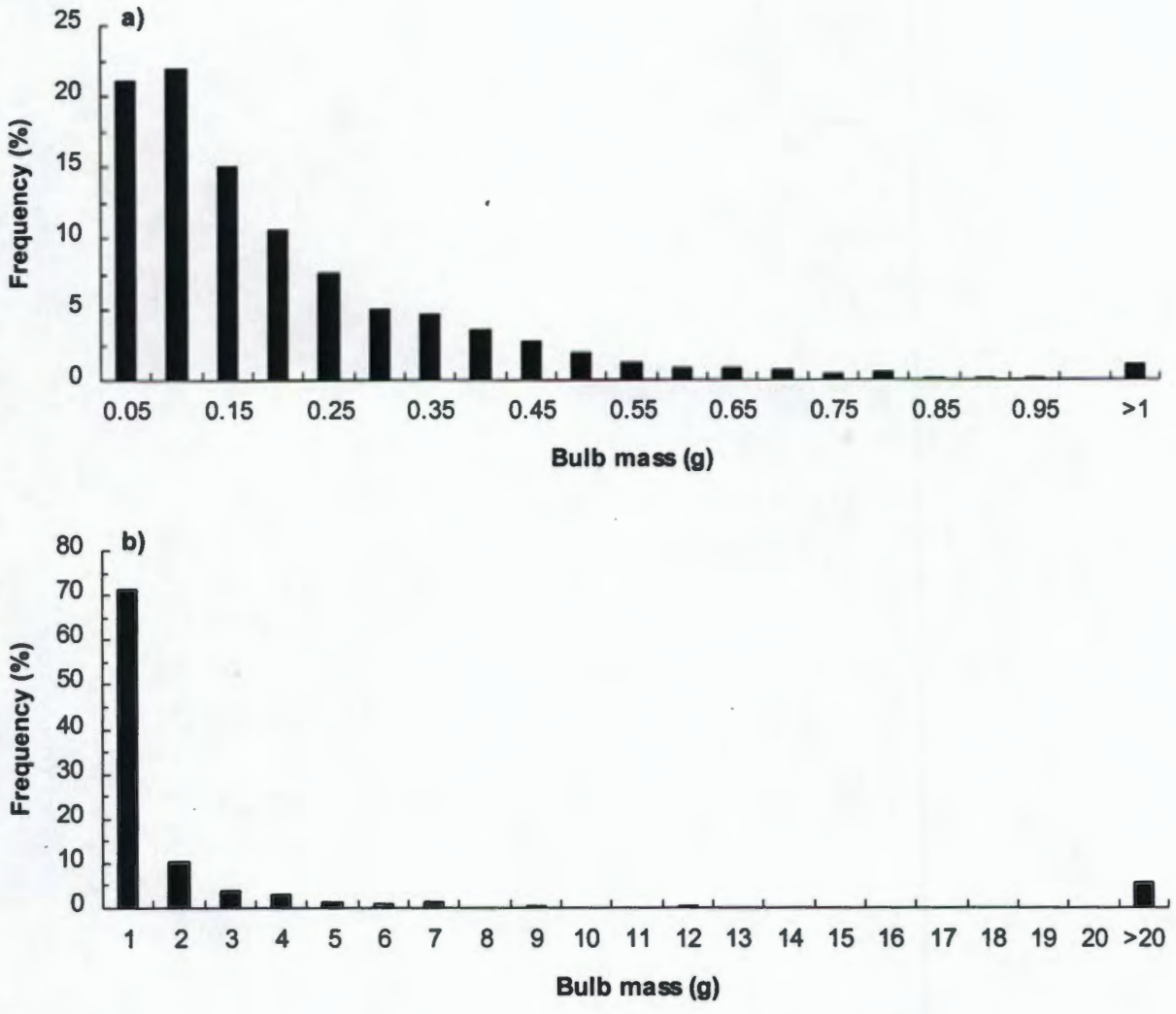

Figure 5.3: The size-frequency distributions of geophytes collected in random quadrats at (a) Sir Lowry's Pass and (b) Steinkopf.

Three different bulb categories were defined for each of the two sites, *viz.* small, medium and large bulbs. The size-frequency distributions for geophytes collected in random 25 x 25 cm quadrats (for methods see Chapter 4) at Sir Lowry's Pass and Steinkopf (Figure

5.3) were used to determine the frequencies of occurrence of the different bulb categories at each site. In Chapter 3 I showed that foraging common mole-rats selectively consume smaller bulbs and store large bulbs. For Steinkopf, it was assumed that small bulbs (≤ 1 g) are immediately eaten, medium bulbs (> 1 g, < 10 g) have an equal probability of being eaten or stored and large bulbs (≥ 10 g) are stored. Although, bulbs are generally much smaller at Sir Lowry's Pass, smaller bulbs are nevertheless still selectively consumed and large bulbs stored (Chapter 4), thus the fate of individual bulbs at this site was determined as for Steinkopf, but small and large bulbs were defined instead as those having masses ≤ 0.1 g and ≥ 0.55 g respectively, and medium bulbs those lying between these extremes.

Energetic budget

A simplified net energetic budget was used as an index of foraging success in the model. A daily net energetic value E_{net} (in kJ.mole-rat^{-1}.d^{-1}) was calculated as the difference between total daily energetic gain and expenditure. Energetic gain E_{gain} was calculated simply as:

$$E_{gain} = wt \times \varepsilon \qquad (5.3)$$

where *wt* = the total mass (g) of bulbs consumed (or stored) per colony per day, and ε = mean energy content (kJ.g^{-1}) of bulbs at each site. Bulbs at Sir Lowry's Pass have a marginally greater mean energy content than those at Steinkopf (Table 5.1).

Energetic loss E_{loss} was calculated as:

$$E_{loss} = \left(t_B v_B \times t_A v_A \times t_D v_D(s)\right) \cdot \overline{m} \qquad (5.4)$$

where t_B, t_A, t_D are respectively the total times (hr) per colony per day spent in a basal resting state (B), engaged in activities such as running and handling food (A), and actively digging (D); $v_B, v_A, v_D(s)$ are the metabolic costs ($kJ.g^{-1}.hr^{-1}$) associated with activity states B, A and D respectively; and $\overline{m}$ is the average mass (g) of a mole-rat. Values of the parameters $v_B, v_A, v_D(s)$ and $\overline{m}$ are given in Table 5.3. Note that digging metabolic cost is a function of the soil condition index *s* because the rate of activity is increased under favourable soil conditions (Lovegrove 1989). To calculate the total time spent in state A each day, it was assumed that a mole-rat makes a single return trip to the nest each time a bulb has to be stored. A constant running speed of 0.0069 $m.s^{-1}$ was assumed. As bulbs at Sir Lowry's Pass are mostly relatively small, a constant handling time of 2.5 $s.bulb^{-1}$ was assumed. For Steinkopf, handling times for small (mass ≤ 1g), medium (1g < mass ≤ 5g) and large (mass > 5g) bulbs were respectively set at 2.7, 3.7 and 4 $s.bulb^{-1}$ (T.A. Branch & S. Croeser unpublished data).

To facilitate comparisons between the two sites, an average E_{net} value was calculated as:

$$\overline{E}_{net} = \frac{\sum_{n}\left(E_{gain} - E_{loss}\right)}{n} \qquad (5.5)$$

where *n* = the number of days. Average E_{net} values estimated by the model do not accurately reflect mole-rat energetic budgets because several additional factors (e.g. the cost of keeping warm) are ignored. Rather, E_{net} values are used as an index of the relative performance of the animals under a range of different scenarios.

RESULTS

Foraging energetics

The results of a base-case scenario for each of the two sites are summarised in Table 5.4. Each base-case was calculated as the average of 100 simulations using a single mole-rat only. This ensured that the co-efficient of variation attached to each of the $\overline{E}_{net}$ values was less than 10%. Estimated $\overline{E}_{net}$ values for Sir Lowry's Pass were 2.7 to 3.6 times greater than those predicted for Steinkopf (Table 5.4). Estimated $\overline{E}_{net}$ values for Steinkopf were influenced by precipitation; energetic rewards were 1.3 times greater for simulations using the wet rainfall series than those using the dry series (Table 5.4).

Table 5.4: Summary of model output

Variable	Sir Lowry's Pass	Steinkopf (wet)	Steinkopf (dry)
$\overline{E}_{net}$	609	223	170
STD	35.4	13.2	14.0
b (m)	72	126	104
STD	30	68	49

$\overline{E}_{net}$ = net daily energetic return (kJ.mole-rat^{-1}.d^{-1}), STD = standard deviation, *b* = burrow length

Figure 5.4a shows the predicted relationship between per capita net energetic gain and group size. For both sites, $\overline{E}_{net}$ values decreased with an increase in the number of mole-rats per burrow system (Figure 5.4a). Although a proportionately greater decrease was estimated for Sir Lowry's Pass, per capita net energetic gains at this site were nevertheless consistently higher than at Steinkopf, for all group sizes. For both the arid and mesic sites, $\overline{E}_{net}$ values eventually converged towards a constant (Figure 5.4a).

Although model results suggested that per capita energetic gain (ignoring energetic costs from processes such as heat loss) is reduced with an increase in the number of mole-rats in a colony, the model highlighted the fact that colony members may play an important role in reducing the risks associated with foraging in an unpredictable environment (Figure

5.5). For example, with only a single mole-rat in a burrow system at Steinkopf, the model estimated that, on

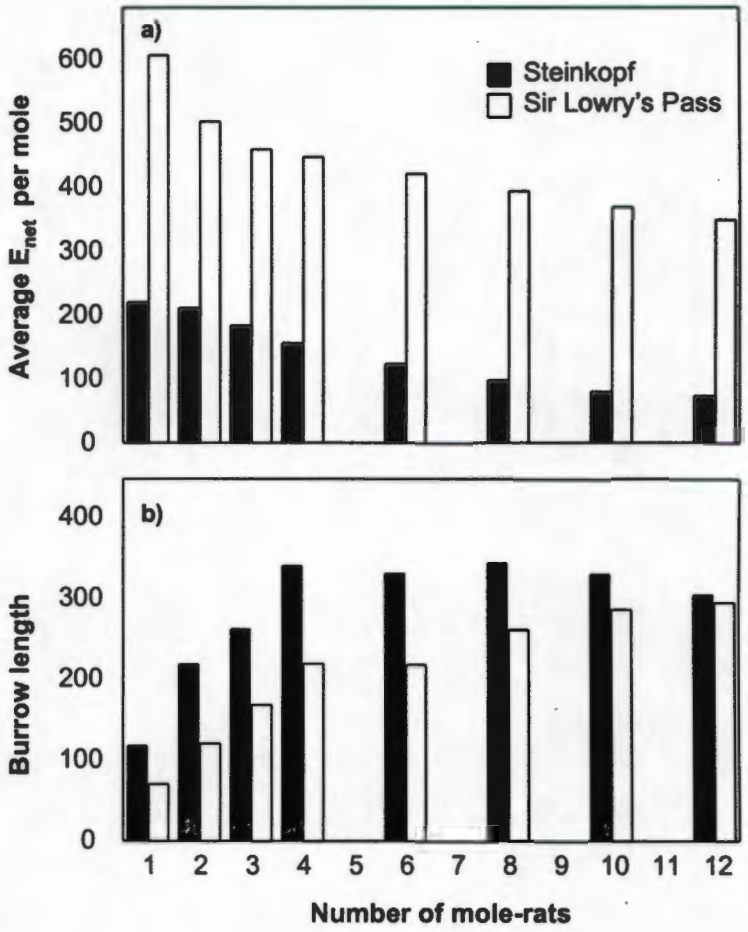

Figure 5.4: The estimated relationship between colony size and (a) per capita net energetic gain (E_{net}), and (b) burrow system length, for the two study sites.

average, total daily energetic expenditure exceeded daily gains as much as 8% of the time over a three month period. With two mole-rats present, this figure drops to 1.7%, while four or more mole-rats are necessary to ensure that a negative daily energetic budget is incurred less than 1% of the time (Figure 5.5). These estimates are based on the wet data series for Steinkopf, the results were even more dramatic when the dry series was used; with a single mole-rat in a system, the model estimated that total daily energetic expenditure exceeded daily gains more than 10% of the time over a three month period, with two mole-rats present,

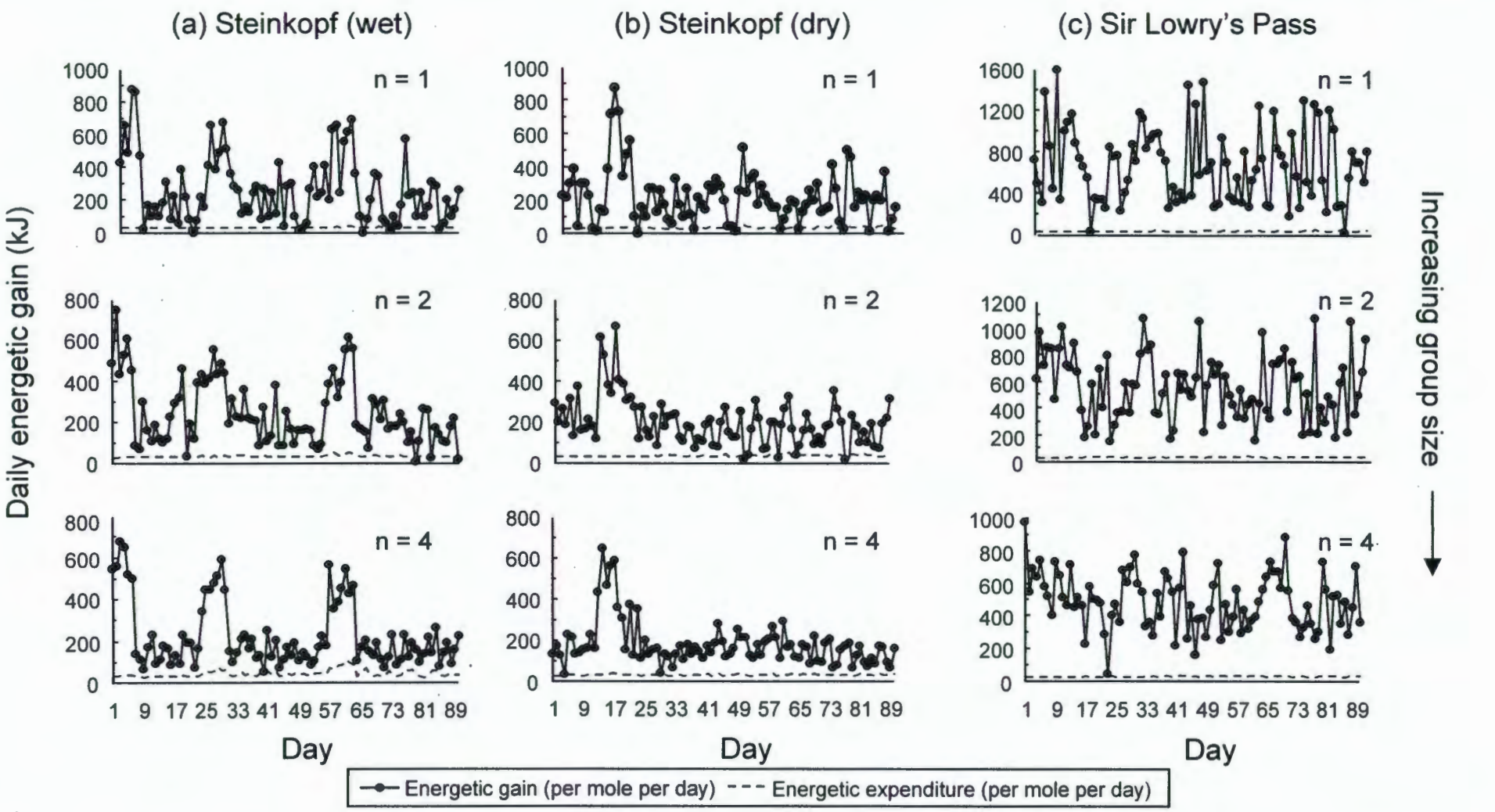

Figure 5.5: Estimated daily energetic gain (kJ) and energetic expenditure (kJ) for *C. h. hottentotus* colonies of different size (n = 1, 2 or 4 mole-rats) at (a) Steinkopf during a wet season, (b) Steinkopf during a dry season and (c) Sir Lowry's Pass. The figure indicates the frequency with which daily energetic expenditure exceeds energetic gains, yielding a negative energetic budget.

this figure drops to 1.8%, while with four mole-rats present, a negative daily energetic budget is incurred approximately 0.2% of the time (Figure 5.5).

Resource characteristics

The effect on mole-rat foraging success of changing the underlying resource distribution from a clumped to a more even distribution was investigated by successively increasing the parameter *k* in the negative binomial distribution employed. When assessing the effects of *k*, absolute food availability was held constant at each site. For both sites, mole-rat foraging success (per capita energetic returns) improved with a more even spread in bulb distribution (Figure 5.6a). Energetic benefits were predicted to be consistently higher for mole-rats foraging at Sir Lowry's Pass.

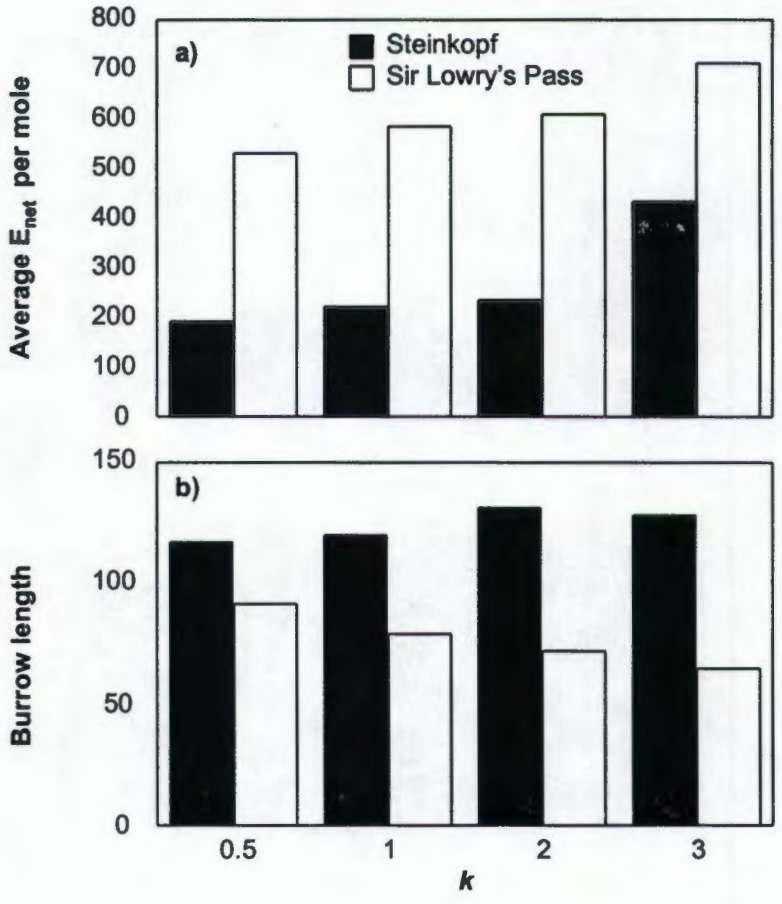

Figure 5.6: The estimated effect of changing the overdispersion parameter (*k*, *i.e.* the underlying resource distribution pattern) on (a) per capita net energetic gain (E_{net}), and (b) burrow system length, for the two study sites.

The effect on mole-rat foraging success of changing the underlying resource density was investigated by successively increasing the bulb density ($\bar{x}$) from 50 to 1000 bulbs.m^{-2}. For both sites, mole-rat foraging success (per capita energetic returns) improved with an increase in bulb density (Figure 5.7a). For both the arid and mesic sites $\overline{E}_{net}$ values eventually tended towards a constant. Energetic benefits were predicted to be consistently greater for mole-rats foraging at Sir Lowry's Pass.

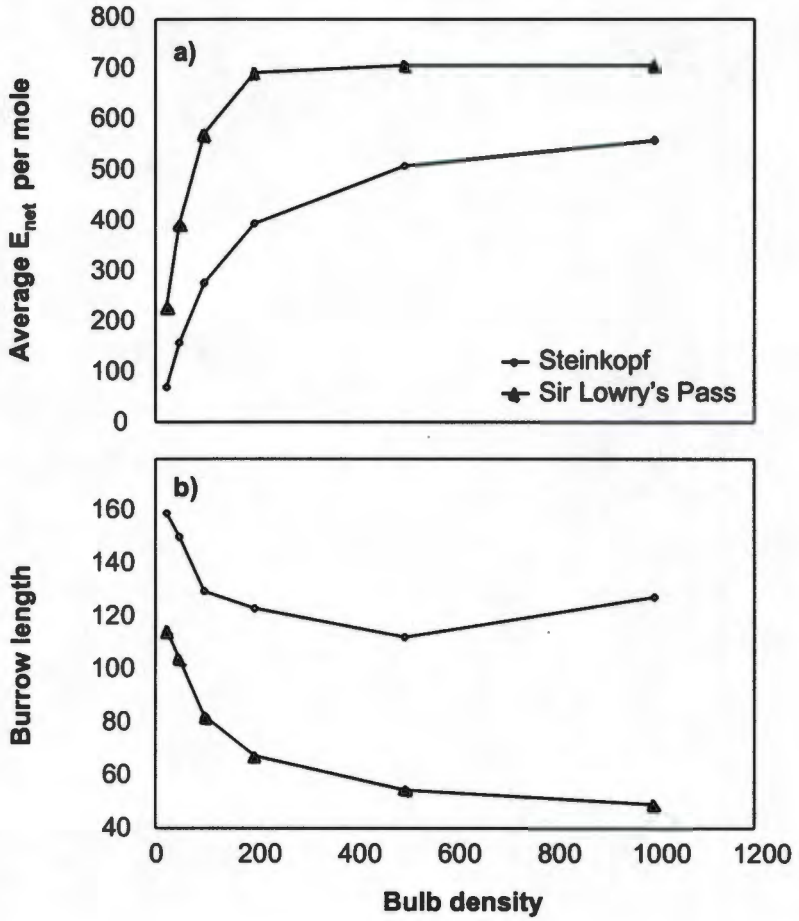

Figure 5.7: The estimated effect of changing the resource density (bulbs.m^{-2}) on (a) per capita net energetic gain (E_{net}), and (b) burrow system length, for the two study sites.

Burrow architecture

Despite using the same burrowing constraints for the Steinkopf and Sir Lowry's Pass simulations, the model predicted that markedly different burrow systems would develop over

a three month period in each of the two areas. A single example of a burrow system generated by the model for each of four different scenarios is presented in Figure 5.8. Whereas the Sir Lowry's Pass burrow systems were characterised by a greater number of reticulations, the longest axis of the Steinkopf burrow systems was substantially greater than that of the Sir Lowry's Pass systems (Table 5.4).

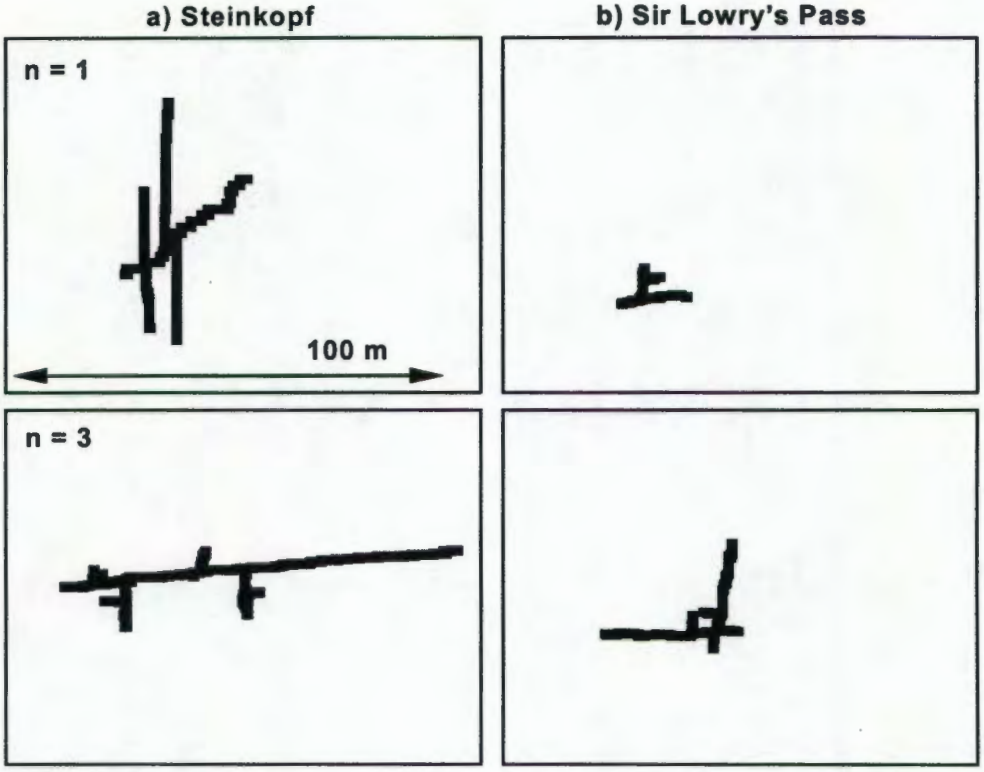

Figure 5.8: Four examples of burrow systems generated by the model for each of four different scenarios: a single animal at Steinkopf (top left); three animals at Steinkopf (bottom left); a single animal at Sir Lowry's Pass (top right); three animals at Sir Lowry's Pass (bottom right).

An increase in the number of mole-rats in a colony resulted in an initial near-linear increase in burrow system length *b* at both sites, but this levelled off with four or more mole-rats present in the Steinkopf system and approximately ten or more in the Sir Lowry's Pass system (Figure 5.4b). Predicted burrow system lengths *b* were consistently longer at Steinkopf than at Sir Lowry's Pass for all group sizes. Burrow system lengths *b*, which were

simulated to develop over a three month period at each site, were on approximately the same scale as observed in the field, assuming equivalent colony sizes (Table 5.1).

A decrease in the patchy nature of food supplies at Sir Lowry's Pass resulted in a decrease in burrow length *b* (Figure 5.6b). This effect was less marked for the Steinkopf site. For both sites an increase in bulb density resulted in a marked decrease in burrow system length (Figure 5.7b).

Soil condition

The model is driven partly by a soil condition input series, the importance of which was assessed by contrasting scenarios in which soils are assumed to be (a) moist and (b) dry for the entire three month period. Using the Steinkopf model, the energetic rewards in the former case were estimated to be 3.5 times greater than in the latter case. Burrow system length *b* under a moist soil condition scenario was estimated at 2.9 times that under a dry soil scenario. The importance of soil hardness in determining energetic rewards was highlighted further by the fact that under constant moist soil conditions, mole-rats were predicted to increase their average energetic rewards 2.2 times relative to the base case. The results of running the Steinkopf model with the Sir Lowry's Pass soil input series suggested a 1.16 times increase in energetic rewards because of the reduced frequency of dry soil conditions.

Sensitivity analysis

To test the sensitivity of the model to the various parameters, model parameters were individually increased and decreased by 50% and the effect on model results quantified by calculating $\overline{E}_{net}$ and burrow length *b* as a proportion of the base-case values obtained for the Steinkopf site. Model results were most sensitive to the mole-rat digging rate as well as other parameters which constrained the daily extension of the burrow system, i.e. d_{max} and

t_{max}. (Figure 5.9). Changes in bulb energetic content resulted in approximately proportional changes in $\overline{E}_{net}$ estimates, but had no effect on estimates of *b* (Figure 5.9). Results are only presented if a 50% change in a parameter resulted in a greater than 5% change in $\overline{E}_{net}$.

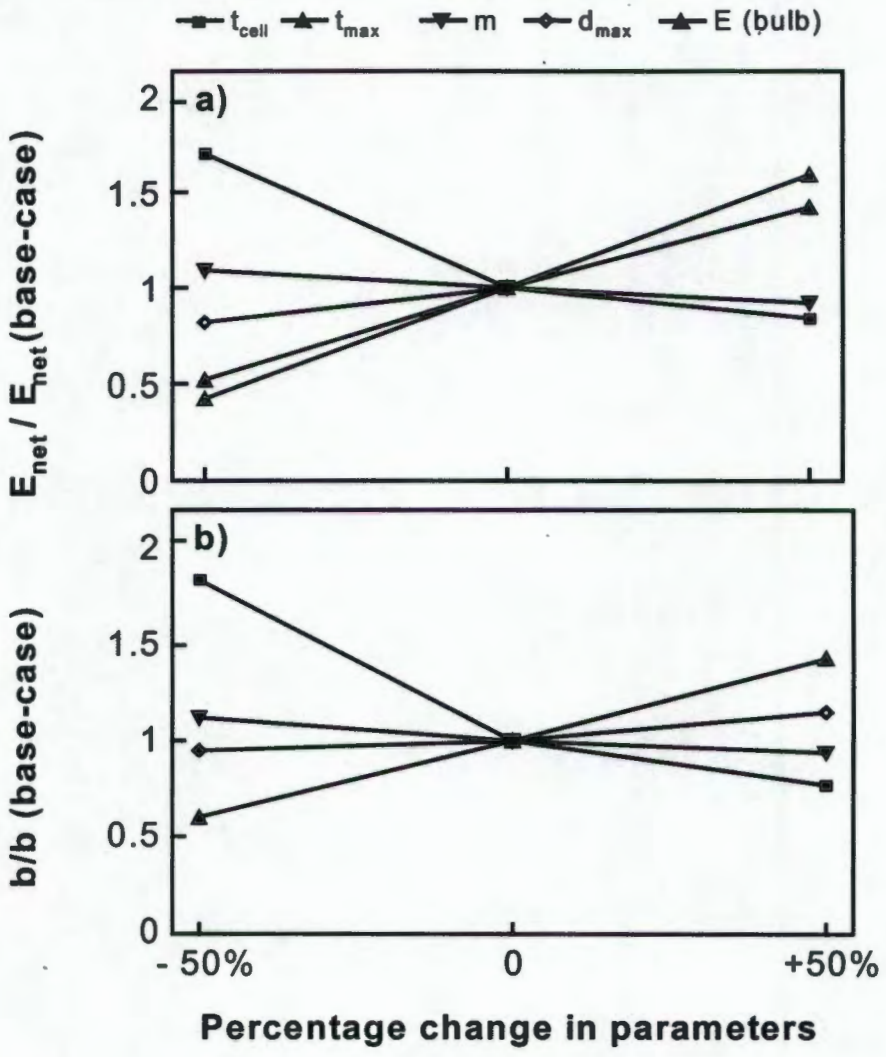

Figure 5.9: Sensitivity analysis results for the foraging model. The figures show the effect, relative to base-case values, on (a) E_{net} and (b) burrow length (*b*), of sequentially increasing and decreasing model parameters as indicated.

DISCUSSION

The simulation model presented in this chapter is not the first attempt to model foraging in the Bathyergidae. Lovegrove and Wissel (1988) and Lovegrove (1991) mathematically

derived a stochastic foraging model which they termed the Sociality-Risk Hypothesis (SRH). This model differs from the SRH in several respects, most notably: (1) our model design and construction were based on rigorous empirical data; (2) the empirical data were collected in two different habitats occupied by the same species, facilitating an intraspecific comparison and thus eliminating phylogenetic effects; and (3) the model provides a quantitative and dynamic framework to explore aspects of the AFDH as an explanation for the evolution of mole-rat sociality.

The model was robust with respect to its parameters because small changes in their values did not result in disproportionately large changes in model output. As expected, model results were most sensitive to the maximum number of hours of active behaviour permitted per mole-rat per day t_{max} because this parameter essentially constrained the daily extension of the burrow system, and hence the mole-rats' access to food resources.

The model predicts that individual mole-rats foraging at Sir Lowry's Pass will enjoy substantially greater energetic returns than those foraging at Steinkopf. Absolute differences in total available energy do not account for this divergence, for, although energy levels (per unit area) at Sir Lowry's Pass were 1.6 times greater than at Steinkopf (Table 5.1), the model suggests that net energetic returns at the mesic site are between 2.7 and 3.6 times those at the arid site. Jarvis *et al.* (1994) note that both solitary and social bathyergids generally occur in habitats with similar mean amounts of energy available to them. They suggest it is the pattern of resource distribution and density, not total available energy *per se*, which ultimately constrains foraging efficiency and shapes group-living. It follows that at Steinkopf, the high energetic costs and low probabilities involved in locating widely dispersed geophytes by blind burrowing in an arid area, where rainfall is low and sporadic, may interact to produce poor per capita net energetic returns to foraging individuals (Lovegrove & Painting 1987; Jarvis *et al.* 1994; 1998). Alteration of the resource density and resource dispersion pattern (clumped/even) parameters in the simulation model provide additional

support for this assertion. Increasing the resource density or changing the resource distribution pattern from a more patchy to a more even dispersion resulted in a substantial increase in per capita energetic returns. These findings suggest that the pattern of resource distribution and density influence the magnitude of energetic returns, ultimately directing foraging efficiency. Thus the dominant selective pressure shaping mole-rat foraging constraints, and hence promoting group living, may be the unpredictability of the food environment rather than absolute food availability. As illustrated by the model this effect is most pronounced in a more arid environment characterised by an underlying distribution that is patchy in both space and time.

An important result which emerged from the simulations was that per capita energetic returns decreased with increasing group size, suggesting that, compared to a solitary forager, there is no energetic advantage to an individual foraging cooperatively within a group. The concept of "risk sensitive behaviour" (Weissburg 1986) proposes that the survival benefits to individuals foraging cooperatively involves a reduction in the risk of poor returns while foraging alone, rather than the maximisation of net energetic returns (Caraco 1980; Caraco *et al.* 1980; Real *et al.* 1982; Caraco & Lima 1985; Lovegrove & Wissel 1988). Risk is defined as the probability of faring poorly whilst foraging, due to the stochastic nature of food resources (Caraco 1981). Consequently, cooperative foraging in mole-rats is probably best viewed from the perspective of risk reduction rather than the optimisation of energetic returns alone. The results from the simulation model revealed that an increase in group size significantly reduced the probability of a mole-rat incurring a negative daily energetic budget, *e.g.* at Steinkopf a colony size of 4 animals, reduced this risk to less than 1%. Failure to meet their energetic budget may have potentially fatal consequences for foraging mole-rats. Lovegrove and Wissel (1988) suggest that simultaneous cooperative foraging reduces the distances an individual must burrow before any individual in the colony encounters a geophyte, thereby reducing the risk of unproductive foraging. Thus, the most

important function of cooperative foraging may be risk reduction, as, despite having to tolerate reduced per capita energetic benefits, mole-rats foraging in groups substantially minimise the risk of not meeting their daily energetic requirements. As illustrated by the model, this effect is most pronounced in arid environments characterised by clumped, widely dispersed food resources and low and sporadic rainfall. The major implications of these findings are that: (1) group size does not increase individual energetic benefits; (2) the benefit of cooperative foraging is that it greatly reduces the risks of unproductive foraging; and (3) the benefits of cooperative foraging are most pronounced in arid regions. As such our results support Lovegrove and Wissel (1988) and Lovegrove' s (1991) SRH, as well as other similar models such as Thompson *et al.* (1975).

Two important ramifications follow from these results; firstly, it is critical for mole-rats to store food supplies to reduce the risk of incurring a negative daily energetic budget. Unsuccessful foragers are guaranteed access to the colony's food cache and are assured of meeting their daily energy requirements. By storing food, mole-rats can ensure a ready food supply to see them through nutritionally stressful periods, and thus it is perhaps not surprising that food caching is a widespread phenomenon amongst the bathyergids (Genelly 1965; Du Toit *et al.* 1985; Davies & Jarvis 1986; Lovegrove & Jarvis 1986; Bennett 1988; Jarvis *et al.* 1998; Spinks 1998). Secondly, the model findings suggest that colony sizes should exceed a certain minimum number to reduce foraging risk. At Steinkopf, the model predicts that colony sizes of four animals will effectively eliminate the risk of incurring a negative daily energetic budget. The model prediction is supported by the observation that the mean group size at both sites was five animals (Table 5.1).

The simulation model output supports the general view that food resources play a central role in determining the pattern of burrowing by subterranean foragers (Andersen 1982; 1987; Reichman *et al.* 1982; Sparks & Andersen 1988; Heth 1989; Davis & Kalisz 1992). The model predicts that burrow system dimensions and architecture will differ

markedly between Steinkopf and Sir Lowry's Pass. Systems from the arid site were longer than those from the mesic site, and distinctly linear in construction, whilst the short systems from Sir Lowry's Pass exhibited a more reticulate architecture. Jarvis and Bennett (1990; 1991) and Jarvis *et al.* (1994) note that burrow length/architecture appears to be correlated with the availability of food, and they suggest that with increasing aridity mole-rats must dig longer burrow systems to gain access to sufficient quantities of the widely dispersed and clumped food resources in these arid areas. Consequently, the long linear burrows at Steinkopf probably reflect the low density and associated longer foraging distances between individual resources or resource clumps, whereas the short reticulated systems at Sir Lowry's Pass reflect the high densities of geophytes. This contention is supported by the model prediction that burrow length will decrease with an increase in resource density or a decrease in the patchy nature of food supplies. Model results thus predict that in an arid environment, animals expend much time and energy extending their burrow system in search of food, whereas in a more mesic environment, time and energy are spent instead on harvesting the numerous small bulbs. These findings support my suggestion (Chapter 4) that differences in burrow dimensions and architecture between the two sites are primarily a function of differences in the underlying resource distributions.

The AFDH predicts that the solitary Bathyergidae are excluded from arid regions as the cost of burrowing long unproductive distances is not energetically viable for a solitary forager (Lovegrove & Wissel 1988; Jarvis *et al.* 1994; 1998). One of the biggest constraints on subterranean foraging is the absolute distance a solitary animal is able to burrow. Even when conditions are optimal for excavation, digging is constrained by the maximum rate of incisor growth, the energetic costs of burrowing and the risk of overheating (Vleck 1979; 1981; McNab 1966; Lovegrove 1989; Jarvis & Bennett 1991). The model output indicates that an increase in group size substantially increases burrow system length[3]. Therefore, by

[3] This effect is only pronounced *e.g.* with < 5 mole-rats at Steinkopf, thereafter an increase in group size does not substantially increase burrow length in the model (Figure 5.4)

foraging cooperatively, and thereby diluting any foraging constraints, mole-rats can maximise burrow system size and the concomitant probability of encountering stochastic food resources. As mentioned previously, Lovegrove and Wissel (1988) suggest that simultaneous cooperative foraging reduces the distances any one individual must burrow before encountering a geophyte. Thus, although absolute burrow system length will increase with increasing group size, per capita burrowing distance and hence energetic costs should decrease.

Soil hardness was an important factor determining energetic rewards in the foraging model, because it influenced digging rates and energetic expenditure. Because less energy is expended to extend a burrow system in moist soil, the common mole-rat typically extends its burrow system after periods of rain (Vleck 1979; 1981; Lovegrove & Painting 1987; Lovegrove 1989; Jarvis *et al.* 1994; 1998). Mole-rats in the model were assumed to burrow four times faster in moist than in dry soils, and the model predicted that energetic rewards are increased 3.5 times if soils are constantly moist versus constantly dry. Daily resource rewards will obviously increase with an increase in the distance and speed that a subterranean rodent burrows per day (Lovegrove 1989). The foraging success of a mole-rat may therefore be expected to fluctuate considerably as a function of patterns of rainfall. This contention is supported by the model prediction that per capita energetic returns for mole-rats foraging at Steinkopf during a "wet" season were 1.3 times greater than those of mole-rats foraging at Steinkopf during a "dry" season. This is an important result as models of social evolution in the Bathyergidae typically emphasise the role of resource characteristics, often at the expense of climatic considerations. However, these findings stress that an understanding of the factors shaping foraging behaviour, and hence ultimately group living, in the bathyergids requires consideration of all habitat characteristics, including food resources and climatic variables.

CONCLUSION

Solomon and Getz (1997) propose that important insights into mammalian social evolution will be gained by evaluating the effects of habitat variables on cooperative breeding. In particular they suggest that the effect of habitat variables should be examined intraspecifically in optimal and sub-optimal habitats. A simple simulation model of the type presented here may complement such field studies by providing a quantitative and dynamic framework within which to explore the effects of habitat characteristics on mole-rat foraging, and thereby more clearly define the linkages between habitat variables and foraging behaviour, and ultimately sociality in the Bathyergidae. Quantifying the consequences of habitat idiosyncrasies and foraging decisions in terms of a simple, yet pertinent, currency *i.e.* per capita energetic returns, facilitates a robust and objective approach to investigating these factors.

In conclusion the results of the foraging model presented in this chapter indicate that the low density of patchily dispersed food resources, and the low, sporadic rainfall, and concomitant low soil moisture levels in arid environments interact to elevate foraging costs and reduce energetic returns, and ultimately constrain foraging efficiency in the common mole-rat. Moreover, the model suggests that increased group size and cooperative foraging dilutes foraging costs and reduces the risks of unproductive foraging, and as such represents an evolutionarily stable adaptation to foraging and survival in arid areas. These findings therefore support the underlying premise of the AFDH that mole-rat coloniality and co-operative foraging have evolved in response to the energetic costs of foraging and the distribution of critical resources in arid environments.

Chapter 6

Influence of aridity and reproductive status on male and female reproduction.

ABSTRACT

The comparative reproductive attributes of common mole-rats collected from Sir Lowry's Pass and Steinkopf were investigated. It was predicted that non-reproductive animals from the arid population would exhibit a more profound reproductive control than those inhabiting mesic areas. In addition, the influence of breeding season on male and female reproduction was investigated in an attempt to separate the effects of seasonality from those of reproductive status. Gross anatomical and histological morphometrics of the testes and selected sperm and endocrine parameters were investigated in 112 males from 49 wild caught colonies. Furthermore, ovarian and uterine gross anatomical morphometrics and histology and selected endocrine parameters were examined in 80 females from 42 wild caught colonies. Reproductive and non-reproductive males from both Steinkopf and Sir Lowry's Pass revealed no differences in any of the testicular, sperm or endocrine parameters studied. The absence of a well-defined physiological suppression of reproduction in male common mole-rats is typical of social suppression in male mammals. Similarly, for both the arid and mesic locality, reproductive and non-reproductive females exhibited a similar degree of reproductive function, the only clear-cut status-related differences were associated with the occurrence of pregnancy in reproductive females from both areas. Thus, the results from this investigation fail to reveal clear status-related inter-habitat difference in reproductive activity in the common mole-rat. Evidently incest avoidance between philopatric colony mates is the pervasive mode of reproduction control in subordinate common mole-rats from both localities, and in subordinate cryptomids in general. Hence the absence of inter-habitat variance in the mechanism of reproductive regulation. Consequently, status-related differences in reproductive function cannot provide insight into differences in colony cohesion and fidelity, and hence the degree of social elaboration between arid and mesic areas. Furthermore, with respect to reproductive periodicity, males from both localities exhibited no apparent seasonality in reproductive function: spermatogenesis, sperm quality (motility and percentage normal morphology) basal LH and LH response to exogenous GnRH were similar in the reproductively active and inactive periods. Seasonal cyclicity was evident in the reproductive anatomy and testosterone concentrations of reproductive females from both study areas, and is hypothesised to be a consequence of the occurrence of pregnancy in breeding females during the breeding period. Ovarian histology revealed that all adult females from both localities showed clear evidence of ovarian activity and follicular development during the non-breeding period suggesting that reproductive functions are not completely switched off, and that female common mole-rats from both localities do not become seasonally reproductively quiescent. This maintenance of reproductive activity

during the non-reproductive period is essential in *C. h. hottentotus* males and females, as this period coincides with the period of maximal dispersal opportunities. Such reproductive activeness in dispersing animals may aid intersexual recognition, and assist pair-bond formation thereby facilitating later outbreeding.. Consequently, dispersal and subsequent outbreeding opportunities appear to be important determinants of reproductive function in common mole-rats from both arid and mesic sites, moderating season and status-related effects on reproductive function.

INTRODUCTION

In defining the eusociality continuum Sherman *et al.* (1995) note that "Cooperative breeding and eusociality are not discrete phenomena, but rather form a continuum of fundamentally similar social systems whose main differences lie in the distribution of lifetime reproductive success among group members.". In so doing, Sherman *et al.* (1995) recognise that reproductive differences are central to all definitions of sociality, and thus to the quintessential understanding of social evolution within all animal groups. Consequently, any enquiry into the evolution of bathyergid sociality would be incomplete without an evaluation of the concomitant changes in reproductive attributes.

Paralleling the remarkable variation in bathyergid socio-biology is an equally intriguing variance in reproductive biology. This is particularly prevalent in the social species. Reproduction within all social mole-rat colonies is highly skewed (*sensu* Vehrencamp 1983a; 1983b), typically being monopolised by a few dominant individuals whilst the remaining colony members are reproductively quiescent (Bennett & Jarvis 1988a; Faulkes *et al.* 1990a; 1991; Jarvis & Bennett 1990; 1991; Bennett *et al.* 1997; 1998). However, the mechanisms mediating reproduction in the subordinate colony members exhibit profound inter-specific variation (Faulkes *et al.* 1990a; 1991; 1994; Faulkes & Abbott 1991; 1997; Bennett *et al.* 1993; 1994; 1997; Spinks *et al.* 1997). Thus the naked mole-rat, *Heterocephalus glaber*, exhibits physiological suppression in subordinate colony members of both sexes (Abbott *et al.* 1989; Faulkes *et al.* 1990a; 1991; 1994; Faulkes & Abbott 1991; 1997). In non-reproductive male *H. glaber* social cues are physiologically translated into

diminished spermatogenic activity and sperm quality, whilst in non-reproductive females they translate into a block to follicular maturation and ovulation (Faulkes *et al.* 1990a; 1991; 1994; Faulkes & Abbott 1991; 1997). In striking contrast, the Mashona mole-rat, *Cryptomys darlingi*, apparently lacks a physiological suppression, as incest avoidance precludes breeding between philopatric colony mates in this obligate outbreeder (Bennett *et al.* 1997). The Damaraland mole-rat, *Cryptomys damarensis*, lies between these two extremes. While non-reproductive females show physiological suppression and behavioural inhibition to incest, non-reproductive males lack a physiological component to suppression and exhibit only incest avoidance (Bennett *et al.* 1993; 1994; Bennett 1994; Faulkes *et al.* 1994; Rickard & Bennett 1997). Bennett *et al.* (1997; 1998) suggest that this variation in the mechanism of reproductive modulation may be correlated with environmental factors, with arid adapted species being characterised by a physiological component to reproductive suppression and mesic-adapted species exhibiting only behavioural regulation of access to reproduction, via incest taboos.

Previous studies of common mole-rat reproduction are limited (Bennett 1988; 1989; Spinks *et al.* 1997). This chapter investigates the reproductive capacities of both reproductive and non-reproductive common mole-rats collected from arid and mesic areas. Specifically inter-habitat differences in the comparative reproductive characteristics of dominant and subordinate colony members were examined. Given the suggested influence of aridity on the regulation of reproduction within social mole-rat colonies (mentioned above) it was predicted that non-reproductive animals from the arid population would exhibit a more profound reproductive control than those inhabiting mesic areas. Such inter-habitat differences may in turn reflect differences in colony cohesion and fidelity, and hence the degree of social development.

Interpretations of the effects of reproductive status on *C. h. hottentotus* reproduction may be confounded by the reproductive periodicity prevalent within this species. As outlined in Chapter 1, the common mole-rat is apparently unique among the social bathyergids in

breeding seasonally (Bennett *et al.* 1991; Jarvis & Bennett 1991; Spinks *et al.* 1997). Long-term mark-recapture studies reveal that young are born in summer (late November to January), during which time a maximum of two litters may be produced and reared (Skinner & Smithers 1990; Jarvis & Bennett 1991; A.C. Spinks unpublished data). This reproductive periodicity is typical of both surface-dwelling and subterranean mammals inhabiting seasonal environments (see for example Wehrenberg & Dyrenfurth 1983; Gorman & Stone 1990; Mills *et al.* 1992; Parreira & Cardoso 1993; Kaplan & Mead 1994; Page *et al.* 1994). Annual alterations in environmental factors, modified by social factors, provide the proximate cues for such reproductive periodicity (Clarke 1981; Bronson & Periggo 1987; Ims 1990; Louw 1993; Bronson & Heideman 1994; Turek & Van Cauter 1994). Consequently, differences in reproductive characteristics between the breeding and non-breeding periods are also assessed to ensure that seasonal effects on the reproductive characteristics of males and females did not obscure the effects of status.

MATERIALS AND METHODS

The animals used in this study were caught at Sir Lowry's Pass and Steinkopf using modified Hickman live-traps (Hickman 1979a). A total of 192 common mole-rats from 49 wild-caught colonies, were used in this study. Site-specific sample sizes are summarised in Table 6.1.

To control for the effects of breeding season on reproductive characteristics, animals were caught during both the breeding and non-breeding periods. The breeding season for *C. h. hottentotus*, defined as the period when most mating is likely to occur, lasts from September to early November. During the non-breeding period mole-rats were caught in May-June, and during the breeding period in September and early November (September and November groups were combined for subsequent analyses, as statistical analysis revealed no significant differences).

Table 6.1: The number of reproductive and non-reproductive male and female *C. h. hottentotus* used in this investigation. Also shown is the number of colonies from which these individuals were drawn.

	Sir Lowry's Pass		Steinkopf	
	Individuals	Colonies	Individuals	Colonies
Male	67	25	45	24
Reproductive	22	-	21	-
Non-reproductive	45	-	24	-
Female	35	23	45	19
Reproductive	19	-	18	-
Non-reproductive	16	-	27	-
Total‡	102	25	90	24

‡ totals are for the total number of individuals and colonies from each study locality used in this investigation.

Applying the criteria of Bennett (1989; 1992) and Rosenthal *et al.* (1992), reproductive male common mole-rats were identified on the basis of being the heaviest male in the colony. Bennett (1989; 1992) and Rosenthal *et al.* (1992) have conclusively shown that the reproductive male is the largest and most dominant colony member. During the breeding season reproductive female common mole-rats could readily be identified if they were gravid, or by the presence of a perforate vagina and swollen teats. During the non-breeding period, although reduced, teats were still evident. The presence/absence of placental scars on the uterine horns, indicated the reproductive status of sacrificed animals. In addition Bennett (1989; 1992) and Rosenthal *et al.* (1992) have demonstrated that the reproductive female tends to be the largest and most dominant female colony member. No animals less than 40 g in weight were used in this study, since post-mortem examination of the gross reproductive anatomy and histology of males and females has revealed that animals less than 40 g in weight are sexually immature (A. C. Spinks unpublished data).

Plasma luteinizing hormone

Blood sampling

Plasma luteinizing hormone (LH) concentrations were assessed using the same technique described by Faulkes *et al.* (1991) and Bennett *et al.* (1993). Animals were hand-held and blood samples were obtained from veins in the foot. Approximately 300-400 µl of whole blood was collected by capillary action using heparinized micro-haematocrit tubes. After collection the samples were kept cool for a maximum of 1 hr before being centrifuged for 5 min at 500 *g*, and the plasma was stored at -70 °C until LH determination.

GnRH administration

To investigate possible differential LH responses of the pituitary to stimulation by Gonadotrophin Releasing Hormone (GnRH), the effects of administration of exogenous GnRH were investigated in reproductive and non-reproductive male common mole-rats from both localities. In all experiments 2 µg exogenous GnRH was administered subcutaneously as a single 200 µl injection. Blood samples were taken before and 20 min after a single subcutaneous injection. In all controls sterile physiological saline was administered subcutaneously as a single 200 µl injection. Again, blood samples were taken before and 20 min after a single subcutaneous injection. The GnRH was synthesised in the laboratory of R.P. Millar (Chemical Pathology, University of Cape Town), using solid phase methodology (the purity of GnRH was > 98% homogeneity) (Millar *et al.* 1989), and was stored at -70 °C until required.

Luteinizing hormone bioassay

Luteinizing hormone was measured using an *in vitro* bioassay based on the production of testosterone by dispersed mouse Leydig cells (Van Damme *et al.* 1974), as previously described and validated in the naked mole-rat by Faulkes *et al.* (1990a, 1991), in the

Damaraland mole-rat by Bennet *et al.* (1993) and in the Mashona mole-rat by Bennett *et al.* (1997). Details of the assay have been described previously (Harlow *et al.* 1984; Hodges *et al.* 1987; Abbott *et al.* 1988). Plasma samples were assayed in duplicate at two dilution's (1:20 and 1:40), as a routine check for parallelism, and compared with a rat LH standard (the rLH antigen preparation: rLH-1-7 from NIDDK, Baltimore) over the range 0.0625-2 miu.ml^{-1}. The testosterone produced was measured by radioimmunoassay as described by Hodges *et al.* (1987).

Checks for parallelism were carried out to validate the LH bioassay for plasma taken from animals after GnRH treatment. Dilution's of the common mole-rat plasma samples taken before and after GnRH treatment were parallel to and not significantly different from the reference preparation. The sensitivity of the assay (determined at 90% binding) was 0.1 miu per tube. Intra- and inter-assay mean coefficients of variation for repeated determination of an LH quality control (1.53 miu.ml^{-1}) were 10% and 16%, respectively.

Plasma steroid hormones

Plasma testosterone concentrations were assessed in both males and females.

Collection of plasma

Animals were killed by inhalation of halothane, and blood was immediately collected by cardiac puncture. The whole blood was centrifuged and the plasma collected and frozen, at -70 °C, until required.

Testosterone assay

Concentrations of plasma testosterone were determined on diethyl ether-extracted plasma by radioimmunoassay. Details of the assay have been described by Bennett (1988) and Bennett (1994). Plasma samples were treated by extracting 100 µl plasma aliquots with 6 ml

of alkaline diethyl ether dried down under a stream of nitrogen gas, at 30-40 °C. Testosterone determinations were performed by redissolving the extracted steroid in 0.4 ml of 1% methanol phosphate buffer saline. Duplicate 100 µl samples of the redissolved extracts were used for the assay. One hundred microlitres of testosterone antiserum was added to each assay tube and the mixture was incubated at room temperature (25 °C) for 30 min. This was followed by the addition of 100 µl [1,2,6,7-^{3}H] testosterone TRK 402 (sp. act. 80-105 Ci/mmol; Radiochemical Centre Amersham, Bucks, UK), to each tube (≈ 10 000 cpm). These were incubated at 4 °C overnight. Unbound testosterone was absorbed with 500 µl of dextran-coated charcoal (Norit A charcoal 1.0 g and 0.1 g of Dextran T-40 in 400 ml assay buffer) at 4 °C for 10 min, then pelleted by centrifugation at 3000 rpm for 15 min at 4 °C. Antibody-bound testosterone was decanted into scintillation vials, to which 7 ml scintillation fluid was added. The contents of each vial were mixed and counted on a Tricarb scintillation counter for 2 min.

The antiserum was raised in rabbits against testosterone-3-carboxymethyl-oxime conjugated to bovine serum albumin as described by Millar & Kewley (1976). Cross-reaction with all major naturally occurring steroids was < 0.1%, except for dihydrotestosterone for which it was 5.1%. Cross-reaction was not tested in mole-rat plasma samples. Extraction efficiency, which was routinely monitored by determining the recovery of a tracer amount of (^{3}H) testosterone (≈1000cpm) added to each sample, was 84.01% (± 0.81% SE, n = 98). Samples were corrected for procedural losses. Intra-assay variation was not determined. The inter-assay precision, expressed as the coefficient of variation for repeated measures of a quality control, was 16.95% (n = 7). Non-specific binding was 1.06 ± 0.13% (n = 7) of total counts; zero binding accounted for 29.46 ± 1.61% (n = 7) of total counts. The testosterone assay has been validated in the Cape Porcupine *Hystrix africaeaustralis* (Van Aarde & Skinner 1986a; 1986b) and Damaraland mole-rat (Bennett 1994).

Removal and preparation of reproductive tract tissue

Following the collection of plasma from euthanised animals, the reproductive tracts were removed. In males only the testes, which are abdominally situated, were removed. In females the entire reproductive tract, including ovaries and uterine horns, was removed. Tissues used for anatomy and histology were immediately fixed in Bouin's solution, for a minimum of 7 days, and then transferred to 70% alcohol for storage.

In males used for the assessment of sperm motility and morphology, the testes, together with the attached vas deferentia and epididymides, were removed from recently killed animals and placed in Ham's F10 culture medium (Gibco, Cat. No. 074-01200A, Grand Island, New York), on a preheated microscope stage (34°C). These tissues were processed as described below (sections on sperm morphology and sperm motility).

Gonadal anatomy

It was assumed that any size changes in the tissue examined, resulting from fixation, would be constant across all samples.

Testicular anatomy

Testes were blotted to remove excess fixative, and individually weighed to the nearest milligram. Maximum testis length and width was measured using a dissecting microscope fitted with a graticule. Testicular volume was calculated using the formula for the volume (V) of an ellipsoid *i.e.* $V = 4/3\pi ab^2$ where a = 1/2 maximum length; b = 1/2 maximum width (Woodall and Skinner, 1989).

Ovarian and uterine anatomy

The tissue was blotted to remove excess fixative, and the entire reproductive tract including ovaries weighed to the nearest milligram. Ovaries were dissected from the reproductive tract, and individually weighed to the nearest milligram[1]. The following anatomical dimensions were measured (Figure 6.1), using either a dissecting microscope fitted with a graticule or digital vernier callipers: maximum ovarian length and breadth; the length of each uterine horn from the cervix to the start of the oviduct; the diameter of the uterine horns expressed as the average of three measures taken at points approximately quarter, half and three-quarters of the way along the length of each uterine horn. Ovarian volume was calculated using the formula for the volume (V) of an ellipsoid *i.e.* $V = 4/3\pi ab^2$ where a = 1/2 maximum length; b = 1/2 maximum breadth (Woodall and Skinner 1989). The presence and number of embryo's and placental scars were also recorded.

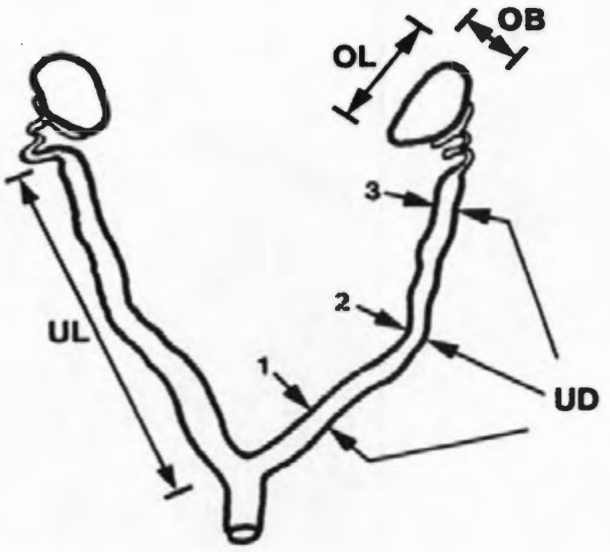

Figure 6.1: Diagrammatic representation of the ovaries and reproductive tract of a female common mole-rat, showing the positions of the anatomical measures recorded for this study. UL = uterine horn length; UD = uterine horn diameter (average of three measures); OL = ovarian length; OB = ovarian breadth (modified with permission from Faulkes 1990).

Gonadal histology

Tissue samples were processed using standard histological techniques (Culling 1975).

[1] Due to the difficulty of controlling for morphometrics changes resulting from pregnancy, reproductive tracts from pregnant females were not included in the assessment of anatomical morphometrics,

Testicular histology

Sections of 7 µm were cut from the equatorial region of each testis, and stained with haematoxylin and eosin. For each animal, several histological measurements, both quantitative and qualitative, were assessed:

(1) Mean seminiferous tubule diameter and seminiferous tubule epithelial thickness were determined from 15 circular seminiferous tubule cross-sections, from a single testis. All measurements were recorded using a compound microscope fitted with a graticule.

(2) Testes were classified for functional state using the spermatogenic index adopted for European voles, *Microtus agrestis*, by Grocock and Clarke (1974), as follows: index 5 = large seminiferous tubules and complete spermatogenesis; index 4 = complete spermatogenesis but elongated spermatozoa and spermatids; index 3 = further reduction in the number of spermatozoa and spermatids; index 2 = no elongated spermatids but round spermatids still occur; index 1 = small tubules containing only Sertoli cells, spermatogonia and primary spermatocytes; index 0 = very small tubules containing only Sertoli cells and spermatogonia, and a few visible spermatocytes. For each animal, the spermatogenic index for 40 seminiferous tubules was determined, and this was averaged to give a single value per animal.

(3) Testes were classified for spermatozoa abundance, using an index ranging from two to zero, as follows: index 2 = fully formed spermatozoa present in the tubules and common/abundant in number; index 1 = fully formed spermatozoa present, but few in number; index 0 = although maturing/elongating spermatids present, no fully formed spermatozoa occur in tubules. For each animal, the spermatozoa abundance index for 40 seminiferous tubules was determined, and this was averaged to give a single value per animal.

(4) The state of interstitial tissue was assessed using a modified version of the interstitial cell index adopted for European voles, *Microtus agrestis*, by Grocock and Clarke

(1974), as follows: index 3 = interstitial cell patches large and abundant, and cell nuclei are round; index 2 = interstitial cell patches are smaller and less abundant, cell nuclei still round; index 1 = interstitial cell patches are small and most nuclei are no longer round. The interstitial cell index for each animal was assessed by looking at all the testicular sections for that animal, and assigning an index describing the typical interstitial cell state. Interstitial cell state was fairly constant for each animal, and varied little between sections

(5) To investigate seasonal fluctuations in Leydig cell activity, the nuclear diameters of 10 randomly selected Leydig cells per testis (all from a single section), were measured using a compound microscope fitted with a graticule. Griffiths (1984) used the same measure to assess seasonal fluctuations in Leydig cell activity of elephant seals, *Mirounga leonina*.

(6) The sexual maturity of males was classified according to the criteria suggested by Kirkpatrick (1955), Hoffmann and Kirkpatrick (1956) and Pudney (1976) for grey squirrels, *Sciurus carolinensis*, and fox squirrels, *S. niger*. Five stages were identified: infantile = small seminiferous tubules with small or no lumena; prepubertal = most tubules containing primary spermatocytes in the interiors; functional = most seminiferous tubules full with sperm production; degenerating = *early stage* - loose primary and secondary spermatocytes, and other cellular debris cluttering the tubule, *middle stage* - more cellular debris cluttering the tubules, and shrinking tubules, *late stage* - advanced degeneration with shrinking tubules and disappearing lumina; redeveloping = forming lumina and layers of developing spermatocytes in tubules. The first two stages were regarded as immature and the rest as adult. For all aspects investigated in this study, only data collected from adult animals were used.

Ovarian histology

Fifteen serial sections of 7 µm were cut at three levels through both the left and right ovary of each female, and counter-stained with haematoxylin and eosin. These sections were used to qualitatively assess the state of ovarian activity in each animal. The ovaries of all females under investigation contained primordial, early primary and primary follicles, and consequently only the presence of secondary follicles, tertiary/Graafian follicles, corpora lutea and luteinized unruptured follicles (LUF's) were recorded. Ovarian follicles were classified according to Wheater *et al.* (1987) and Bennett *et al.* (1994), as follows;

(1) *Primordial follicle*: a primary oocyte surrounded by a single layer of flattened follicular cells. The primary oocyte has a large nucleus, prominent nucleolus and little cytoplasm.

(2) *Early primary follicle*: enlarged follicle containing a greatly enlarged oocyte, surrounded by one of more layers of cuboidal follicular cells. The zona pellucida is sometimes present between the oocyte and the surrounding follicular cells, although it may develop slightly later *i.e.* in the primary follicle.

(3) *Primary follicle*: further enlarged follicle in which the follicular cells have proliferated to form a layer several cells thick, the zona granulosa. The external tissue layer, the theca, has begun to differentiate into the theca interna and the theca externa.

(4) *Secondary follicle*: situated deeper in the ovarian cortex. The zona pellucida has proliferated greatly, and the follicular antrum appears, in which follicular fluid accumulates. The oocyte has almost reached mature size and becomes eccentrically situated. The theca interna and theca externa are now well developed.

(5) *Tertiary/Graafian follicle*: The oocyte stops growing. The follicular antrum becomes markedly enlarged and the zona granulosa forms a layer of even thickness around the periphery of the follicle. The oocyte is surrounded by a thin layer of cells, the corona radiata, which is attached to the zona pellucida by thin bridges of cells.

(6) *Corpus luteum*: a very large structure. After ovulation the zona pellucida is absent, lost with the ovum. The zona granulosa cells increase in size and become steroid secreting.

(7) *Luteinized unruptured follicle (LUF):* unlike the corpus luteum, the zona pellucida of the ova can be seen, clearly indicating the absence of ovulation. The zona granulosa cells increase in size and become steroid secreting.

LUF density was recorded on a nominal index of 0-3, index 0 = zero LUF's and index 3 = high density of LUF's. The LUF density index for each animal was assessed by looking at all the ovarian sections for that animal, and assigning an index describing the typical LUF density. LUF density was fairly constant for each female, and varied little between sections and between ovaries.

Sperm motility

For male common mole-rats, epididymides were dissected away from the testes and cleared of surrounding adipose and connective tissue, and blood vessels. Spermatozoa were extracted from a cleanly dissected portion of the cauda epididymis, into Ham's F10 culture medium. A 10 µl drop of sperm suspension was then placed in a 1 ml motility bath and examined on a preheated microscope stage (34°C), using negative phase contrast optics at a magnification of x160. The base of the motility bath consisted of an optical coverslip, to allow for optimal microscopic conditions. The images were recorded onto videotape using a VHS recorder and a colour video camera. Sperm motility was analysed using a computerised image analysis system (Sperm Motility Quantifier, Wirson Scientific and Precision Equipment, Auckland Park, Johannesburg). This system has been used successfully on a range of mammalian and amphibian species (Kaskar *et al.* 1993; 1994; Van der Horst *et al.* 1995).

The recordings of sperm motion were captured with a frame skip of zero, at an analysis rate of 50 Hz. The average number of frames analysed was 21.1 ± 0.3 frames, with a minimum and a maximum of 10 and 32 frames in the sperm trajectory respectively. The following motility parameters were measured: curvilinear velocity; straightline velocity; average path velocity; linearity; amplitude of lateral head displacement; wobble; straightness; dance; radian; curvature; percentage motility and percentage progressive motility (see Appendix II for explanation of motility measures). A minimum of 200 spermatozoa, including at least 100 motile spermatozoa, were analysed for each animal.

Sperm morphology

For male *C. h. hottentotus*, spermatozoa were aspirated from the cauda epididymis into Ham's F10 culture medium. A 10 µl sample of sperm suspension was incubated for 5 min at 34°C in 20 µl eosin-nigrosin stain, mounted on a glass slide, and examined under oil emersion at a magnification of x1000. A total of 200 spermatozoa were analysed per animal. Spermatozoa were categorised as normal or having one of the following structural defects: head defect (bicephalic, macrocephalic, microcephalic, other); tail-/head-less; mitochondrial sheath defect, cytoplasmic droplet; bent midpiece; flagellar defect (bent primary piece, looped tail, coiled/knotted tail, biflagellate, circular tail) (Plates 6.1 & 6.2). Similar categories of sperm morphology have been used for the domestic ferrett, *Mustela putorius furo*, the black-footed ferrett, *Mustela nigripes*, (Curry *et al.* 1989) and the Florida panther, *Felis concolor*, (Barone *et al.* 1994).

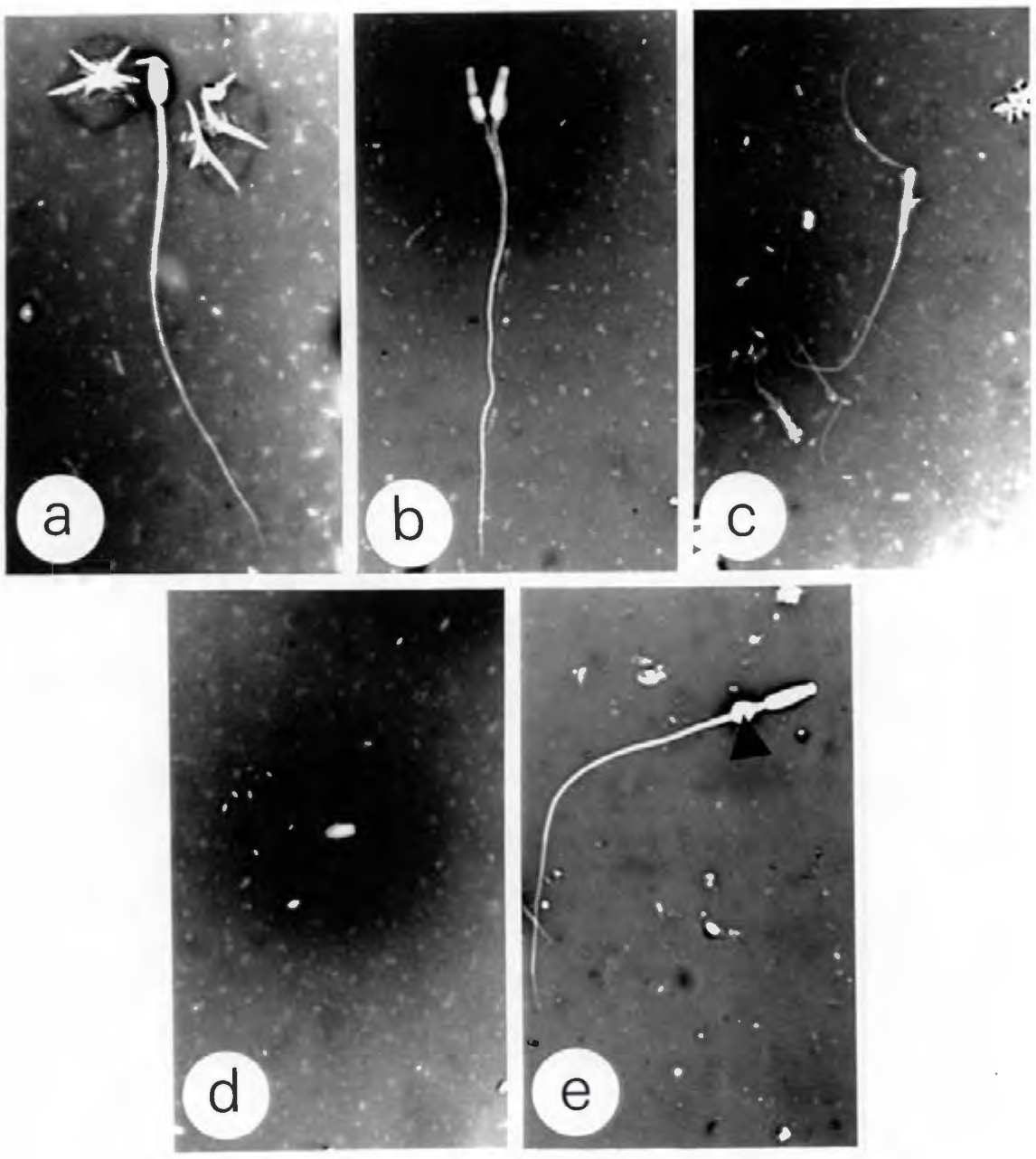

Plate 6.1: Photographs to show sperm morphology categories; (a) normal, (b) bicephalic (head defect), (c) headless, (d) tailless, and (e) cytoplasmic droplet (indicated by arrow) and marginally bent primary piece (flagellar defect). All photographs taken under oil emersion at a magnification of x1000 (Photographs© by Andrew Spinks).

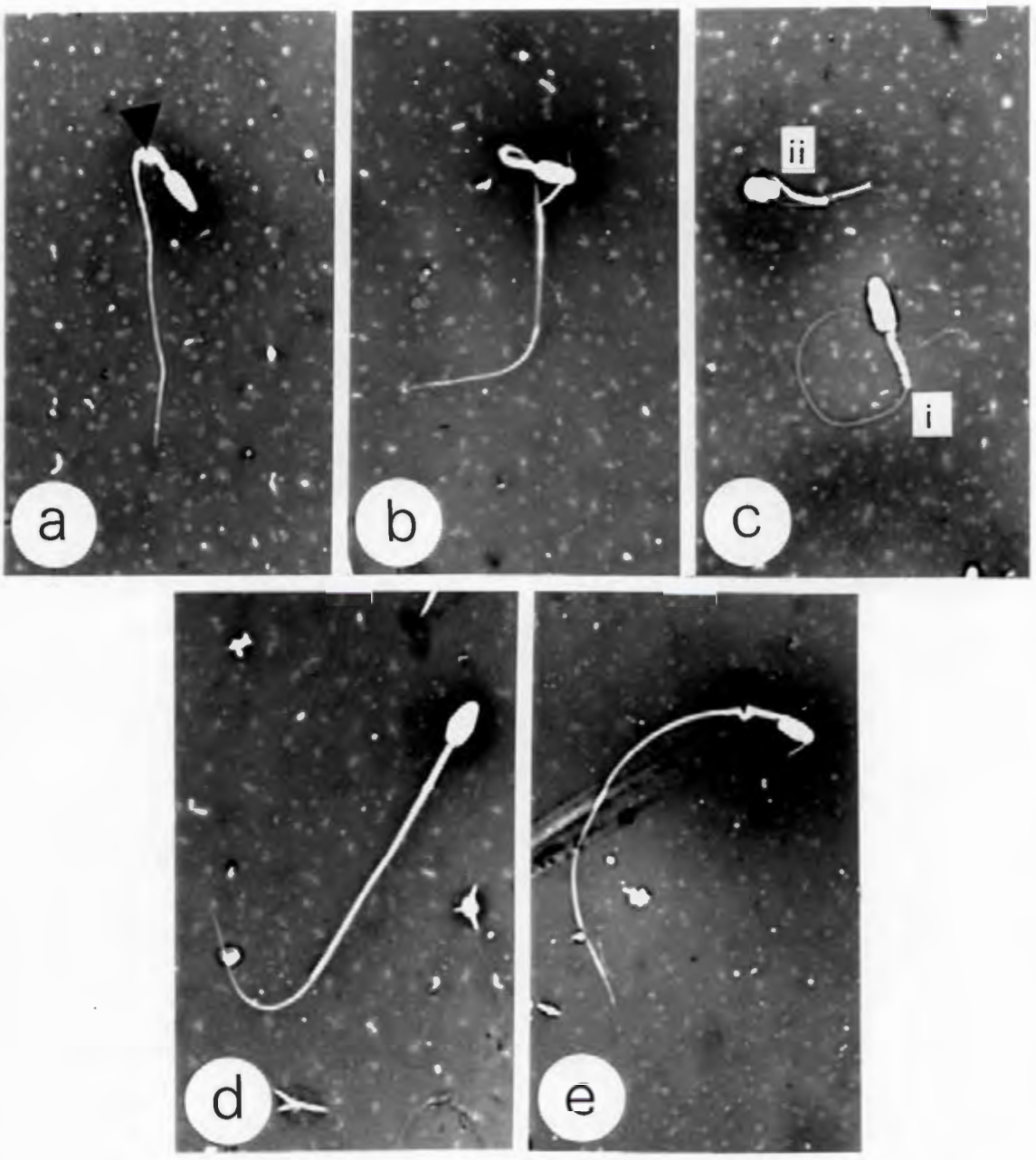

Plate 6.2: Photographs to show sperm morphology categories; (a) bent midpiece and cytoplasmic droplet (indicated by arrow), (b) bent midpiece and bent primary piece (flagellar defect), (c) looped tail (i), coiled/knotted tail (ii) (both flagellar defects), (d) bent primary piece (flagellar defect), and (e) circular tail (flagellar defect) and cytoplasmic droplet (indicated by arrow). All photographs taken under oil emersion at a magnification of x1000 (Photographs© by Andrew Spinks).

Statistical analyses

Regression analysis revealed a strong correlation between body mass and measurements of testicular and ovarian gross anatomy, and testicular histological morphometrics. Consequently, body mass was introduced as a covariant during subsequent analysis of these parameters. In contrast, none of the endocrine or sperm morphology or motility variables recorded correlated significantly with body mass. Accordingly, these parameters were not standardised relative to body mass.

For sperm morphology, sperm motility and female reproductive tract anatomical morphometrics, factor analysis failed to identify a restricted subset of determinant factors, accounting for most of the variance. Thus, for the purposes of this study, all sperm morphology and motility measures, and all female reproductive tract anatomical measures were analysed.

For reproductive anatomy and histology, sperm motility and morphology, plasma steroid concentrations and basal plasma bioactive LH concentrations comparative testing was done using the Multifactor Analysis of Variance (MANOVA) (Zar 1984). Where significant interactions were indicated, One-way Analysis of Variance (ANOVA) was used (Zar 1984). Responses to GnRH challenges were analysed statistically using the Mann Whitney U-test (Zar 1984). In making statistical comparisons, the individual animal was considered to be the appropriate unit of replication and comparison. Consequently, when reporting averages for experimental groups and performing analyses of variance, computations were made using one value per animal (replicate measures made from a single animal were averaged to provide one value per animal).

Differences in spermatogenic index, spermatozoa abundance index and interstitial cell index between males of different reproductive status, from the two localities and in and out of the breeding period, were not tested statistically. These measures facilitate identification of reproductive activity within a male, but are too coarse to allow for fine,

statistical differentiation between groups. Similarly, ovarian histology was used to qualitatively assess the state of ovarian activity in each female. Consequently, differences in ovarian histology between females, were not tested statistically.

RESULTS 1: THE EFFECTS OF REPRODUCTIVE STATUS

Males

For males collected from both study sites, differences in reproductive status were not reflected in any of the parameters evaluated. Thus there were no significant differences between reproductive and non-reproductive males in the anatomical, histological, sperm motility, sperm morphological or endocrine measurements determined in this investigation.

Testicular anatomy and histology

Testis mass and volume did not differ significantly between reproductive (Sir Lowry's Pass [SLP]: n = 18, Steinkopf [ST]: n = 15) and non-reproductive males (SLP: n = 37, ST: n = 17; Figure 6.2) from either Sir Lowry's Pass or Steinkopf. Moreover, diameter and epithelial thickness of the seminiferous tubules were similar for reproductive (SLP: n = 14, ST: n = 10) and non-reproductive males (SLP: n = 29, ST: n = 6; Figure 6.3) from both sites.

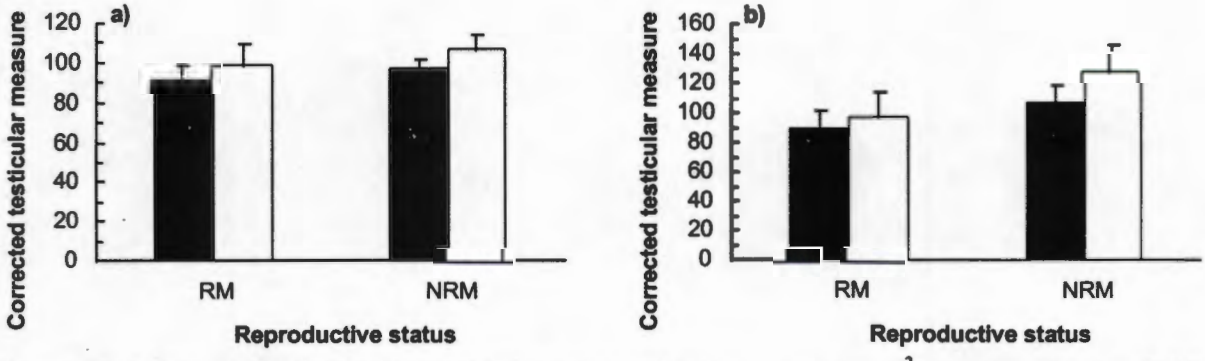

Figure 6.2: Mean (± SE) testicular mass (■, in mg) and volume (□, in mm^3) for reproductive (RM) and non-reproductive (NRM) *C. h. hottentotus* males collected at (a) Sir Lowry's Pass; and (b) Steinkopf. Values are corrected for body mass by the extraction of residuals.

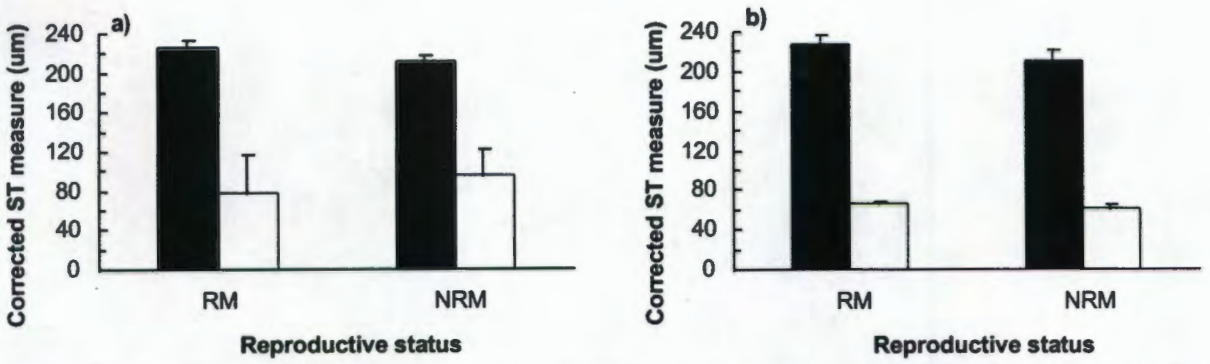

Figure 6.3: Mean (± SE) seminiferous tubule diameter (■) and seminiferous tubule epithelial diameter (□) for reproductive (RM) and non-reproductive (NRM) *C. h. hottentotus* males collected at (a) Sir Lowry's Pass; and (b) Steinkopf. Values are corrected for body mass by the extraction of residuals. ST = seminiferous tubule.

Table 6.2: Comparative testicular histological features for reproductive (RM) and non-reproductive (NRM) *C. h. hottentotus* males collected from (1) Sir Lowry's Pass, and (2) Steinkopf.

Variable	Sir Lowry's Pass		Steinkopf	
	RM (n = 14)	NRM (n = 29)	RM (n = 10)	NRM (n = 6)
Spermatogenic index	3.68 ± 0.09	3.42 ± 0.07	3.44 ± 0.13	3.03 ± 0.19
Sperm abundance index	1.07 ± 0.04	0.98 ± 0.04	0.98 ± 0.06	0.92 ± 0.13
Interstitial cell index	2.57 ± 0.17	2.43 ± 0.11	2.70 ± 0.15	2.33 ± 0.21
Leydig cell nuclear diameter	6.85 ± 0.22 [a]	6.72 ± 0.14 [a]	7.57 ± 0.21 [b]	7.69 ± 0.26 [b]
Sexual maturity‡	100%	100%	100%	100%

All results are expressed as mean ± SE; RM = reproductive males; NRM = non-reproductive males; BP = breeding period; NBP = non-breeding period; ‡ sexual maturity indicates the percentage of males investigated who had functional testes (see Methods and Materials); a: MANOVA, $F_{(1, 42)} = 0.19, p = 0.67$; b: MANOVA, $F_{(1, 15)} = 0.13, p = 0.72$.

As suggested by the spermatogenic index, all males exhibited complete spermatogenesis and the testicular functional state did not differ markedly between reproductive and non-reproductive males from either locality (Table 6.2). Furthermore, the sperm abundance index and interstitial cell index revealed that sperm and interstitial cell abundance respectively, were comparable for males of both status from Sir Lowry's Pass and Steinkopf (Table 6.2). There was no significant difference in Leydig cell nuclear diameter between reproductive and non-reproductive males from either study site

(Table 6.2). All males used in this investigation were sexually mature, their testes being categorised as *functional* (see Methods & Materials; Table 6.2).

Sperm motility and morphology

An analogous pattern was evident in the sperm parameters. As mentioned, spermatogenesis was observed in the testes of all animals in the study (Table 6.2). For both study localities there was no significant difference between the sperm motility parameters of reproductive and non-reproductive males (Table 6.3). Reproductive and non-reproductive males from both sites had a comparable percentage of spermatozoa with normal morphology (Table 6.3). Furthermore, at Sir Lowry's Pass both groups showed an equivalent distribution of sperm defects (Figure 6.4a). At Steinkopf, although the distribution of most sperm defects was statistically comparable between males of different status, non-reproductive males had significantly more spermatozoa with bent midpieces' than did reproductive males (Figure 6.4b)

Endocrinology

Basal LH concentrations were not significantly different between reproductive [SLP: 3.81 ± 1.05 miu.ml^{-1} (13), ST: 2.72 ± 0.36 miu.ml^{-1} (17)] and non-reproductive [SLP: 3.93 ± 0.49 miu.ml^{-1} (25), ST: 4.93 ± 1.22 miu.ml^{-1} (20)] males from either locality (SLP: MANOVA, $F_{(1, 37)} = 0.002$, $p = 0.96$; ST: MANOVA, $F_{(1, 35)} = 2.78$, $p = 0.11$).

There was no significant difference in pre- and post-LH concentrations in response to a single 200 µl challenge of physiological saline in male common mole-rats (Mann Whitney U-test, $U = 0.18$, $n = 20$, $p = 0.86$). Due to the small sample size, the saline challenge results for all males irrespective of season, status or locality were combined for statistical

Table 6.3: Comparative sperm motility and sperm morphology characteristics for reproductive (RM) and non-reproductive (NRM) *C. h. hottentotus* males collected (1) from Sir Lowry's Pass, and (2) from Steinkopf.

Motility variable	Sir Lowry's Pass				Steinkopf			
	RM	NRM	*F-ratio*	*p*	RM	NRM	*F-ratio*	*p*
Sperm motility								
VCL (mms^{-1})	148.36 ± 4.39(8)	149.54 ± 4.10(8)	0.04	0.9	129.37± 3.89(8)	128.58 ± 6.96(8)	0.01	0.9
VSL (mms^{-1})	120.84 ± 5.89(8)	118.86 ± 5.00(8)	0.06	0.8	98.62 ± 5.17(8)	96.43 ± 8.58(8)	0.04	0.8
VAP (mms^{-1})	131.64 ± 5.95(8)	130.36 ± 4.39(8)	0.03	0.9	109.54 ± 5.08(8)	107.60 ± 8.44(8)	0.04	0.9
Linearity (%)	76.37 ± 2.07(8)	75.16 ± 1.92(8)	0.18	0.7	72.72 ± 2.02(8)	71.01 ± 3.25(8)	0.19	0.7
ALH (mm)	4.40 ± 0.17(8)	4.62 ± 0.09(8)	1.65	0.2	4.36 ± 0.07(8)	4.50 ± 0.11(8)	1.09	0.3
Wobble	0.85 ± 0.02(8)	0.85 ± 0.01(8)	0.15	0.7	0.82 ± 0.02(8)	0.81 ± 0.03(8)	0.20	0.7
STR	0.87 ± 0.01(8)	0.87 ± 0.02(8)	0.06	0.8	0.87 ± 0.01(8)	0.86 ± 0.02(8)	0.35	0.6
Dance (mm^2s^{-1})	403.79 ± 39.59(8)	505.90 ± 29.76(8)	4.25	0.06	414.03 ± 17.96(8)	427.88 ± 40.79(8)	0.90	0.8
Radian (mm)	1.42 ± 0.05(8)	1.43 ± 0.07(8)	0.002	1.0	1.69 ± 0.06(8)	1.69 ± 0.12(8)	0.002	1.0
Curvature	0.41 ± 0.01(8)	0.40 ± 0.03(8)	0.01	0.9	0.41 ± 0.01(8)	0.38 ± 0.02(8)	2.76	0.1
% motile	62.57 ± 4.10(8)	61.27 ± 4.82(8)	0.04	0.9	73.94 ± 6.85(8)	62.82 ± 5.41(8)	1.78	0.2
% prog. motile	56.82 ± 4.08(8)	55.56 ± 5.08(8)	0.04	0.9	68.08 ± 6.28(8)	56.52 ± 5.87(8)	1.91	0.2
Sperm morphology								
Normal morphology (%)	28.71 ± 1.71(7)	25.29 ± 1.80(7)	2.08	0.2	25.83 ± 0.95(7)	24.90 ± 2.32(5)	0.16	0.7

All results are expressed as mean ± SE(*n*); RM = reproductive males; NRM = non-reproductive males; BP = breeding period; NBP = non-breeding period; VCL = curvilinear velocity; VSL = straightline velocity; VAP = average path velocity; ALH = amplitude of lateral head displacement; STR = straightness; prog. = progressively.

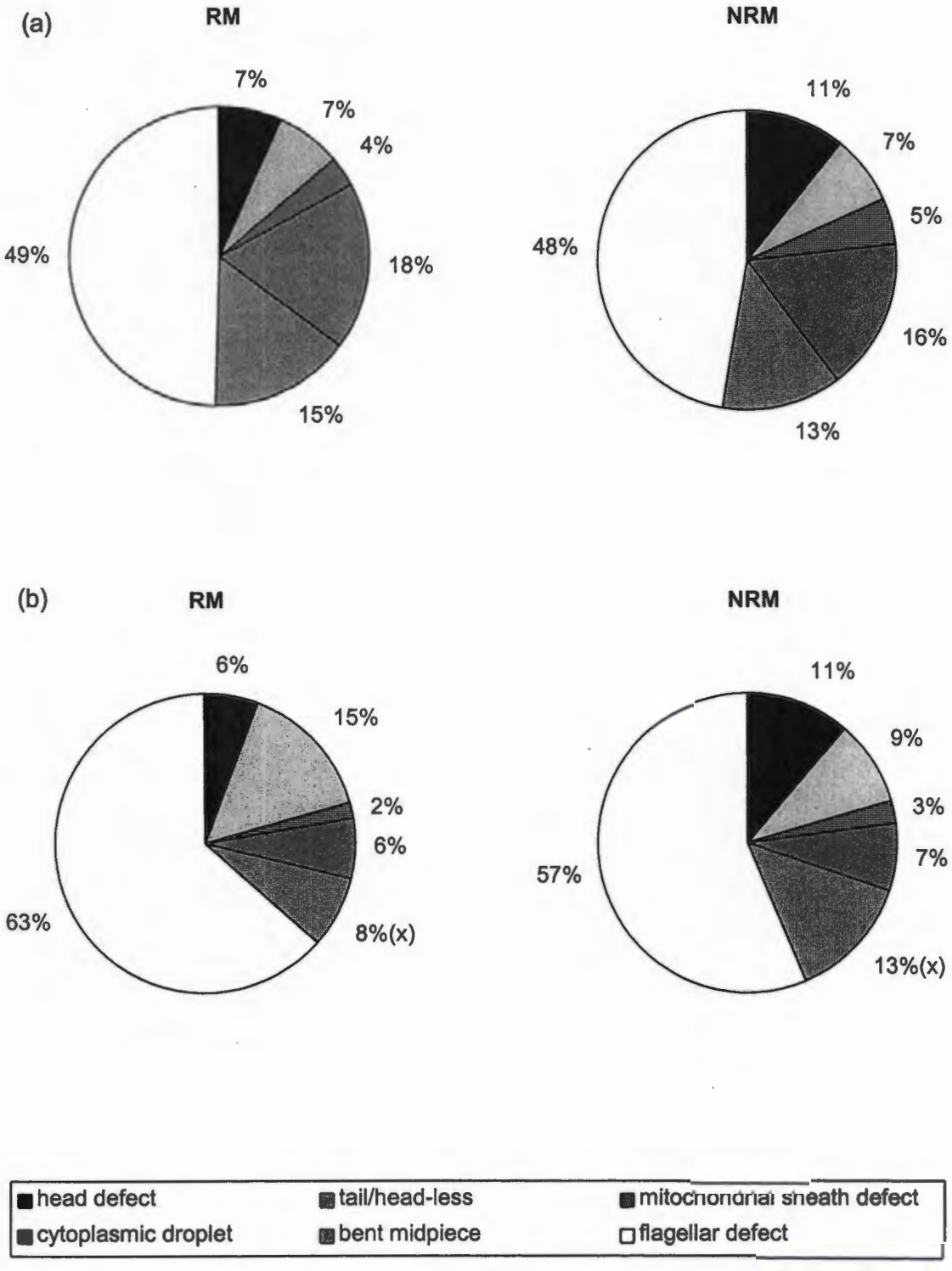

Figure 6.4 The distribution of sperm defects in reproductive (RM) and non-reproductive (NRM) *C. h. hottentotus* males (a) collected at Sir Lowry's Pass; and (b) collected at Steinkopf, x: MANOVA, $F_{(1,12)} = 6.78, p = 0.03$.

analysis (control results are included in Figures 6.5 & 6.15 for reference purposes). This was considered appropriate as the aim of the saline challenge is simply to control for procedural effects on plasma bioactive LH concentrations, negating the need to distinguish between animals of differing status and from different localities. The absence of a significant response to the saline challenge effectively excludes the experimental protocol as a determinant of the outcome of the GnRH challenge.

For both Sir Lowry's Pass and Steinkopf there was a significant response in reproductive (SLP: $n = 8$, ST: $n = 12$) and non-reproductive males (SLP: $n = 15$, ST: $n = 17$) to a single subcutaneous challenge of 2µg GnRH (Figure 6.5). There was no significant difference in the magnitude of the LH response between reproductive and non-reproductive males from both localities, and post-challenge plasma bioactive LH concentrations did not differ significantly between animals of differing reproductive status (SLP: MANOVA, $F_{(1, 22)} = 0.23$, $p = 0.65$; ST: MANOVA, $F_{(1, 28)} = 2.53$, $p = 0.12$; Figure 6.5).

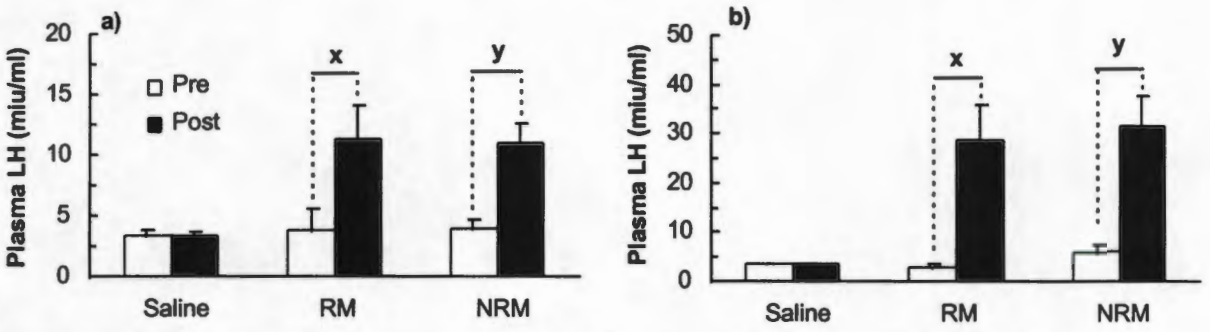

Figure 6.5: Concentrations of plasma bioactive LH (mean ± SE) in reproductive (RM) and non-reproductive (NRM) *C. h. hottentotus* males, before (Pre) and 20 min after (Post) a single s.c. injection of GnRH or saline: (a) collected at Sir Lowry's Pass, x: Mann Whitney U-test, $U = 2.37$, $p = 0.02$, y: Mann Whitney U-test, $U = 3.32$, $p = 0.009$; and (b) collected at Steinkopf, x: Mann Whitney U-test, $U = 3.61$, $p = 0.0003$, y: Mann Whitney U-test, $U = 3.84$, $p = 0.0001$.

Because the material used for the analysis of plasma testosterone concentrations was collected from sacrificed animals, sample sizes were necessarily small, making unequivocal testing of differences difficult. Nevertheless, the results show that plasma testosterone concentrations did not differ significantly between reproductive (SLP: $n = 8$, ST:

n = 4) and non-reproductive males (SLP: n = 18, ST: n = 11) from both localities (SLP: MANOVA, $F_{(1, 25)} = 2.09$, $p = 0.16$; ST: MANOVA, $F_{(1, 14)} = 1.11$, $p = 0.31$; Figure 6.6).

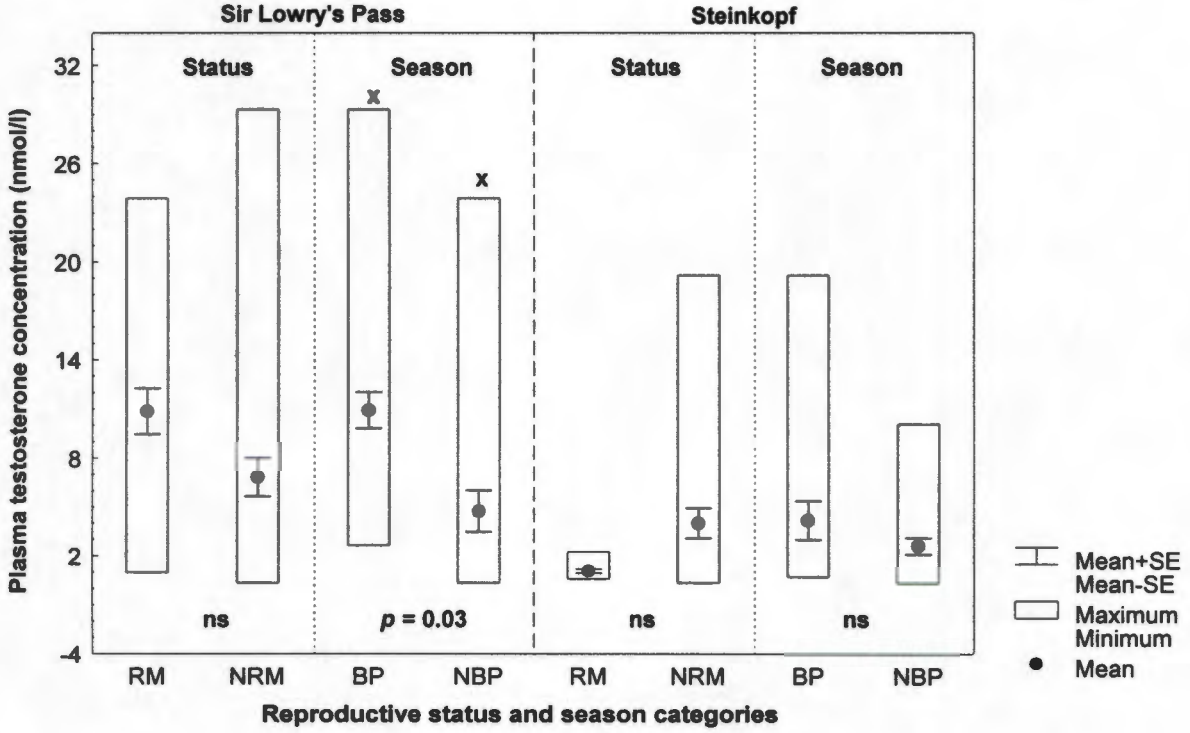

Figure 6.6 Concentrations of plasma testosterone (mean ± SE, and range) in *C. h. hottentotus* males, collected at Sir Lowry's Pass and Steinkopf. For each locality data are presented for reproductive (RM) and non-reproductive (NRM) males, and for males caught during the breeding (BP) and non-breeding (NBP) periods. x: MANOVA, $F_{(1, 25)} = 5.20$, $p = 0.03$; ns = non significant

Females

For females collected from both localities differences in reproductive status were reflected in many of the parameters under investigation. There were marked differences between reproductive and non-reproductive females in the gross anatomical and some endocrine measurements evaluated in this study.

Ovarian and uterine anatomy

The reproductive tracts of reproductive females (SLP: n = 11, ST: n = 10) from both localities were significantly heavier than those of non-reproductive females (SLP: n = 9, ST: n = 20; Figure 6.7). Moreover, reproductive females (n = 15) from Sir Lowry's Pass exhibited a

significantly greater ovarian mass than non-reproductive females (n = 9; Figure 6.7a). Similarly, although the difference was not statistically significant (MANOVA, $F(1, 33) = 0.17$, $p = 0.69$), the ovaries of reproductive females (n = 14) from Steinkopf were notably heavier than those of non-reproductive females (n = 20; Figure 6.7b). Ovarian volume did not differ significantly between reproductive (SLP: n = 16, ST: n = 14) and non-reproductive females (SLP: n = 9, ST: n = 20; Figure 6.7) from either locality.

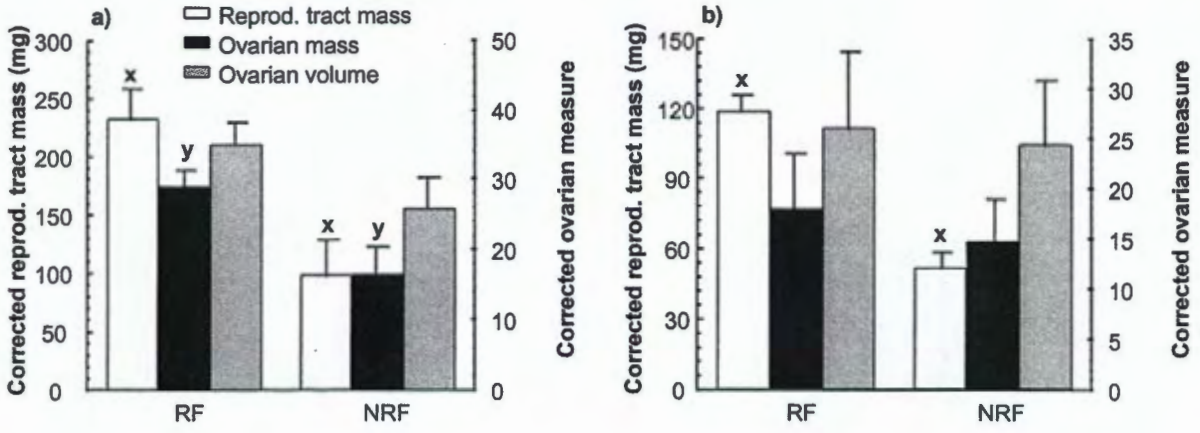

Figure 6.7: Mean (± SE) reproductive tract mass (mg; left axis), ovarian mass (mg; right axis) and ovarian volume (mm^3; right axis) for reproductive (RF) and non-reproductive (NRF) *C. h. hottentotus* females collected at (a) Sir Lowry's Pass, x: MANOVA, $F_{(1, 19)} = 9.12$, $p = 0.009$; y: MANOVA, $F_{(1, 23)} = 4.47$, $p = 0.05$; and (b) Steinkopf, x: MANOVA, $F_{(1, 29)} = 87.13$, $p < 0.00001$. Values are corrected for body mass by the extraction of residuals.

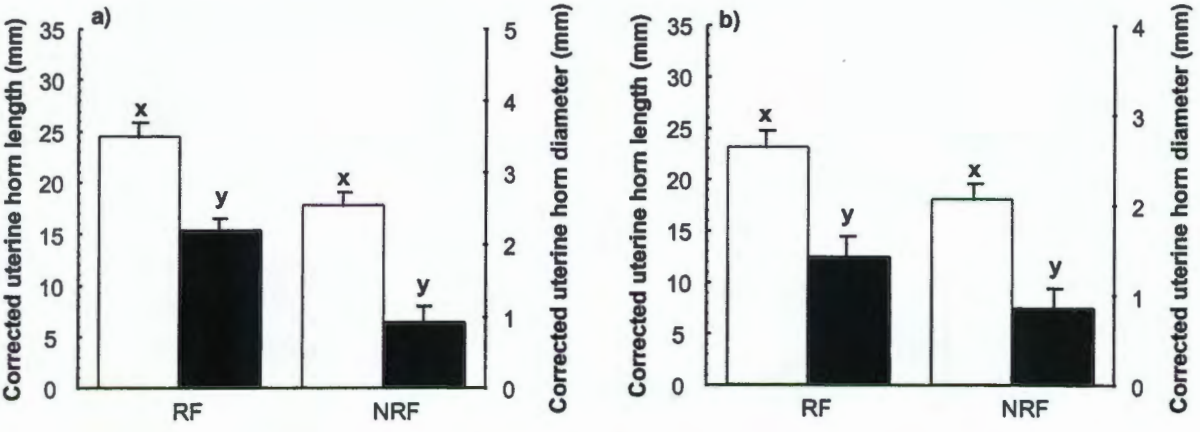

Figure 6.8: Mean (± SE) uterine horn length (mm; left axis) and uterine horn diameter (mm; right axis) for reproductive (RF) and non-reproductive (NRF) *C. h. hottentotus* females collected at (a) Sir Lowry's Pass, x: MANOVA, $F_{(1, 19)} = 20.97$, $p = 0.0003$; y: MANOVA, $F_{(1, 19)} = 68.68$, $p < 0.00001$; and (b) Steinkopf, x: MANOVA, $F_{(1, 29)} = 12.96$, $p = 0.001$, y: MANOVA, $F_{(1, 29)} = 34.73$, $p < 0.00001$. Values are corrected for body mass by the extraction of residuals.

The length and diameter of the uterine horns differed significantly between reproductive (SLP: $n = 11$, ST: $n = 10$) and non-reproductive females (SLP: $n = 9$, ST: $n = 20$; Figure 6.8) from Sir Lowry's Pass and Steinkopf. For both localities the uterine horns of reproductive females were significantly longer and wider than those of non-reproductive females (Figure 6.8).

Ovarian histology

Status-related differences in ovarian histology are graphically summarised in Figure 6.9. The basic pattern of status-related differences appears to be similar for Sir Lowry's Pass and Steinkopf. For both localities, most reproductive (SLP: $n = 12$, ST: $n = 10$) and non-reproductive females (SLP: $n = 11$, ST: $n = 10$) exhibited secondary follicles and tertiary (or Graafian) follicles in their ovaries (Figure 6.9). However, at both Steinkopf and Sir Lowry's Pass, LUF's were evident in a greater percentage of non-reproductive than reproductive females, this being most marked for Sir Lowry's Pass animals (Figure 6.9). For both study sites, only the ovaries of reproductive females had corpora lutea (Figure 6.9).

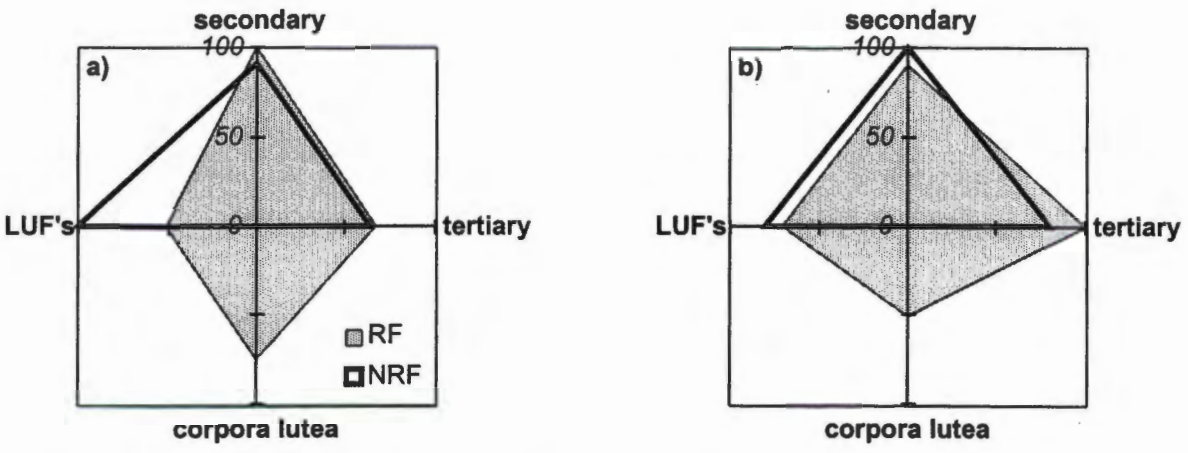

Figure 6.9: Radar diagrams showing the percentage of reproductive (RF) and non-reproductive (NRF) *C. h. hottentotus* females collected at (a) Sir Lowry's Pass and (b) Steinkopf, exhibiting secondary and tertiary follicles, corpora lutea and luteinized unruptured follicles in their ovaries. Each axis represents the overall percentage of females of each status from each locality exhibiting a particular follicular type.

Status-related differences were also evident in LUF density. Reproductive females [SLP: 0.8 ± 0.2 (13), ST: 1.7 ± 0.4 (10)] from both localities had notably lower LUF densities than non-reproductive females [SLP: 2.2 ± 0.3 (11), ST: 2.2 ± 0.4 (10)].

Endocrinology

Basal LH concentrations were not significantly different between reproductive [SLP: 5.15 ± 1.09 miu.ml^{-1} (11), ST: 4.40 ± 0.72 miu.ml^{-1} (17)] and non-reproductive [SLP: 4.19 ± 0.73 miu.ml^{-1} (15), ST: 3.50 ± 0.48 miu.ml^{-1} (15)] females from either locality (SLP: MANOVA, $F_{(1, 25)} = 1.02$, $p = 0.32$, ST: MANOVA, $F_{(1, 31)} = 1.12$, $p = 0.30$).

There was no significant difference in pre- and post-LH concentrations in response to a single 200 µl challenge of physiological saline in female common mole-rats (Mann Whitney U-test, $U = 0.15$, $n = 10$, $p = 0.88$). As for the males, the saline challenge results for all females, irrespective of season, status or locality were combined for statistical analysis (control results are included in Figures 6.10 & 6.19 for reference purposes). The absence of a significant response to the saline challenge effectively excludes the experimental protocol as a determinant of GnRH challenge outcome.

For females from Steinkopf there was a significant response in reproductive ($n = 14$) and non-reproductive females ($n = 12$) to a single subcutaneous challenge of 2 µg GnRH (Figure 6.10b). There was no significant difference in the magnitude of the LH response between reproductive and non-reproductive females from Steinkopf, and post-challenge plasma bioactive LH concentrations did not differ significantly between animals of differing reproductive status (MANOVA, $F_{(1, 25)} = 3.26$, $p = 0.08$).

In contrast, although both reproductive ($n = 9$) and non-reproductive female ($n = 13$) *C. h. hottentotus* from Sir Lowry's Pass exhibited a slight response to a single subcutaneous challenge of 2 µg GnRH (Figure 6.10a), this response was non-significant. However, there

was a significant difference in the magnitude of the LH response between reproductive and non-reproductive females from Sir Lowry's Pass, and post-challenge plasma bioactive LH concentrations were significantly higher in reproductive females (MANOVA, $F_{(1, 21)} = 6.39$, $p = 0.02$; Figure 6.10a).

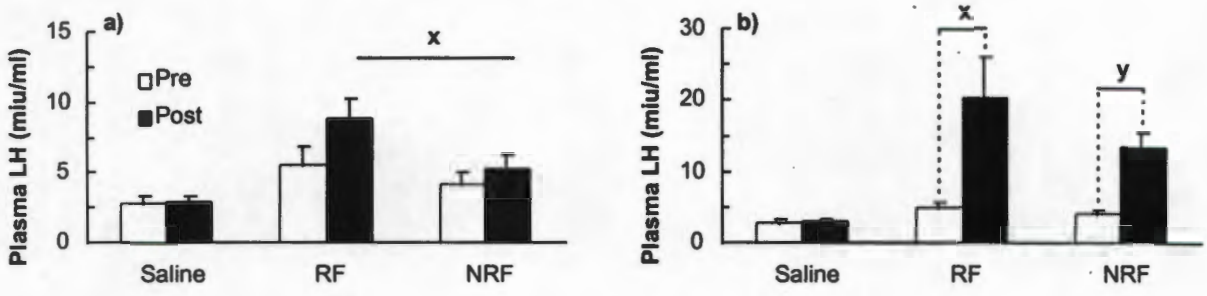

Figure 6.10: Concentrations of plasma bioactive LH (mean ± SE) in reproductive (RF) and non-reproductive (NRF) *C. h. hottentotus* females, before (Pre) and 20 min after (Post) a single s.c. injection of GnRH or saline: (a) collected at Sir Lowry's Pass, x: MANOVA, $F(1, 21) = 6.39$, $p = 0.02$; and (b) collected at Steinkopf, x: Mann Whitney U-test, $U = 2.32$, $p = 0.02$, y: Mann Whitney U-test, $U = 3.50$, $p = 0.0005$.

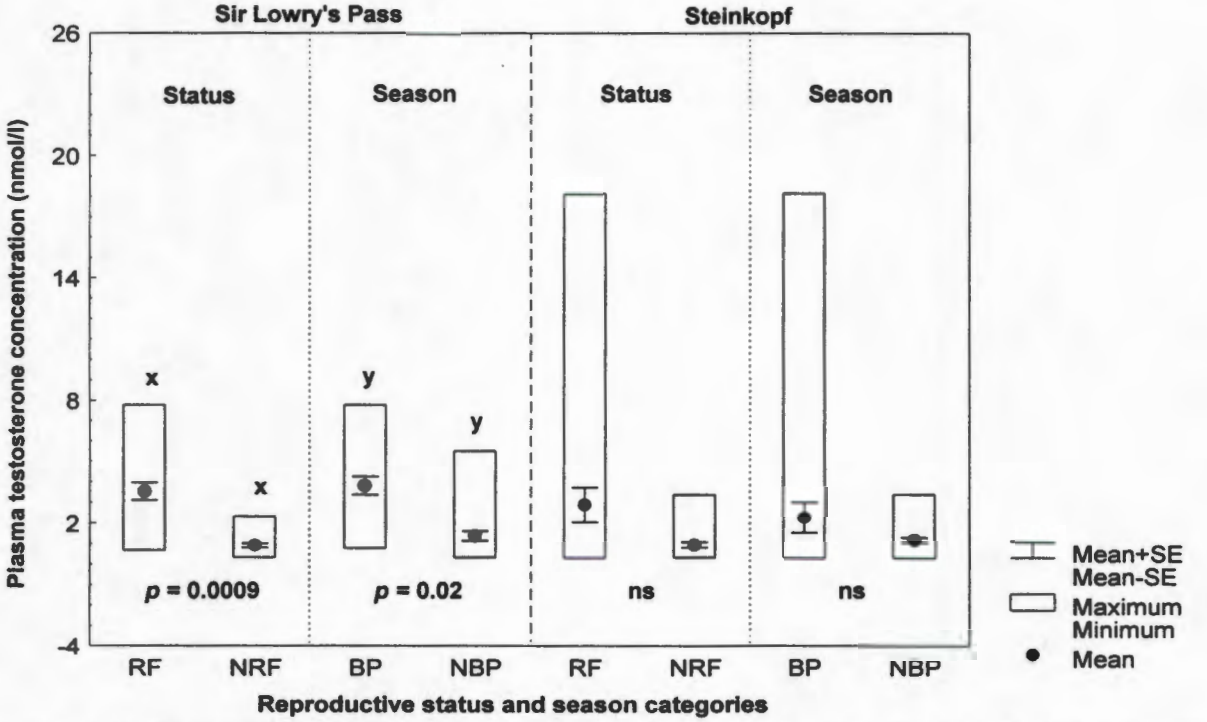

Figure 6.11 Concentrations of plasma testosterone (mean ± SE, and range) in *C. h. hottentotus* females, collected at Sir Lowry's Pass and Steinkopf. For each locality data are presented for reproductive (RF) and non-reproductive (NRF) females, and for females caught during the breeding (BP) and non-breeding (NBP) periods. x: MANOVA, $F_{(1, 19)} = 16.51$, $p = 0.0009$; y: MANOVA, $F_{(1, 19)} = 7.47$, $p = 0.02$; ns = non significant.

Reproductive females (n = 11) from Sir Lowry's Pass exhibited significantly higher plasma testosterone concentrations than non-reproductive females (n = 9; Figure 6.11). Although not statistically significant (MANOVA, $F_{(1, 25)} = 2.60$, $p = 0.12$), a similar pattern was evident at Steinkopf, with reproductive females (n = 11) exhibiting markedly higher testosterone concentrations than non-reproductive females (n = 15; Figure 6.11).

RESULTS 2: SEASONAL DIFFERENCES

The main aim of this chapter is to investigate the effects of reproductive status on *C. h. hottentotus* male and female reproductive characteristics. However, as outlined in the introduction to this chapter, interpretations of the effects of reproductive status may be confounded by the reproductive periodicity prevalent within the common mole-rat (Chapter 1). Consequently differences in reproductive characteristics between the breeding and non-breeding periods were assessed to ensure that the effects of seasonality did not obscure the effects of reproductive status.

Males

Testicular anatomy and histology

Seasonal differences in reproductive characteristics in males collected from Sir Lowry's Pass were revealed in the analyses of testicular anatomical and histological morphometric data. Males caught during the breeding period (n = 35) had testes of a significantly smaller mass and volume than those captured outside the breeding season (n = 20; Figure 6.12a). Furthermore, the diameter of the seminiferous tubules of males during the breeding season (n = 25) were significantly smaller than those of males outside the breeding period (n = 18; Figure 6.13a). Although not statistically significant, seminiferous tubule epithelial diameter

was also markedly smaller in males caught during the breeding period than during the non-breeding period (MANOVA, $F_{(1, 42)} = 2.10$, $p = 0.16$; Figure 6.13a).

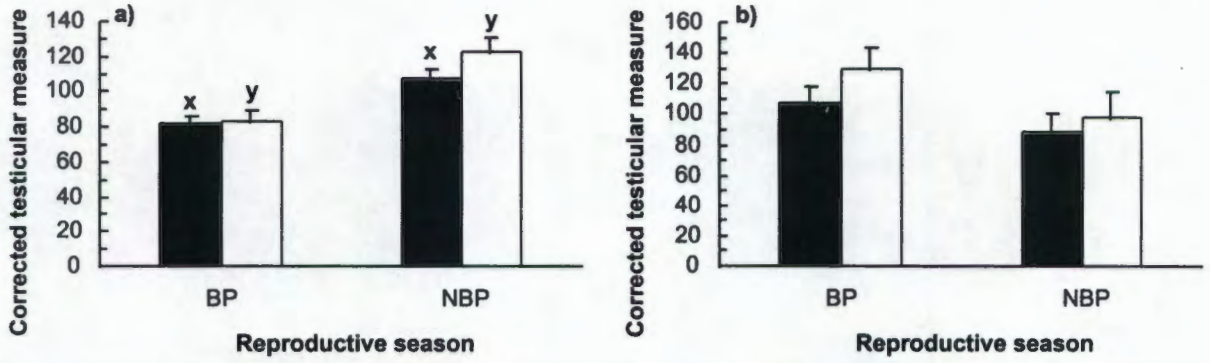

Figure 6.12: Mean (± SE) testicular mass (■, in mg) and volume (□, in mm^3) for *C. h. hottentotus* males caught during the breeding (BP) and non-breeding (NBP) periods, (a) males collected at Sir Lowry's Pass, x: MANOVA, $F_{(1, 54)} = 16.32$, $p = 0.0002$; y: MANOVA, $F_{(1, 54)} = 17.41$, $p = 0.0001$; and (b) males collected at Steinkopf. Values are corrected for body mass by the extraction of residuals.

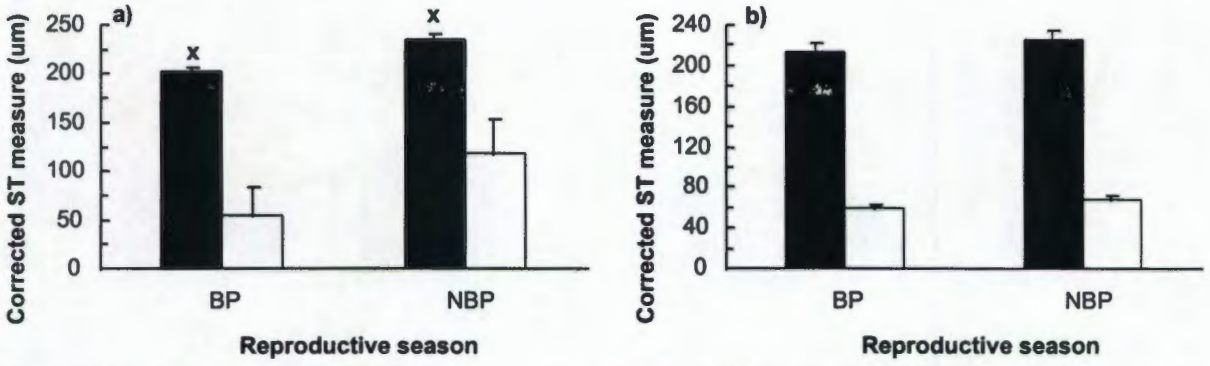

Figure 6.13: Mean (± SE) seminiferous tubule diameter (■) and seminiferous tubule epithelial diameter (□) for *C. h. hottentotus* males caught during the breeding (BP) and non-breeding (NBP) periods, (a) males collected at Sir Lowry's Pass, x: MANOVA, $F_{(1, 42)} = 27.26$, $p < 0.00001$; and (b) males collected at Steinkopf. Values are corrected for body mass by the extraction of residuals. ST = seminiferous tubule.

In contrast to these results, males from Steinkopf exhibited no seasonal manifestations on testicular anatomical and histological morphometrics. Testis mass and volume did not differ significantly between males caught during the breeding ($n = 17$) and non-breeding periods ($n = 15$; Figure 6.12b). Moreover, diameter and epithelial thickness of the seminiferous tubules were similar for males secured during ($n = 9$) and outside ($n = 7$; Figure 6.13b) the breeding period.

Implicit from the spermatogenic index is that all males exhibited complete spermatogenesis both during and outside the breeding period, and for both study populations (Table 6.4). Furthermore, the sperm abundance index and interstitial cell index for males from both Sir Lowry's Pass and Steinkopf revealed that sperm and interstitial cell abundance respectively were comparable during the breeding and non-breeding periods (Table 6.4). There were no significant differences in Leydig cell nuclear diameter between animals caught during the breeding and non-breeding periods at either study site (Table 6.4). All males used in this investigation were sexually mature, their testes being categorised as *functional* (see Methods & Materials; Table 6.4).

Table 6.4: Comparative testicular histological features for *C. h. hottentotus* males caught during the breeding (BP) and non-breeding (NBP) periods (1) collected from Sir Lowry's Pass, and (2) collected from Steinkopf.

Variable	Sir Lowry's Pass		Steinkopf	
	BP (n = 25)	NBP (n = 18)	BP (n = 9)	NBP (n = 7)
Spermatogenic index	3.41 ± 0.08	3.65 ± 0.06	3.27 ± 0.15	3.31 ± 0.20
Sperm abundance index	0.95 ± 0.04	1.09 ± 0.04	0.96 ± 0.08	0.94 ± 0.10
Interstitial cell index	2.58 ± 0.12	2.33 ± 0.14	2.33 ± 0.17	2.86 ± 0.14
Leydig cell nuclear diameter	6.68 ± 0.14 [a]	6.89 ± 0.16 [a]	7.55 ± 0.22 [b]	7.71 ± 0.24 [b]
Sexual maturity[‡]	100%	100%	100%	100%

All results are expressed as mean ± SE; RM = reproductive males; NRM = non-reproductive males; BP = breeding period; NBP = non-breeding period; [‡] sexual maturity indicates the percentage of males investigated who had functional testes (see Methods and Materials); a: MANOVA, $F_{(1, 42)} = 1.13, p = 0.30$; b: MANOVA, $F_{(1, 15)} = 0.24, p = 0.64$.

Sperm motility and morphology

Any seasonal differences in testicular anatomical and histological features did not reflect changes in spermatogenic activity or sperm motility. As mentioned, the testes of all males under investigation showed evidence of spermatogenesis. Moreover, all sperm motility parameters investigated were comparable for males caught during the breeding and non-

breeding periods, for both study localities (Table 6.5). Although, for both sites, the percentage of spermatozoa with normal morphology did not differ significantly between males captured during and after the breeding period (Table 6.5), there were significant differences in the distribution of sperm defects between these periods for animals collected at Sir Lowry's Pass (Figure 6.14a). Males caught during the breeding period had significantly fewer spermatozoa with cytoplasmic droplets, and significantly more spermatozoa with flagellar defects, than did those caught outside the breeding period (Figure 6.14a). By contrast males collected from Steinkopf showed an equivalent distribution of sperm defects during both in and out of the breeding season (Figure 6.14b)

Endocrinology

Basal LH concentrations were not significantly different between males caught during [SLP: 3.33 ± 0.30 miu.ml^{-1} (22), ST: 4.87 ± 1.18 miu.ml^{-1} (21)] or after [SLP: 4.65 ± 1.03 miu.ml^{-1} (16), ST: 2.57 ± 0.30 miu.ml^{-1} (15)] the breeding period at either locality (SLP: MANOVA, $F_{(1, 37)} = 1.90$, $p = 0.18$; ST: MANOVA, $F_{(1, 35)} = 2.79$, $p = 0.10$).

As outlined previously there was no significant difference in pre- and post-LH concentrations in response to a single 200 µl challenge of physiological saline in male common mole-rats (control results are included in Figures 6.5 & 6.15 for reference purposes).

For both Sir Lowry's Pass and Steinkopf there was a significant response to a single subcutaneous challenge of 2µg GnRH in males both during (SLP: $n = 7$, ST: $n = 17$) and outside (SLP: $n = 16$, ST: $n = 12$) the breeding period (Figure 6.15). There was no significant seasonal difference in the magnitude of the LH response of animals caught at Steinkopf, and post-challenge plasma bioactive LH concentrations were not

Table 6.5: Comparative sperm motility and sperm morphology characteristics for *C. h. hottentotus* males caught during the breeding (BP) and non-breeding (NBP) periods (1) collected from Sir Lowry's Pass, and (2) collected from Steinkopf.

Motility variable	Sir Lowry's Pass				Steinkopf			
	BP	NBP	*F-ratio*	*p*	BP	NBP	*F-ratio*	*p*
Sperm motility								
VCL (mms^{-1})	148.25 ± 4.46(8)	149.60 ± 4.03(8)	0.05	0.8	127.47 ± 4.96(8)	130.47 ± 6.20(8)	0.13	0.7
VSL (mms^{-1})	120.29 ± 6.12(8)	119.41 ± 4.75(8)	0.01	0.9	96.20 ± 6.95(8)	98.85 ± 7.19(8)	0.07	0.8
VAP (mms^{-1})	131.79 ± 5.69(8)	130.22 ± 4.71(8)	0.04	0.8	106.68 ± 6.52(8)	110.46 ± 7.33(8)	0.14	0.7
Linearity (%)	76.48 ± 2.37(8)	75.05 ± 1.51(8)	0.24	0.6	72.14 ± 3.11(8)	71.58 ± 2.27(8)	0.02	0.9
ALH (mm)	4.69 ± 0.13(8)	4.32 ± 0.12(8)	4.55	0.053	4.47 ± 0.11(8)	4.38 ± 0.07(8)	0.55	0.5
Wobble	0.86 ± 0.02(8)	0.84 ± 0.01(8)	1.01	0.3	0.82 ± 0.03(8)	0.82 ± 0.02(8)	0.02	0.9
STR	0.87 ± 0.02(8)	0.88 ± 0.01(8)	0.21	0.7	0.87 ± 0.02(8)	0.86 ± 0.01(8)	0.15	0.7
Dance (mm^2s^{-1})	430.32 ± 38.62(8)	479.37 ± 39.17(8)	0.98	0.4	425.46 ± 36.80(8)	416.45 ± 25.31(8)	0.38	0.9
Radian (mm)	1.42 ± 0.07(8)	1.43 ± 0.06(8)	0.03	0.9	1.76 ± 0.08(8)	1.62 ± 0.10(8)	1.00	0.4
Curvature	0.42 ± 0.03(8)	0.39 ± 0.02(8)	1.33	0.3	0.40 ± 0.02(8)	0.39 ± 0.01(8)	0.23	0.6
% motile	62.11 ± 5.50(8)	61.73 ± 3.15(8)	0.003	1.0	62.00 ± 6.34(8)	74.76 ± 5.76(8)	2.34	0.2
% prog. motile	57.24 ± 5.53(8)	55.14 ± 3.42(8)	0.10	0.8	56.73 ± 6.20(8)	67.87 ± 6.02(8)	1.77	0.2
Sperm morphology								
Normal morphology (%)	25.00 ± 2.41(6)	28.50 ± 1.23(8)	2.13	0.2	25.57 ± 1.37(5)	25.36 ± 1.62(7)	0.006	0.9

All results are expressed as mean ± SE(*n*); RM = reproductive males; NRM = non-reproductive males; BP = breeding period; NBP = non-breeding period; VCL = curvilinear velocity; VSL = straightline velocity; VAP = average path velocity; ALH = amplitude of lateral head displacement; STR = straightness; prog. = progressively.

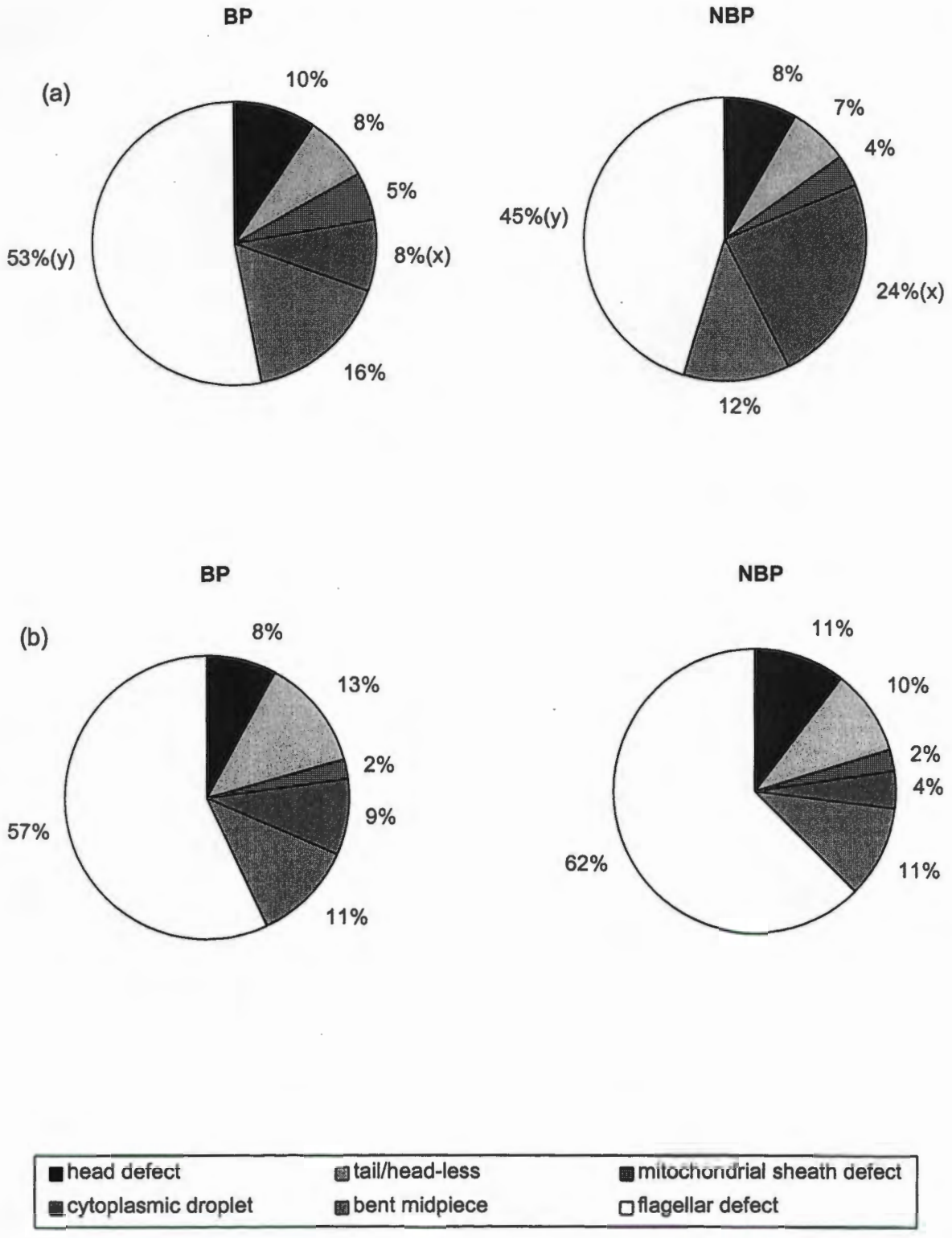

Figure 6.14 The distribution of sperm defects in *C. h. hottentotus* males caught during the breeding (BP) and non-breeding (NBP) periods (a) collected at Sir Lowry's Pass, x: MANOVA, $F_{(1, 13)} = 20.41$, $p = 0.0009$; y: MANOVA, $F_{(1, 13)} = 5.74$, $p = 0.04$; and (b) collected at Steinkopf.

significantly different (MANOVA, $F_{(1, 28)} = 2.53$, $p = 0.12$; Figure 6.15b). By contrast males from Sir Lowry's Pass exhibited significantly lower post-challenge plasma LH concentrations during the breeding period than outside of it (Figure 6.15a).

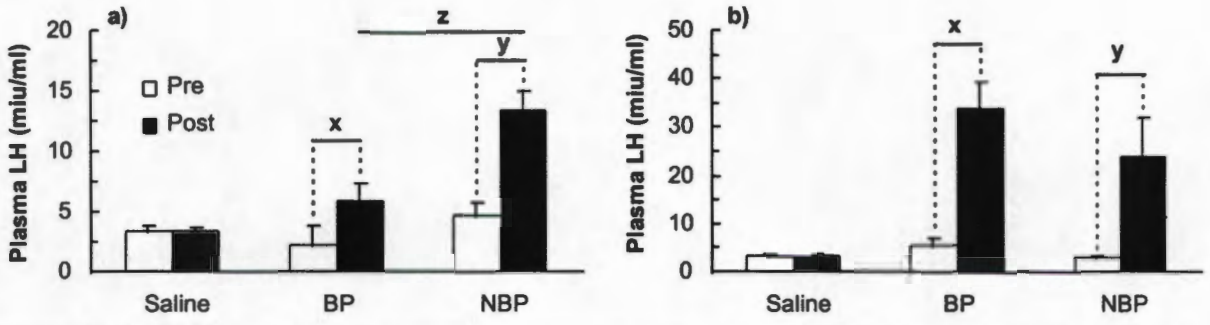

Figure 6.15: Concentrations of plasma bioactive LH (mean ± SE) in *C. h. hottentotus* males caught during the breeding (BP) and non-breeding (NBP) periods, before (Pre) and 20 min after (Post) a single s.c. injection of GnRH or saline: (a) collected at Sir Lowry's Pass, x: Mann Whitney U-test, $U = 2.43$, $p = 0.02$, y: Mann Whitney U-test, $U = 3.68$, $p = 0.0002$; z: MANOVA, $F_{(1, 22)} = 8.24$, $p = 0.01$; and (b) collected at Steinkopf, x: Mann Whitney U-test, $U = 4.51$, $p < 0.00001$, y: Mann Whitney U-test, $U = 2.83$, $p = 0.005$.

Males caught at Sir Lowry's Pass caught during the breeding period ($n = 14$) exhibited significantly higher plasma testosterone concentrations than those secured during the non-breeding period ($n = 12$; Figure 6.6). Although not statistically significant (MANOVA, $F_{(1, 14)} = 0.50$, $p = 0.50$), a similar pattern was evident at Steinkopf, with males collected during the breeding season ($n = 6$) exhibiting marginally higher testosterone concentrations than those collected outside the breeding season ($n = 9$; Figure 6.6).

Females

Ovarian and uterine anatomy

Seasonal differences in reproductive characteristics of females collected from both Sir Lowry's Pass and Steinkopf were revealed in the analysis of ovarian and uterine anatomical morphometrics. The reproductive tracts of females caught during the breeding period (SLP: $n = 7$, ST: $n = 17$) were significantly heavier than those of females outside the breeding period (SLP: $n = 13$, ST: $n = 13$; Figure 6.16), for both study populations. Furthermore,

females from both localities collected during the breeding period (SLP: n = 12, ST: n = 21) had ovaries of a significantly larger mass and volume than those captured outside the breeding season (SLP: n = 13, ST: n = 13; Figure 6.16)

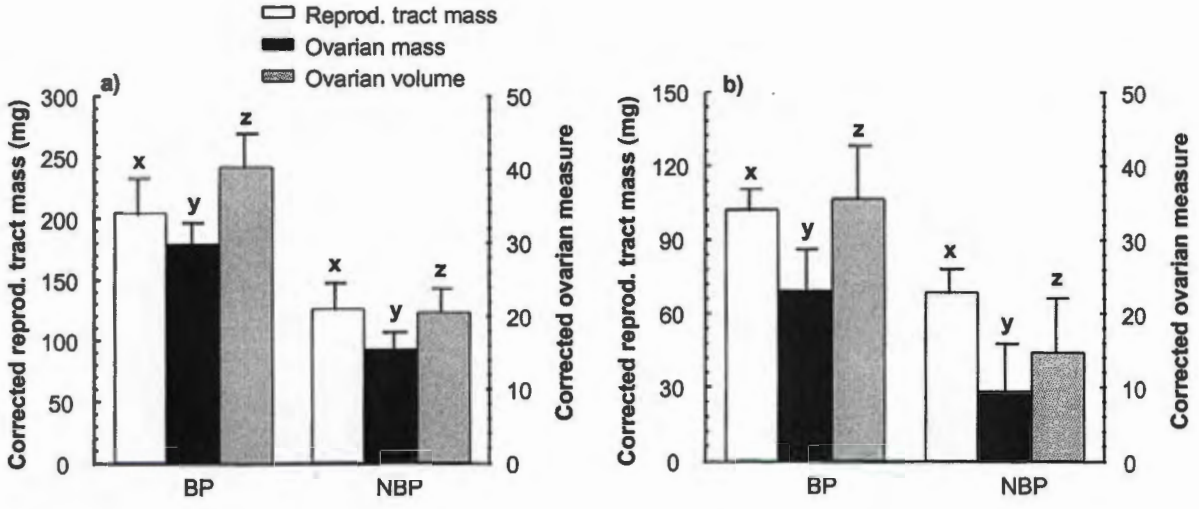

Figure 6.16: Mean (± SE) reproductive tract mass (mg; left axis), ovarian mass (mg; right axis) and ovarian volume (mm^3; right axis) for *C. h. hottentotus* females caught during the breeding (BP) and non-breeding (NBP) periods, (a) females collected at Sir Lowry's Pass, x: MANOVA, $F_{(1, 19)} = 5.92$, $p = 0.03$; y: MANOVA, $F_{(1, 23)} = 11.39$, $p = 0.003$; z: MANOVA, $F_{(1, 24)} = 13.79$, $p = 0.001$; and (b) females collected at Steinkopf, x: MANOVA, $F_{(1, 29)} = 21.91$, $p = 0.0001$; y: MANOVA, $F_{(1, 33)} = 4.13$, $p = 0.05$; z: MANOVA, $F_{(1, 33)} = 4.18$, $p = 0.05$. Values are corrected for body mass by the extraction of residuals.

Due to significant interactions between reproductive status and season for reproductive tract mass, ovarian mass and ovarian volume, ANOVA's were conducted for reproductive and non-reproductive females, from each locality during and outside the breeding season (Table 6.6). When seasonal variation in ovarian and uterine anatomy is analysed separately for reproductive and non-reproductive females it is apparent that seasonal changes are restricted to reproductive females (Table 6.6). For both localities, reproductive females caught during the breeding period exhibited a significantly greater reproductive tract mass, ovarian mass and ovarian volume than those secured outside the breeding period (Table 6.6). By contrast no seasonal differences were apparent in non-reproductive females from both localities (Table 6.6).

Table 6.6: Comparative ovarian and uterine anatomy for reproductive (RF) and non-reproductive (NRF) *C. h. hottentotus* females collected from Sir Lowry's Pass and Steinkopf during the breeding (BP) and non-breeding (NBP) periods. Data presented after MANOVA analysis indicated significant interaction between reproductive status and season. All values are corrected for body mass by the extraction of residuals.

Variable	RF		NRF	
	BP	NBP	BP	NBP
Sir Lowry's Pass				
Reprod. tract mass (mg)‡	372.31 ± 44.21[b]	181.54 ± 31.38[b]	42.17 ± 10.33	54.08 ± 7.17
Ovarian mass (mg)	48.75 ± 4.04[c]	21.22 ± 4.33[c]	5.99 ± 0.88	6.17 ± 0.61
Ovarian volume (mm^3)	62.52 ± 4.23[c]	24.51 ± 4.83[c]	8.95 ± 1.26	10.49 ± 0.87
Uterine horn length (mm)	18.86 ± 1.73[c]	30.32 ± 1.31[c]	17.04 ± 1.47	18.72 ± 1.04
Steinkopf				
Reprod. tract mass (mg)‡	145.0 ± 12.71[b]	93.17 ± 10.38[b]	57.54 ± 3.21	48.57 ± 4.47
Ovarian mass (mg)	41.74 ± 9.75[a]	8.02 ± 11.27[a]	10.03 ± 0.62	7.73 ± 0.87
Ovarian volume (mm^3)	62.79 ± 14.41[a]	11.98 ± 16.66[a]	16.72 ± 1.24	12.99 ± 1.73

All results expressed as means ± SE; a, b, c = statistically significant groups (ANOVA); a = $p \leq 0.05$; b = $p \leq 0.01$; c = $p \leq 0.005$; ‡ reprod. = reproductive

Uterine horns in females captured during the non-breeding period ($n = 7$) at Sir Lowry's Pass were significantly longer than those in females caught during the breeding period ($n = 13$; Figure 6.17a). When seasonal variation in uterine horn length is analysed separately for reproductive and non-reproductive females it is apparent that as with the ovaries seasonal changes are restricted to reproductive females (Table 6.6). By comparison, the uterine horns of females collected during both the breeding ($n = 17$) and non-breeding periods ($n = 13$) at Steinkopf were of similar length (MANOVA, $F_{(1, 29)} = 0.01$, $p = 0.91$; Figure 6.17b). Uterine horn diameter did not differ significantly between females caught during (SLP: $n = 7$, ST: $n = 17$) and outside (SLP: $n = 13$, ST: $n = 13$) the breeding period, from both localities (SLP: MANOVA, $F_{(1, 19)} = 2.35$, $p = 0.15$; ST: MANOVA, $F_{(1, 29)} = 2.57$, $p = 0.12$; Figure 6.17).

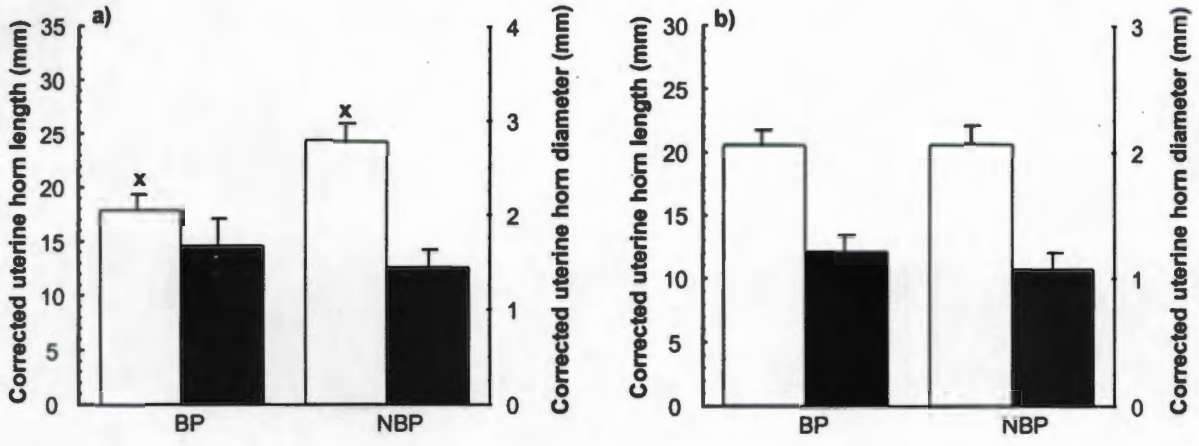

Figure 6.17: Mean (± SE) uterine horn length (mm; left axis) and uterine horn diameter (mm; right axis) for *C. h. hottentotus* females caught during the breeding (BP) and non-breeding (NBP) periods, (a) females collected at Sir Lowry's Pass, x: MANOVA, $F_{(1, 19)} = 20.09$, $p = 0.0004$; and (b) females collected at Steinkopf. Values are corrected for body mass by the extraction of residuals.

Ovarian histology

Seasonal differences in ovarian histology are graphically summarised in Figure 6.18. The basic patterns differ marginally between Sir Lowry's Pass and Steinkopf. For both localities, most females caught during the breeding (SLP: $n = 10$, ST: $n = 12$) and non-breeding periods (SLP: $n = 13$, ST: $n = 8$) exhibited secondary follicles and tertiary follicles in their ovaries (Figure 6.18). An equal percentage of females collected during and outside the breeding period at Steinkopf had LUF's (Figure 6.18). By contrast a greater percentage of females caught outside the breeding period at Sir Lowry's Pass had LUF's, relative to those caught during the breeding period (Figure 6.18). Whilst females exhibited corpora lutea only during the breeding period at Steinkopf, two females from Sir Lowry's Pass showed evidence of corpora lutea during the non-breeding period (Figure 6.18).

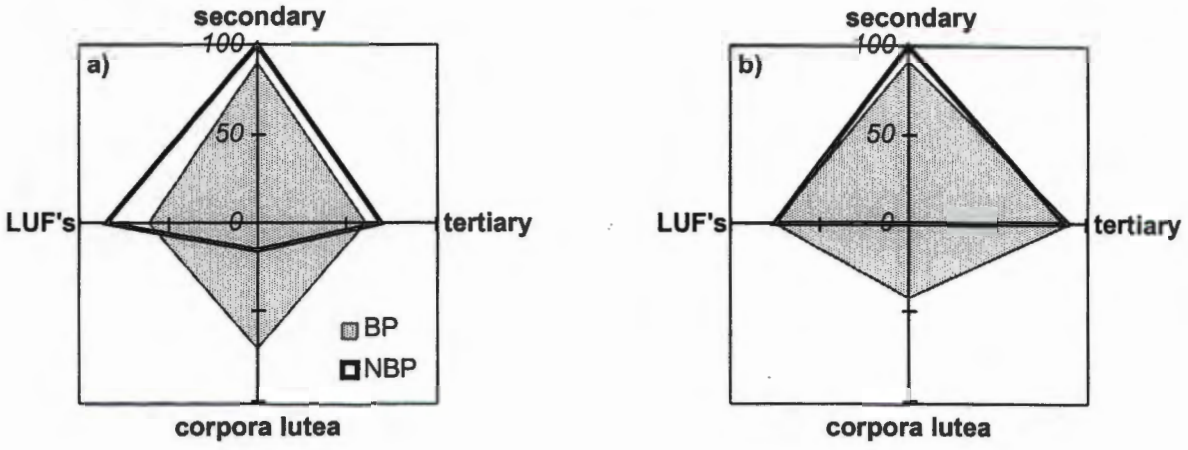

Figure 6.18: Radar diagrams showing the percentage of *C. h. hottentotus* females caught during the breeding (BP) and non-breeding (NBP) periods, (a) from Sir Lowry's Pass and (b) from Steinkopf, exhibiting secondary and tertiary follicles, corpora lutea and luteinized unruptured follicles in their ovaries. Each axis represents the overall percentage of females of each status from each locality exhibiting a particular follicular type.

Seasonal differences were evident in LUF density for females collected at Sir Lowry's Pass. Females secured during the breeding period [1 ± 0.3 (11)] had markedly lower LUF densities than females captured outside the breeding season [1.8 ± 0.3 (13)]. By comparison LUF density was similar for females caught during both the breeding [1.9 ± 0.4 (12)] and non-breeding [2 ± 0.5 (8)] periods at Steinkopf.

Endocrinology

For females caught at Sir Lowry's Pass basal LH concentrations during the breeding period [2.80 ± 0.34 miu.ml^{-1} (14)] at Sir Lowry's Pass were significantly lower than those outside the breeding season [6.69 ± 1.00 miu.ml^{-1} (12); Figure 6.19a]. In contrast at Steinkopf basal LH concentrations were not significantly different between females secured during [4.07 ± 0.57 miu.ml^{-1} (23) or after [3.74 ± 0.67 miu.ml^{-1} (9)] the breeding period (MANOVA, $F_{(1, 31)} = 0.26$, $p = 0.62$).

As outlined previously there was no significant difference in pre- and post-LH concentrations in response to a single 200 µl challenge of physiological saline in female common mole-rats (controls included in Figures 6.10 & 6.19 for reference purposes).

For animals from Steinkopf, there was a significant response to a single subcutaneous challenge of 2 µg GnRH in females secured during the breeding period (n = 17; Figure 6.19b). By contrast, the response outside the breeding period was slight and non-significant (n = 9; Mann Whitney U-test, U = 0.97, p = 0.33; Figure 6.19b). Furthermore, there was a significant difference in the magnitude of the LH response between females caught at Steinkopf during the breeding and non-breeding periods. Females caught during the breeding period exhibited significantly higher post-challenge plasma bioactive LH concentrations than those caught during the non-breeding period (MANOVA, $F_{(1, 25)}$ = 8.45, p = 0.008; Figure 6.19b).

Although females captured during both the breeding (n = 10) and non-breeding periods (n = 12) at Sir Lowry's Pass exhibited a slight response to a single subcutaneous challenge of 2 µg GnRH (Figure 6.19a), this response was non-significant. However, there was a significant difference in the magnitude of the LH response between females secured at Sir Lowry's Pass during the breeding and non-breeding periods. Females caught outside the breeding period exhibited significantly higher post-challenge plasma bioactive LH concentrations than those caught during the breeding period (MANOVA, $F_{(1, 21)}$ = 10.86, p = 0.004; Figure 6.19a).

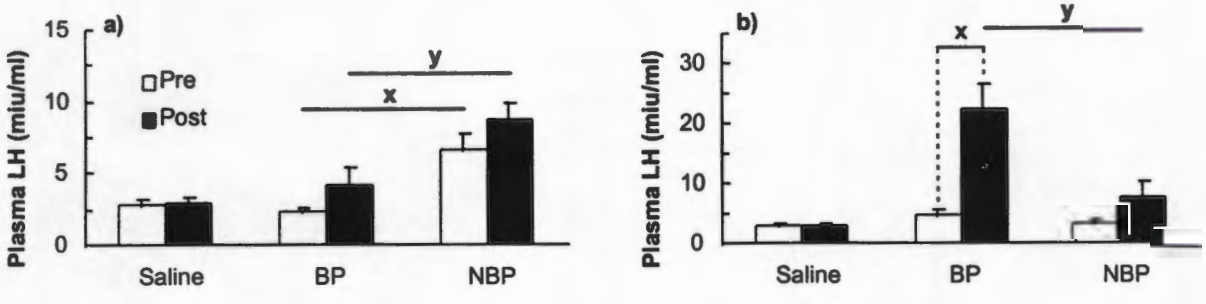

Figure 6.19: Concentrations of plasma bioactive LH (mean ± SE) in *C. h. hottentotus* females caught during the breeding (BP) and non-breeding (NBP) periods, before (Pre) and 20 min after (Post) a single s.c. injection of GnRH or saline: (a) collected at Sir Lowry's Pass, x: MANOVA, $F_{(1, 25)}$ = 15.60, p = 0.0006; y: MANOVA, $F_{(1, 21)}$ = 10.86, p = 0.004; and (b) collected at Steinkopf, x: Mann Whitney U-test, U = 4.41, p < 0.00001, y: MANOVA, $F_{(1, 25)}$ = 8.45, p = 0.008 .

Females caught during the breeding period ($n = 8$) at Sir Lowry's Pass exhibited significantly higher plasma testosterone concentrations than those caught during the non-breeding period ($n = 12$; Figure 6.11). Although not statistically significant (MANOVA, $F_{(1, 25)} = 2.02$, $p = 0.17$), a similar pattern was evident at Steinkopf, with females collected during the breeding period ($n = 14$) exhibiting markedly higher testosterone concentrations than those collected outside the breeding period ($n = 12$; Figure 6.11). When seasonal variation in plasma testosterone concentration is considered separately for reproductive and non-reproductive females it is apparent that seasonal changes are restricted to reproductive females. At both localities reproductive females exhibited a dramatic increase in testosterone concentrations in the breeding period (SLP: 5.54 ± 0.84 nmol.l^{-1}, ST: 5.38 ± 2.20 nmol.l^{-1}) relative to the non-breeding period (SLP: 1.87 ± 0.76 nmol.l^{-1}, ST: 0.89 ± 2.01 nmol.l^{-1}). In contrast non-reproductive females exhibited comparable testosterone concentrations both during (SLP: 0.96 ± 0.39 nmol.l^{-1}, ST: 0.59 ± 0.22 nmol.l^{-1}) and outside (SLP: 0.89 ± 0.28 nmol.l^{-1}, ST: 1.50 ± 0.27 nmol.l^{-1}) the breeding period.

DISCUSSION

Reproductive status

In many rodents, the regulation and restraint of reproductive function is an adaptive response to environmental factors such as increased population density (Brown & MacDonald 1984). Reproductive suppression is also widespread in hierarchical groups of cooperatively breeding mammals, where dominant individuals may inhibit the reproduction of subordinates via behavioural, and other interactions (Abbott 1987; Abbott *et al.* 1988). Social competition and reproductive suppression in subordinate individuals play a major role in determining individual reproductive success in such mammalian species (Keller & Reeve 1994). Examples of social suppression of reproduction reach an extreme in singular (*sensu* French 1997) cooperatively breeding species where reproduction is restricted to a single

female and one or two males *e.g.* naked mole-rats (Abbott *et al.* 1989; Faulkes *et al.* 1990a; 1991); common marmoset monkeys, *Callithrix jacchus jacchus*, (Abbott 1984; Abbott *et al.* 1989); dwarf mongooses, *Helogale parvula*, (Rood 1980; Creel *et al.* 1992); slender-tailed meerkats, *Suricata suricatta* (Doolan & MacDonald 1996) and wild dogs, *Lycaon pictus* (Malcolm & Marten 1982; Creel *et al.* 1997).

Results from the present study indicate that common mole-rat males from both localities display a similar status-related reproductive capacity to that of the Damaraland and Mashona mole-rat (Bennett *et al.* 1993; 1997; Faulkes *et al.* 1994), namely reproductive quiescence in non-reproductive males does not translate into repressed testicular and hormonal function. Thus for both Steinkopf and Sir Lowry's Pass, testicular anatomy and histology, spermatogenesis, sperm motility, sperm morphology, sperm abundance, interstitial cell abundance and activity, plasma testosterone concentrations, basal bioactive LH concentrations and LH responses to exogenous GnRH were similar for reproductive and non-reproductive males. This absence of a physiologically well-defined suppression of reproduction in male common, Damaraland and Mashona mole-rats is typical of social-suppression in male mammals (*e.g.* Creel *et al.* 1992; Faulkes *et al.* 1994).

In contrast to the males, status-related differences were apparent in the anatomy of the female reproductive tract. Reproductive females from both localities had heavier reproductive tracts and ovaries, and longer and wider uteri than non-reproductive females. Reproductive female Damaraland and naked mole-rats also exhibit enlarged ovaries and large, thick-walled and well vascularised uteri (Faulkes 1990; Bennett *et al.* 1994). In contrast the non-reproductives of these species have small ovaries, and reduced, flaccid uteri. These differences are related to the fact that reproductive females bear offspring, whilst non-reproductive females do not. The enlarged ovaries reflect the presence of large corpora lutea, and the enlarged uterus serves to nourish and support the developing embryos. In support of this contention, post-mortem examination of all the reproductive females revealed the presence of distinct, fleshy placental scars, varying in number from

three to six. The fact that reproductive females show seasonal cyclicity in reproductive tract anatomy[2] (see below) also indirectly supports the notion that status-related differences are related to the occurrence of pregnancy.

Endocrine differences between reproductive and non-reproductive females were revealed in the analysis of plasma testosterone. At both Steinkopf and Sir Lowry's Pass reproductive females exhibited higher plasma testosterone concentrations than non-reproductive females. Bennett (1994) has shown that reproductive female *C. damarensis* exhibit an elevated urinary concentration of testosterone during gestation. Androgens, like testosterone are the precursors to the female steroid hormones oestrogen and progesterone, and this accounts for their elevated concentrations in pregnant females (Baird 1984; Bennett pers. comm.). Consequently, as with the reproductive tract anatomy, the status-related differences in testosterone concentration may simply reflect differences associated with pregnancy. Clarke and Faulkes (1997), in their investigation of dominance in the naked mole-rat, show that plasma testosterone concentrations are elevated in reproductive females, relative to non-reproductive females, irrespective of whether they are pregnant or not. It is well established that testosterone levels correlate with dominance in many mammalian species [*e.g.* plains and Grevy's zebra, *Equus burchelli* and *E. grevyi* (Chaudhuri & Ginsberg 1990); African elephants, *Loxodonta africana* (Poole *et al.* 1984); red deer, *Cervus elaphus* (Lincoln *et al.* 1972)], and Clarke and Faulkes (1997) suggest that the elevated testosterone in reproductive female naked mole-rats is responsible for their heightened aggression, necessary to maintain their dominance rank. In the common mole-rat, dominance status within the colony is also maintained via agonistic interactions (Bennett 1992; Rosenthal *et al.* 1992). The elevated testosterone concentrations in reproductive females from both localities may ensure that these animals can aggressively defend their dominant position, and thereby maintain colony cohesion.

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[2] Although reproductive females exhibit seasonality in reproductive tract anatomy, they always possess larger tracts and ovaries than non-reproductives, even during the non-breeding period (see Table 6.6).

The results for the analysis of basal bioactive LH concentrations and of LH responses to exogenous GnRH for both reproductive and non-reproductive females collected at Steinkopf suggest that reproductive and non-reproductive females exhibit similar basal LH concentrations and a similar LH response to exogenous GnRH. However, the comparative results for Sir Lowry's Pass were rather enigmatic and consequently the significance of inter-habitat differences is difficult to establish. Nevertheless, in view of the prediction made in the introduction, that non-reproductive animals from the arid population would exhibit a more profound reproductive control than those inhabiting mesic areas, it was anticipated that non-reproductive females at Steinkopf would exhibit a diminished LH response to exogenous GnRH, similar to the response seen in non-reproductive female Damaraland mole-rats (Bennett *et al.* 1993). It is evident from the results that this is not the case, reproductive and non-reproductive females demonstrating similar levels of pituitary sensitivity, apparently refuting the prediction.

Disparate to the anatomical and endocrine results there were few status-related differences in ovarian histology. At both localities both reproductive and non-reproductive females exhibited follicular activity both during and outside the breeding period. All females, irrespective of status, exhibited either well developed secondary follicles and/or tertiary (*i.e.* pre-ovulatory) follicles. By comparison corpora lutea were only present in animals previously idenitifed as reproductive females, for both localities. Two interesting corollaries follow from this observation: (1) it confirms that only a small subgroup of females in the population fall pregnant (*i.e.* the reproductive females), supporting the notion that status-related differences in reproductive function are a product of the occurrence of pregnancy; and (2) it provides support for Bennett *et al.*'s (1998) contention that the cryptomids are induced ovulators. Bennett *et al.* (1998) showed an absence of corpora lutea in the ovaries of solitary, unpaired female *C. damarensis*. However, following pairing, females will soon mate and fall pregnant, suggesting the mechanical process of coitus is required for ovulation (Bennett *et al.* 1998). Similarly, the absence of corpora lutea in non-reproductive female common mole-rats,

despite the presence of well developed pre-ovulatory follicles, indicate that this species is also an induced ovulator. Induced ovulation may represent an adaptive reproductive strategy in the unpredictable environments occupied by most cryptomids, enabling them to respond rapidly to dispersal and concomitant outbreeding opportunities.

Luteinized unruptured follicles were present in the ovaries of most females, although LUF's were evident in a greater proportion of the non-reproductive females from both localities, than in the reproductive females. Furthermore, LUF densities were higher in non-reproductive females than in reproductive females. Similarly, Bennett *et al.* (1994) note that non-reproductive female Damaraland mole-rats have a higher LUF density than reproductive females. Luteinized unruptured follicles result from the luteinization of secondary and tertiary follicles (Bennett *et al.* 1998). As mentioned above, the common and Damaraland mole-rats appear to be induced ovulators, consequently the higher density of LUF's in non-reproductives may simply result from the luteinization of unovulated pre-ovulatory follicles. However, the analysis of LUF's must be interpreted with caution, because: (1) their exact function in bathyergid biology is as yet unclear (Bennett *et al.* 1994); and (2) the difficulty of always clearly distinguishing between atretic follicles and LUF's, potentially results in an over-estimate of LUF occurrence and density.

The results from this investigation do not support the prediction that non-reproductive animals from the arid population would exhibit a physiologically more profound reproductive control than those inhabiting mesic areas. In fact, for both Steinkopf and Sir Lowry's Pass reproductive and non-reproductive males and females exhibited a similar degree of reproductive function, the only clear-cut status-related differences were associated with the occurrence of pregnancy in reproductive females from both localities. These findings apparently refute Bennett *et al.*'s (1997; 1998) contention that variation in the mechanism of reproductive modulation may be correlated with environmental factors with arid-adapted species being characterised by a physiological component to reproductive suppression. Optimal skew theory predicts that the degree of reproductive skew in a society will be

influenced by both intrinsic and extrinsic factors, including: (1) the intensity of ecological constraints on independent reproduction; (2) the influence of subordinate cooperation on group productivity; (3) the genetic relatedness of group members; and (4) subordinate fighting ability (Vehrencamp 1983a; 1983b; Keller & Reeve 1994; Reeve & Keller 1995). Reproductive skew is expected to increase with increasing ecological constraints on independent reproduction, as subordinates can expect only small fitness payoffs for leaving if ecological conditions are harsh (Vehrencamp 1983a; 1983b; Keller & Reeve 1994). As a corollary, dominant control of subordinate reproduction is expected to decrease as subordinates may be less inclined to leave. Consequently, in confutation of Bennett *et al.*'s (1997; 1998) notion, optimal skew theory in fact would predict a physiologically less severe degree of reproductive suppression in arid-adapted mole-rat species. In *H. glaber*, the presence of a physiological component to suppression probably relates to the occurrence of inbreeding within this arid-adapted species (see below). However, the occurrence of a physiological component to suppression in female *C. damarensis* presents an intriguing evolutionary enigma. Jarvis (pers. com.) suggests that dominant control over subordinate reproduction in *C. damarensis* serves to protect the reproductive position of the dominant animals. Damaraland mole-rat colonies are potentially susceptible to invasion by foreign conspecifics (J.U.M. Jarvis & N.C. Bennett unpublished data). Invading foreigners would circumvent the incest taboos of subordinate colony members, threatening the reproductive hierarchy and ultimately group cohesion and colony longevity.

As outlined in the introduction, In contrast to the cryptomids, naked mole-rats exhibit physiological manifestations of suppression in subordinates of both sexes (Faulkes & Abbott, 1991; Faulkes *et al.*, 1990a; 1991). These interspecific differences in the extent of reproductive suppression within the social Bathyergidae probably reflect the effects of a number of evolutionary factors. The phylogenetic hypothesis proposed by Allard and Honeycutt (1992) and Faulkes (pers. com.) suggests that the naked mole-rat and the social cryptomids represent divergent groups with relatively independent evolutionary trajectories.

Such findings led Jarvis and Bennett (1993) and Faulkes *et al.* (1994) to postulate that social behaviour and reproductive suppression have evolved separately but in parallel in the Bathyergidae, and have given rise to different physiological mechanisms of suppression in the two taxa. However, as previously alluded to, variation in mating strategies and dispersal may provide a more parsimonious explanation for this infrafamilial divergence in the mechanisms of reproductive control (Faulkes *et al.* 1994). Whereas naked mole-rats appear to be facultative inbreeders (Faulkes *et al.* 1990b; Reeve *et al.* 1990; Honeycutt *et al.* 1991b; Jarvis 1991a; O'Riain *et al.* 1996), laboratory and field studies suggest incest avoidance and concomitant outbreeding in the Damaraland and common mole-rats (Bennett 1994; Jarvis *et al.* 1994; Chapter 9). In both cryptomid species, colony members are typically the offspring of the reproductive pair and do not reproduce until conditions (both social and ecological) favour dispersal and outbreeding (Jarvis *et al.* 1994). Furthermore, recent evidence (Bennett 1994; Burda 1995; Rickard and Bennett 1997) suggests that reproductive quiescence in non-reproductive cryptomids may reflect either incest avoidance (*C. h. hottentotus*, *C. darlingi*) or an interaction between reproductive suppression by parental manipulation and incest avoidance (*C. damarensis*). Incest taboos amongst subordinate colony members in the social cryptomids may negate the need for a rigorous suppression of reproduction. By contrast, in inbred naked mole-rats, the absence of incest avoidance necessitates the evolution of stringent reproductive control and hence the heightened degree of suppression in this species.

Breeding season

In contrast to most subterranean mammals, which are exclusively solitary and highly xenophobic, the bathyergids display a range of sociality, from solitariness to eusociality (Jarvis 1981; Bennett 1989; Jarvis & Bennett 1991; 1993; Chapter 1). While all the solitary species examined exhibit strict reproductive periodicity, the majority of social mole-rats

display no cyclicity in reproductive activity (Jarvis 1969; Van der Horst 1972; Bennett & Jarvis 1988b; Jarvis & Bennett 1991). The common mole-rat, with its seasonal breeding system, is the exception to this general pattern

Reproductive cyclicity in the common mole-rat is presumably a result of it having invaded a seasonal habitat. Both populations used in this study inhabit winter rainfall regions, with most rain falling between May and August. It is well established that periodicity in environmental cues provides the proximate stimulus for seasonality in mammalian reproduction (Clarke 1981; Ims 1990; Bronson and Heideman 1994; Turek & Van Cauter 1994). Furthermore, Bennett *et al.* (1988) and Jarvis and Bennett (1991) recognised that seasonality in temperature and rainfall were important determinants of seasonal breeding in the solitary bathyergids. Louw (1993) notes that seasonal breeding represents an adaptation to maximise the survival of offspring, and hence it is synchronised in such a way that progeny are produced at the most favourable time of the year. The breeding season in both populations of *C. h. hottentotus* will ensure that the young are born at the end of the wet period when access to food resources is maximal (see Chapters 1, 2, 3 & 4), thus ensuring that the reproductive female and newborn offspring satisfy their energetic demands.

Surprisingly the observed pattern of reproductive cyclicity in common mole-rats was not reflected in the gonadal function of males collected from either the arid or mesic localities. Males exhibited no apparent manifestation of season on testicular activity: spermatogenesis; sperm quality (motility and percentage normal morphology); sperm abundance; and interstitial cell abundance and activity were similar in the reproductively active and inactive periods. Furthermore, the absence of a difference in either basal plasma bioactive LH concentrations, or LH responses to exogenous GnRH between males collected at both Sir Lowry's Pass and Steinkopf during and outside the breeding period supports a lack of seasonal periodicity in reproductive function. This maintenance of reproductive activity outside of the breeding season is uncommon amongst seasonal breeding mammals. The solitary, seasonal breeding Cape dune mole-rat, *Bathyergus suillus*, and Cape mole-rat,

Georychus capensis, both exhibit distinctive cyclicity in male reproductive characteristics (Van der Horst 1972; Bennett & Jarvis 1988b). In both species a cessation of spermatogenesis and testicular regression occur during the non-active period. With the onset of the breeding season, testicular recrudescence and a resumption of spermatogenic activity occur (Van der Horst 1972; Bennett & Jarvis 1988b).

An unusual pattern was prevalent in the results: the increased testis mass; testis volume; seminiferous tubule diameter and seminiferous tubule epithelial diameter in males caught at Sir Lowry's Pass during the non-reproductive period. In seasonally breeding mammals, in which cyclicity in male reproductive characteristics has been demonstrated, testicular regression and an associated reduction in testicular morphometrics typically occurs during the non-reproductive period (Clarke 1981; Keverne 1987; Kaplan & Mead 1994; Page *et al.* 1994). In a review of seasonal aspects of testis function, Lincoln (1981) indicated that a reduction in testes size to less that 80% of the seasonal maximum is necessary before there is a reduction is spermatogenic activity. Consequently, these changes in *C. h. hottentotus* males may not be of adaptive significance. This contention is supported by the fact that seasonal differences in testicular anatomical and histological features did not reflect changes in spermatogenesis[3], sperm abundance, sperm motility, percentage of spermatozoa with normal morphology, interstitial cell abundance and activity, basal LH concentrations or LH responses to exogenous GnRH.

Another enigmatic result was the elevated plasma testosterone concentrations in males caught at Sir Lowry's Pass during the reproductive period. This pattern is inconsistent with the similarity in basal LH concentrations, in LH responses to exogenous GnRH and in sperm parameters between males caught during and outside the breeding period. Conventional wisdom regards testosterone as the hormone controlling male reproductive

[3] It is important to recognise that it may be impractical for males to halt spermatogenesis outside the breeding period. In mammals, spermatogenesis is a long process (up to 75 days in humans), and as outlined below, male mole-rats need a ready supply of sperm throughout the year in case opportunities for reproduction arise.

function, however, Wingfield and Moore (1987) and Wingfield *et al.* (1990) suggest that alterations in testosterone levels may more accurately reflect transient patterns of aggressive behaviour than changes in reproductive physiology. Wingfield *et al.*'s (1990) "challenge hypothesis" contends that at the onset of the breeding season, androgen levels rise from a non-breeding baseline to a slightly higher breeding baseline (Figure 1 pg 831 Wingfield *et al.* 1990). These breeding baseline concentrations are sufficient for normal reproductive physiology and behaviour, but are well below the physiological maximum, and have little effect on aggressive behaviour. Temporal patterns of variation in testosterone levels within the breeding season are then predicted to reflect male-male aggression. In the common mole-rat non-breeding testosterone levels appear sufficient to maintain reproductive function. Elevated testosterone levels in Sir Lowry's Pass and Steinkopf males during the breeding period probably reflect heightened levels of aggression associated with mate guarding and mating.

In contrast to the males, reproductive periodicity was evident in the anatomy of the female reproductive tract. Reproductive females from both localities exhibited a greater reproductive tract mass, ovarian mass and ovarian volume during the breeding period. Moreover, the uterine horns of reproductive females from Sir Lowry's Pass were significantly longer during the non-breeding period than during the breeding season. This seasonal alternation supports post-mortem examination of sacrificed females, and reflects the fact that reproductive female common mole-rats, collected at both localities during the breeding season, had large ovaries and swollen, thick-walled and well vascularised uterine horns. By comparison during the non-breeding period their ovaries were reduced and the uteri smaller and flaccid. Temporal changes in the ovarian and uterine morphometrics of seasonal breeding mammals are well established. For example female corn mice, *Calomys musculinus*, European rabbits, *Oryctolagus cuniculus*, and red-giant flying squirrels, *Petaurista petaurista*, show an increase in ovarian size with the onset of the breeding season (Boyd & Myhill 1987; Mills *et al.* 1992; Lee *et al.* 1993). In the female European mole, *Talpa*

europaea, during the reproductive period, the follicular part of the ovary, and the uterus are enlarged (Gorman & Stone 1990). Seasonal changes in the anatomical morphometrics of the reproductive system of female mammals simply reflect the onset of follicular maturation, ovulation and pregnancy; the enlarged ovary is a result of the presence of several large corpora lutea of pregnancy, and the enlarged, well vascularised uterus serves to maintain the developing embryos. That these seasonal differences in *C. h. hottentotus* females are simply a product of pregnancy is supported by the absence of seasonal changes in the reproductive anatomy of non-reproductive females.

Seasonal periodicity in female endocrinology was revealed in the analysis of plasma testosterone and bioactive LH. At both Steinkopf and Sir Lowry's females exhibited an elevated plasma testosterone concentration during the breeding period. Bennett (1994) has shown that reproductive female *C. damarensis* exhibit an elevated urinary concentration of testosterone when they are pregnant. Consequently, as with the reproductive tract anatomy, the seasonal difference in testosterone level probably reflect changes associated with pregnancy. This contention is supported by the fact that only the reproductive females from both localities exhibited a marked seasonal alternation in testosterone concentration. As for reproductive status, the results for the analysis of basal bioactive LH concentrations and of LH responses to exogenous GnRH for females collected at Sir Lowry's Pass during and outside the breeding period were rather esoteric and consequently difficult to interpret. However, the comparative results for Steinkopf suggest that females exhibit a reduced LH response to exogenous GnRH during the non-breeding period. A similar reduced pituitary sensitivity to exogenous GnRH has been implicated as the block to ovulation in subordinate female naked and Damaraland mole-rats (Faulkes *et al.* 1990a; Bennett *et al.* 1993). Consequently, this would suggest that at least at Steinkopf females are anovulatory and thus unable to fall pregnant during the non-breeding period.

Disparate to the anatomical and endocrine results, there was no pattern of seasonal cyclicity in ovarian histology. At both localities females, irrespective of status, showed clear

indications of follicular activity both during and outside the breeding period. However, corpora lutea were generally only present during the breeding period, although the ovaries of two reproductive females from Sir Lowry's Pass had corpora lutea during the non-breeding period. The general absence of corpora lutea during the non-breeding season supports the notion (see above) that females are anovulatory during this period. Luteinized unruptured follicles were present in the ovaries both during and outside the breeding period. However, as outlined above the results for LUF's must be interpreted with caution due to the difficulty of clearly distinguishing between atretic follicles and LUF's. In seasonally breeding mammals, in which cyclicity in female reproductive characteristics has been demonstrated, follicular development is halted during the non-reproductive period, and no secondary or tertiary follicles are present (Clarke 1981; Gorman & Stone 1990). The fact that females from both localities show clear evidence of ovarian activity and follicular development during the non-breeding period suggests that reproductive functions are not completely switched off. However, although basal LH concentrations are sufficient to maintain follicular maturation outside breeding season, the reduced pituitary sensitivity to GnRH of females from Steinkopf will ensure that they are anovulatory during this period (see above).

The results from this investigation thus indicate that, like the males, females from both localities maintain reproductive function (although not complete) outside of the breeding period. This atypical pattern of reproductive activity in common mole-rats, may reflect an interaction between social status and mating strategy. Long-term demographic studies suggest that the common mole-rat is an obligate outbreeder (see Chapter 9), and consequently must disperse to find a mate. As outlined in Chapter 1, mole-rats are forced to restrict extensive burrowing, and hence dispersal, to periods after rainfall, when the reduced soil compaction and increased soil cohesion are energetically optimal for digging (Jarvis and Bennett 1991). In the seasonal habitats occupied by the common mole-rat, with precipitation "concentrated" in winter, dispersal opportunities are maximal outside the breeding period. This would necessitate the maintenance of reproductive activity throughout the year,

particularly during the non-breeding period. This would be particularly important at Steinkopf where the patterns of precipitation are sporadic and unpredictable. Such reproductive activation in dispersing animals may aid intersexual recognition, and facilitate pair-bond formation. The solitary mole-rats, like most subterranean rodents, are typically extremely aggressive, except when they are ready to breed (Bennett and Jarvis 1988b; Jarvis and Bennett 1990; 1991). Sexual recrudescence reduces intersexual aggression, enabling pairing and copulation (Bennett and Jarvis 1988b; Jarvis and Bennett 1990; 1991). Consequently, the continuous reproductive activity in the common mole-rat may enable the strong barriers of territoriality, xenophobia and mutual aggression (see Chapter 9) to be broken down, and information such as sex, status and intention to breed to be relayed. This would afford dispersing animals a greater chance of successful pairing, facilitating outbreeding.

As outlined previously, seasonal breeding represents an adaptation to ensure that offspring are produced at the most favourable time of the year thereby maximising their survival (Louw 1993). Although pairing between foreign common mole-rats is most likely to occur during the non-breeding season, fitness forfeiture would result from the production of young during this period as conditions are not optimal for offspring survival. However, the exact magnitude of fitness costs should differ markedly between arid and mesic localities. In arid areas, low and sporadic precipitation translates into reduced foraging predictability and hence the fitness penalties for producing young at an unsuitable time of the year should be elevated. Consequently, the reduced pituitary sensitivity to GnRH[4] in reproductive females from the arid site during the non-breeding period may act as a safeguard, preventing ovulation and subsequent conception outside the breeding period. This contention is supported by the fact that during a three year demographic study no pregnant females were caught outside the breeding period at Steinkopf, whereas three pregnant females were

[4] Reduced pituitary sensitivity would appear to be a readily reversible phenomenon as a female caught at Steinkopf and returned to the laboratory conceived and fell pregnant outside the breeding period after a year in captivity.

caught during the non-breeding period at Sir Lowry's Pass (A.C. Spinks unpublished data). The maintenance of ovarian activity will mean that following the recrudescence of pituitary function at the onset of the breeding season, these induced ovulators can rapidly ovulate and conceive.

Conclusions

The results from this investigation failed to reveal clear status- or season-related inter-habitat differences in reproductive activity in the common mole-rat. For both Steinkopf and Sir Lowry's Pass reproductive and non-reproductive males and females exhibited a similar degree of reproductive function, the only clear-cut status-related differences were associated with the occurrence of pregnancy in reproductive females from both localities. Evidently incest avoidance between philopatric colony mates is the pervasive mode of reproductive control in subordinate common mole-rats from both localities, and in subordinate cryptomids in general, and hence the absence of inter-habitat variance in the mechanism of reproductive regulation. Consequently, status-related differences in reproductive function cannot provide insight into differences in colony cohesion and fidelity, and hence the degree of social elaboration between arid and mesic areas. Furthermore, although the birth of offspring is restricted to the summer, both males and females retain reproductive function during the winter non-breeding period. As for status, season-related differences were associated with the occurrence of pregnancy in reproductive females from both localities. In conclusion, dispersal and subsequent outbreeding opportunities appear to be important determinants of reproductive function in common mole-rats from both arid and mesic sites, moderating the effects of season and status on reproductive function.

Chapter 7

Comparative demography of wild populations from an arid and a mesic locality

ABSTRACT

The objective of this investigation was to determine whether inter-habitat disparities in demography reflected divergence in the scale of social elaboration between arid and mesic populations of the common mole-rat. Demographic data collected at Steinkopf and Sir Lowry's Pass were used to evaluate three predictions: (1) associated with the increased risks of unproductive foraging in arid environments, colony size should be larger in arid relative to mesic areas; and associated with the need to curtail total colony energy costs (2) individual body size should be smaller in mole-rats from arid areas, and (3) colony recruitment, as reflected in litter size, should be reduced in arid habitats. The results from this investigation provided support for prediction (2) but not for predictions (1) and (3). Thus the predicted inter-site differences in colony size were not apparent. Several explanations are proposed to account for this maintenance of sociality in mesic-occurring common mole-rats, including a lack of time for evolutionary divergence between the study populations, phylogenetic constraints and an altered selective regime. Common mole-rats from Steinkopf exhibited a reduced individual and colony mass relative to those from Sir Lowry's Pass, probably as an adaptation to reduce total colony energy expenditure given the elevated foraging constraints in arid environments. This finding may suggest a heightened degree of social specialisation related to the energetic constraints prevalent in arid areas. Both populations revealed similar small litter sizes and concomitant low recruitment rates. The observed litter sizes probably represent a trade-off between the need to maintain the colony workforce and the need to curtail colony energy expenditure.

INTRODUCTION

The social behaviour of animals is moulded by both extrinsic (*e.g.* predation, climate and habitat heterogeneity) and intrinsic (*e.g.* genetic relatedness) selective factors (Sherman & Morton 1984). Extrinsic selective elements alter demographic patterns, especially dispersal and mortality, thereby shaping the social context within which intrinsic factors like kin selection can operate (Evans 1977; Bekoff 1987). Consequently, demographic data are of considerable importance in understanding the evolution and

adaptive significance of social behaviour (Koenig & Pitelka 1981; Sherman 1981; Sherman & Morton 1984; Jarvis & Bennett 1993; Doolan & MacDonald 1996). However, Sherman and Morton (1984) note that the association between demography and vertebrate social behaviour is poorly understood, primarily as a result of the difficulty of obtaining longitudinal demographic and behavioural data for comparatively long-lived animals such as birds and mammals.

Given the latent relationship between social behaviour and demography, the comparative demographic features of the two study populations of the common mole-rat were investigated. The objective of this investigation was to ascertain whether there were inter-habitat disparities in demography that revealed divergence in the degree of social development. Due to its scope, this demographic study is spread over two chapters. A detailed arid/mesic comparison of colony dynamics, including philopatry, dispersal and recruitment, is undertaken in Chapter 8. In this chapter I address three rather disparate demographic elements suggested to be important in terms of the Aridity Food-Distribution Hypothesis (AFDH):

(1) *Inter-habitat divergence in colony size.* The principle tenet of the AFDH is that increased group-size and cooperative foraging in mole-rats represents an adaptation to the risks of foraging in arid habitats (Lovegrove & Wissel 1988; Lovegrove 1991; Jarvis *et al.* 1994; Lacey & Sherman 1997). Hence the fundamental prediction that colonies of common mole-rats should tend to be larger in arid areas relative to mesic regions.

(2) *Inter-habitat differences in individuals and colony biomass.* It has been suggested that for the energetic benefits of cooperative foraging to be fully realised by the social mole-rats, the total energy expenditure of the colony must be minimised (Jarvis 1978; Lovegrove & Wissel 1988; Jarvis & Bennett 1991). Reduction in body size may effect a significant reduction in absolute energetic costs and hence represent an important adaptation, particularly in arid environments where constraints on foraging are

exaggerated relative to more mesic regions (Jarvis & Bennett 1991; Chapters 3 & 4). Consequently, I predicted that *C. h. hottentotus* occurring in arid habitats would exhibit a reduced individual size, relative to those occurring in mesic areas, thereby curtailing group energetic costs and maximising individual survival.

(3) *Inter-habitat differences in litter size.* Ensuing from the aforementioned need to minimise total colony energy expenditure, Jarvis and Bennett (1991) suggest that energetic costs may be efficiently curtailed through reduced colony recruitment. Hence, I would predict diminished recruitment in common mole-rat colonies from arid habitats relative to those from mesic areas[1]. Recruitment may be curtailed either through the reduction of litter frequency or of litter size. Given that both study populations breed seasonally (Chapter 6) and typically produce only a single litter *per annum* (A.C. Spinks & N.C. Bennett unpublished data), the only way to reduce colony recruitment would be to decrease litter size. Consequently *C. h. hottentotus* from Steinkopf may be expected to produce litters of smaller size than *C. h. hottentotus* from Sir Lowry's Pass.

Whilst the first prediction outlined above concerns the sociobiological consequences of the AFDH directly, the later two pertain to the underlying AFDH predictions, and only indirectly to their sociobiological implications.

METHODS AND MATERIALS

This investigation was conducted on the study populations at Sir Lowry's Pass and Steinkopf. The floristic, edaphic and climatic features for these study localities are outlined in Chapter 2. Common mole-rats from both study sites were trapped at regular intervals

[1] The prediction of low recruitment at Steinkopf does not necessarily contradict the prediction of larger colonies in this area [Prediction (1)]. Although increased recruitment will enhance colony growth, large colonies can also form if individuals remain within the natal colony for an extended period. The low rates of dispersal at Steinkopf (Chapter 8) suggest that this is indeed the case.

over three consecutive years, September 1992 to November 1995 at Sir Lowry's Pass, and September 1993 to September 1996 at Steinkopf. Each year at least two field-trips were undertaken to each study site, one during the breeding period and one during the non-breeding period. Owing to the potentially destructive nature of the capture techniques employed, which required that: (1) a small portion of each burrow system be excavated to capture the resident colony; and (2) animals be kept out of their burrow system until the entire colony was captured, more regular trips were considered potentially disruptive to the study populations. As outlined in Chapter 6 the breeding period for *C. h. hottentotus* is defined as the period when most mating is likely to occur, and lasts from September to November. Field-trips during the breeding period were undertaken in September, October or November, and trips during the non-breeding period were undertaken in February, March, April or June. A total of eight field-trips were made to each study site, each lasting 10 to 12 consecutive days.

Animals were captured using modified Hickman live-traps (Hickman 1979a) baited with sweet potato or natural foods and set in an excavated portion of the burrow system. Traps were checked every 0.5-1 hrs from *ca.* 07h00 to 24h00 each day. Each captured individual was permanently marked by clipping a unique combination of toes, weighed to the nearest 1 g and sexed. Females were assessed for reproductive condition (pregnant, perforate vagina, lactating, presence of teats). Animals were not immediately released, but were housed in plastic containers until the entire colony had been captured, colony members being housed together. Whilst in captivity mole-rats were provided with wood shavings and paper towelling as nesting and were fed on sweet potato or natural foods. A colony was considered to be completely trapped-out if: (1) it was functionally complete (*i.e.* it included a reproductive pair); and (2) no animals came to the traps for three consecutive days after the capture of the last animal. Animals were regarded as belonging to the same colony only if they were collected at the same trap site. Where suspected colony mates were captured at separate sites they were only considered to belong to the same colony if individuals released

at one of the sites were subsequently recaptured at the other site(s). During the course of the investigation reported here, a total of 851 animals were marked during 1591 capture events. At Sir Lowry's Pass (5 ha area) 483 animals from 80 colonies were marked during 868 capture events, whilst at Steinkopf (43 ha area)[2] 368 animals from 76 colonies were marked during 723 capture events.

Data analysis

The analyses of demographic data in this investigation are complicated by the same animals being captured in several capture periods. As a result, samples are not completely independent and accordingly statistical analyses are confounded by the problems of pseudoreplication (*sensu* Hurlbert 1984). However, variables such as colony size and individual mass are not static phenomena, but may show considerable temporal variation. This intrinsic variability in demographic parameters is an important component of the longitudinal (*i.e.* temporal) demography of any species, and cannot be ignored. Moreover, the exclusion of all but the first or the most recent capture data on an individual is arbitrary and may bias the results (Braude 1991). To address this problem individual and colony data are analysed and presented in two ways: (1) at first capture only; and (2) for all captures combined (in this latter case tests may not be statistically valid but are used as an indication of the degree of differences between the study populations). Importantly the conclusions drawn were not significantly influenced by whether only first capture data or all capture data combined, were used. In addition, to illustrate temporal variation in demographic parameters, variables are summarised graphically for each capture session at each site.

Inter-habitat differences in colony size were assessed using only colonies which had been completely trapped out. Differences in the mean colony size between study sites were tested using the Mann-Whitney U-test (Zar 1984). Variability in colony size was expressed

[2] The differences in study site size reflect the differences in population densities at the two sites. At Steinkopf common mole-rat densities range from 1 to 3 mole-rats per hectare, whilst at Sir Lowry's Pass they range between 13 and 24 mole-rats per hectare (see Figure 7.9).

using the co-efficient of variation (V) *i.e.* the standard deviation expressed as a percentage of the mean (Zar 1984). Differences in the co-efficient of variation were tested statistically using the variance ratio test on log-transformed data (Zar 1984). Inter-site differences in the frequency with which colonies of different sizes were captured were assessed using the Fisher exact test on raw data (Zar 1984). Colony biomass was assessed by summing the individual masses of all colony members from complete colonies. Differences in mean colony biomass between Sir Lowry's Pass and Steinkopf were tested using the Mann-Whitney U-test (Zar 1984).

To assess inter-site differences in body mass, individuals were classified as either juveniles (< 40 g) or adults (≥ 40 g); 40 g was selected as the cut-off since post-mortem examination of the gross reproductive anatomy and histology of males and females has revealed that animals greater than 40 g in size are sexually mature (A.C. Spinks unpublished data). Adults were further categorised by sex and reproductive status, *i.e.* as either reproductive males, non-reproductive males, reproductive females or non-reproductive females. Bennett (1989; 1992) and Rosenthal *et al.* (1992) have conclusively shown that the reproductive male is the largest colony member, and this criterion was used to identify the reproductive males in this study. During the breeding season reproductive females could readily be identified when they were gravid, or by the presence of a perforate vagina and enlarged teats. Moreover, Bennett (1989; 1992) and Rosenthal *et al.* (1992) have demonstrated that the reproductive female tends to be the largest female colony member. Divergence between study sites in the mean body mass of corresponding age/sex-status categories was tested using the Mann-Whitney U-test. Furthermore, intra-habitat differences between non-reproductive males and females, and between reproductive males and females were examined using the Mann-Whitney U-test. Intra-site differences in the average body mass of reproductive versus non-reproductive males and reproductive versus non-reproductive females were not tested statistically as differences were confounded by the fact that body mass was used as a variable to assign reproductive status.

Litters were identified as a cohort of unmarked animals, each individual usually ≤ 30 g in size, caught from the same colony during a single capture session. In addition anecdotal information on litter sizes of sacrificed pregnant females and females that gave birth in captivity (either in the field or in the laboratory) were also included. Differences in average litter size between Steinkopf and Sir Lowry's Pass were tested using the Mann-Whitney U-test (Zar 1984). Inter-site differences in the frequency with which litters of different sizes were captured were assessed using the Fisher exact test on raw data (Zar 1984).

Densities of common mole-rats were estimated as the minimum number known alive (Krebs 1966). Traditional density estimates based on mark-recapture data are inappropriate as they assume a random mixing of individuals within the population. This assumption is not valid for colonial species like the common mole-rat. For each trip to each site I could be fairly sure that I had trapped out most of the study population, as: (1) the location of colonies could readily be determined from the presence of soil mounds[3]; (2) all colonies were trapped; and (3) I attempted to trap each colony out completely. Due to the disparity in study site size between Sir Lowry's Pass (5 ha) and Steinkopf (43 ha), animal densities are expressed per unit area. Inter-site differences in common mole-rat densities were tested statistically using the Mann-Whitney U-test (Zar 1984). In all statistical tests $p \leq 0.05$ was considered significant. Summary values are presented as means ± one standard error (sample sizes are given in square brackets). Error bars are not included in line graphs as these obscured the patterns.

[3] When mole-rats dig their burrow systems, excavated soil is pushed onto the surface forming distinctive mounds.

RESULTS

Colony size

Mean colony size did not differ significantly between Steinkopf and Sir Lowry's Pass, irrespective of whether all captures or only first captures were used (all captures Sir Lowry's Pass [SLP]: 5.1 ± 0.2 [142], Steinkopf [ST]: 5.1 ± 0.2 [120], Mann-Whitney U-test, U = -0.21, p = 0.8; first capture SLP: 5.1 ± 0.4 [61], ST: 4.3 ± 0.4 [49], Mann-Whitney U-test, U = 1.89, p = 0.06). In contrast to mean colony size, inter-site differences in modal colony size were dependant on the data set used; for all captures combined, modal colony size was smaller at Steinkopf (mode = 2) than at Sir Lowry's Pass (mode = 5), whilst for first captures only the modal colony size was the same at both sites (mode = 2).

The co-efficient of variation in colony size for all captures combined was identical for Steinkopf (51%) and Sir Lowry's Pass (51%; Variance ratio test, $F_{(120; 142)} = 0.81$, $p > 0.5$). Similarly the co-efficient of variation in colony size at first capture only, did not differ significantly between Steinkopf (64%) and Sir Lowry's Pass (59%; Variance ratio test, $F_{(49; 61)} = 0.95$, $p > 0.5$). These findings suggest that the intrinsic variability in colony size does not differ significantly between the study populations.

Figures 7.1 and 7.2 show the frequencies with which different sized colonies were captured at the two study localities. In absolute terms the frequency distribution of different sized colonies was similar for the two study localities, irrespective of whether all captures or only first captures were used (Figures 7.1a & 7.2a). Using data from either all captures combined or only first captures, colonies of different size occurred with statistically comparable frequency at Steinkopf and Sir Lowry's Pass (all captures: Fisher exact test, $p \geq 0.2$ for all colony sizes; first capture: Fisher exact test, $p \geq 0.4$ for all colony sizes). However, despite the lack of statistical significance, Figures 7.1a and 7.1b do suggest that pairs occurred more frequently at Steinkopf than at Sir Lowry's Pass.

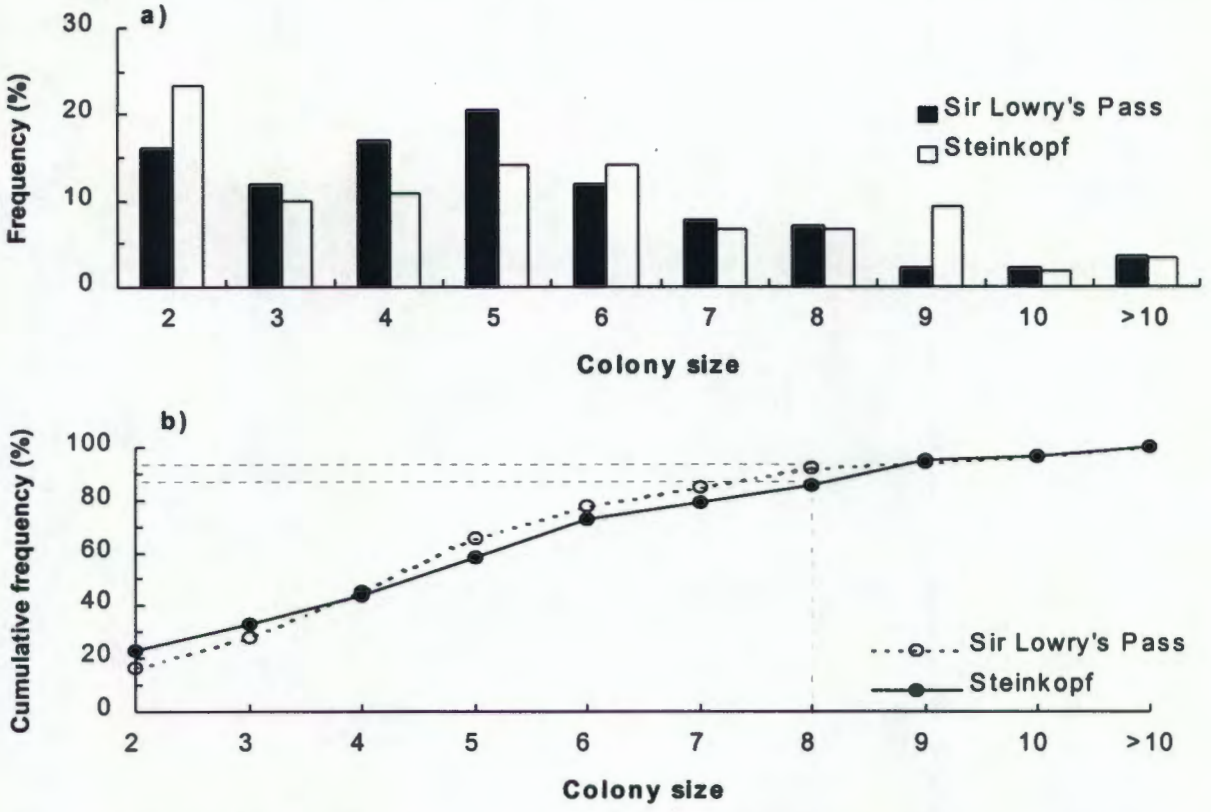


Figure 7.1: Using data for all captures combined (including first captures and recaptures), frequency of different colony sizes of *C. h. hottentotus* captured at Sir Lowry's Pass and Steinkopf: (a) absolute frequency of different colony sizes; (b) cumulative frequency of different colony sizes.

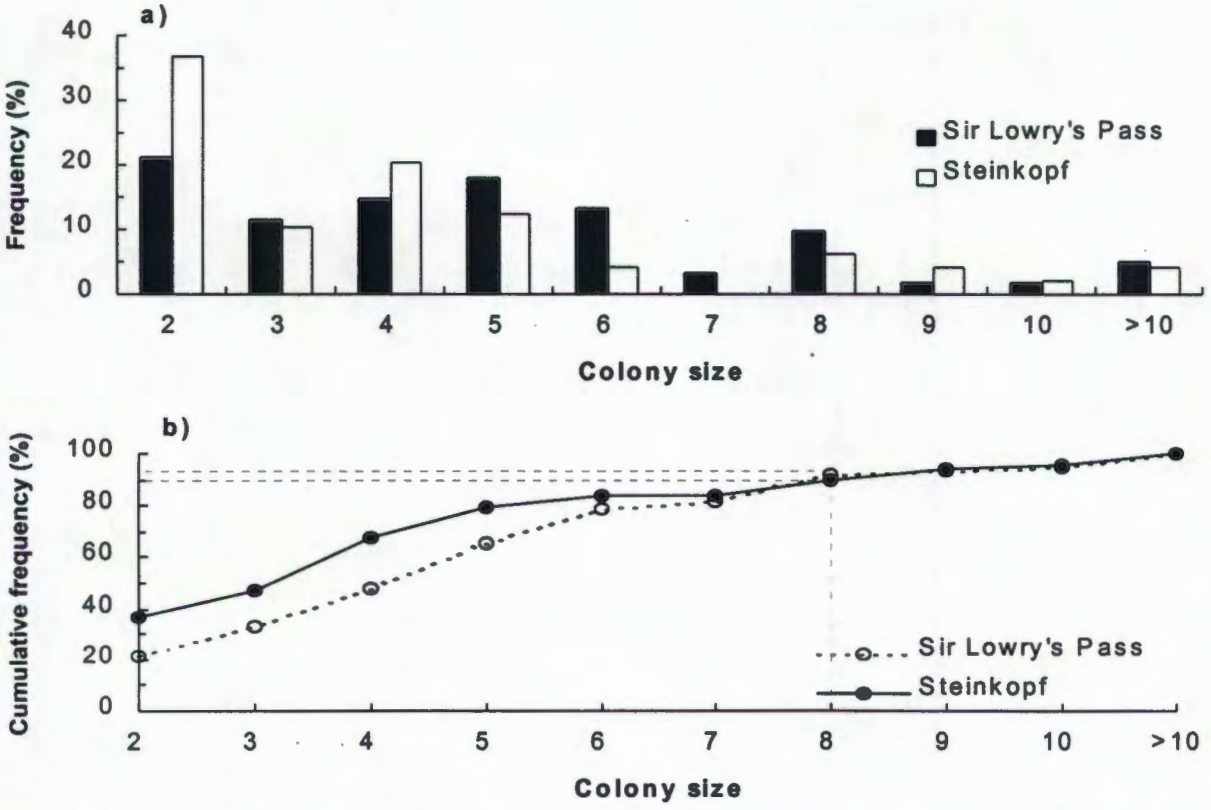


Figure 7.2: Using data for first captures only, frequency of different colony sizes of *C. h. hottentotus* captured at Sir Lowry's Pass and Steinkopf: (a) absolute frequency of different colony sizes; (b) cumulative frequency of different colony sizes.

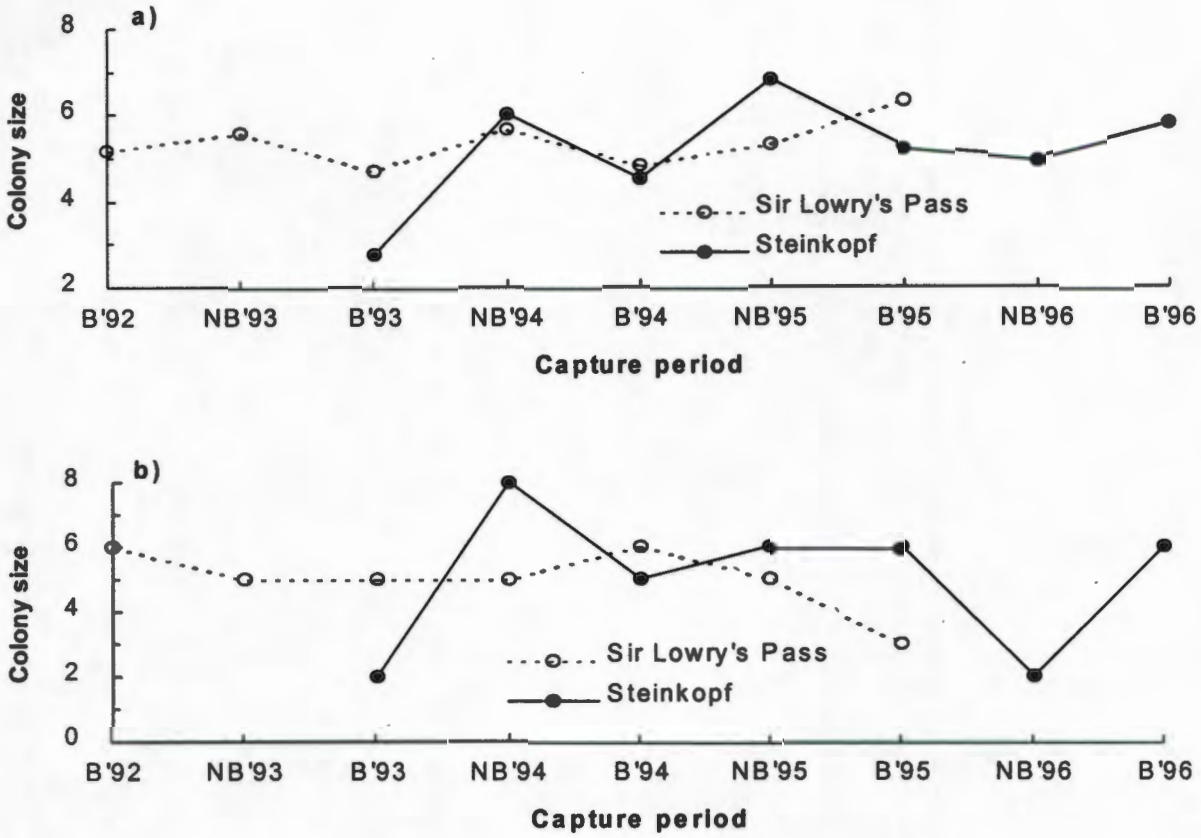


Figure 7.3: Temporal variation in average colony size for complete *C. h. hottentotus* colonies caught at Sir Lowry's Pass and Steinkopf: (a) mean colony size; (b) modal colony size. For the capture periods each label gives the year and whether the data are for the breeding period (B) or non-breeding period (NB).

The cumulative frequency diagrams (Figures 7.1b & 7.2b) reveal that the vast majority of captured colonies range in size from two to eight animals. For all captures combined, 86% of colonies at Steinkopf and 92% of colonies at Sir Lowry's Pass contained two to eight mole-rats (Figure 7.1b), whilst for first captures only 90% of Steinkopf colonies and 92% of Sir Lowry's Pass colonies contained two to eight individuals (Figure 7.2b).

Longitudinal data on colony size (Figure 7.3) revealed that average group sizes were comparable between Sir Lowry's Pass and Steinkopf for most capture periods (Figure 7.3a). The exception was the 1993 breeding period at Steinkopf where mean colony sizes were markedly smaller than for all capture periods at Sir Lowry's Pass, as well as for the other

capture periods at Steinkopf (Figure 7.3a)[4]. Apart from this discrepancy average colony sizes at both sites fluctuated only marginally, oscillating between *ca* four and six individuals per group. In contrast to mean group size, temporal data on modal colony size showed clear differences between sites, however, inter-site differences were equivocal (Figure 7.3b). For Sir Lowry's Pass modal group size was relatively constant at five to six animals per group from the 1992 breeding period to the 1994 breeding period (Figure 7.3b). After this interval, however, modal group size showed a decrease. By comparison, the Steinkopf study population exhibited substantial stochastisity in modal colony size (Figure 7.3b). As with mean colony size, modal colony size during the 1993 breeding period was markedly smaller at Steinkopf than at Sir Lowry's Pass. By the 1994 non-breeding period, modal colony size was greater at Steinkopf than at Sir Lowry's Pass. For the 1994 breeding period and 1995 non-breeding periods modal sizes were comparable for the two sites. However, by the 1995 breeding period, modal group size was again greater at the arid site. In 1996 modal size oscillated widely at Steinkopf.

Individual mass

Common mole-rats from Steinkopf were on average significantly smaller than those from Sir Lowry's Pass (all captures SLP: 75.2 ± 1.0 g [865], ST: 57.8 ± 0.7 g [722], Mann-Whitney U-test, $U = -12.45$, $p < 0.00001$; first capture SLP: 66.9 ± 1.3 g [479], ST: 52.3 ± 1.0 g [369], Mann-Whitney U-test, $U = -7.31$, $p < 0.00001$). Figures 7.4 and 7.5 show the average body mass for different age/sex-status categories of individuals captured at Sir Lowry's Pass and Steinkopf. The resultant patterns are similar whether data from all captures combined (Figure 7.4) or only data from first captures (Figure 7.5) are used: juveniles from Sir Lowry's Pass were on average significantly smaller than those from Steinkopf (all captures: Mann-Whitney U-test, $U = 3.15$, $p = 0.002$; first capture: Mann-Whitney U-test, $U = 2.49$, $p = 0.01$);

[4] At the start of the study at Steinkopf, a large number of the captured colonies where pairs. This would account for the small average colony size in the 1993 breeding period, as well as the modal colony size of 2 (using data for all captures combined) at Steinkopf.

non-reproductive females from both sites were of similar mass (all captures: Mann-Whitney U-test, $U = -0.22$, $p = 0.8$; first capture: Mann-Whitney U-test, $U = -0.85$, $p = 0.4$); non-reproductive males from Sir Lowry's Pass were on average significantly larger than those from Steinkopf (all captures: Mann-Whitney U-test, $U = -9.61$, $p < 0.00001$; first capture: Mann-Whitney U-test, $U = -6.89$, $p < 0.00001$); reproductive females from Sir Lowry's Pass were on average significantly larger than those from Steinkopf (all captures: Mann-Whitney U-test, $U = -7.96$, $p < 0.00001$; first capture: Mann-Whitney U-test, $U = -4.97$, $p < 0.00001$); and reproductive males from Sir Lowry's Pass were on average significantly larger than those from Steinkopf (all captures: Mann-Whitney U-test, $U = -13.83$, $p < 0.00001$; first capture: Mann-Whitney U-test, $U = -8.10$, $p < 0.00001$; Figures 7.4 & 7.5).

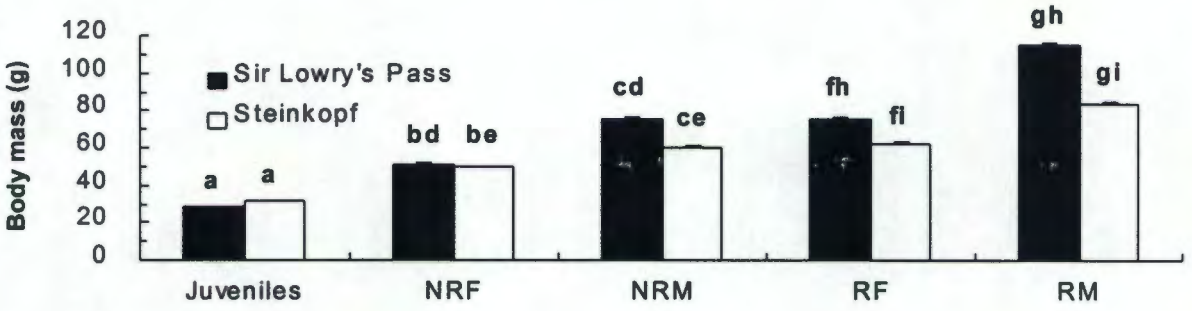


Figure 7.4: Using data for all captures combined (including first captures and recaptures), average body mass for juvenile, non-reproductive female (NRF), non-reproductive male (NRM), reproductive female (RF) and reproductive male (RM) *C. h. hottentotus* captured at Sir Lowry's Pass and Steinkopf. a-i = significantly different groups, any groups sharing a single letter in common are significantly different (see text for details). Data presented as means ± SE. The criteria used to assign individuals to different age/sex-status classes are outlined in the materials and methods.

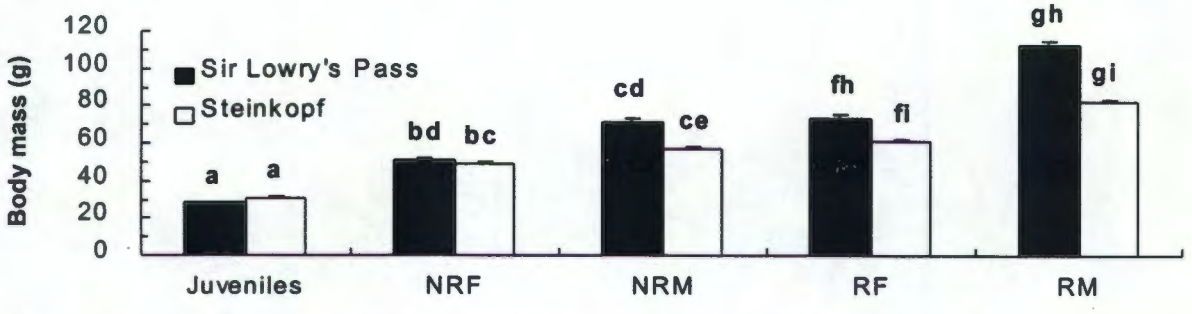
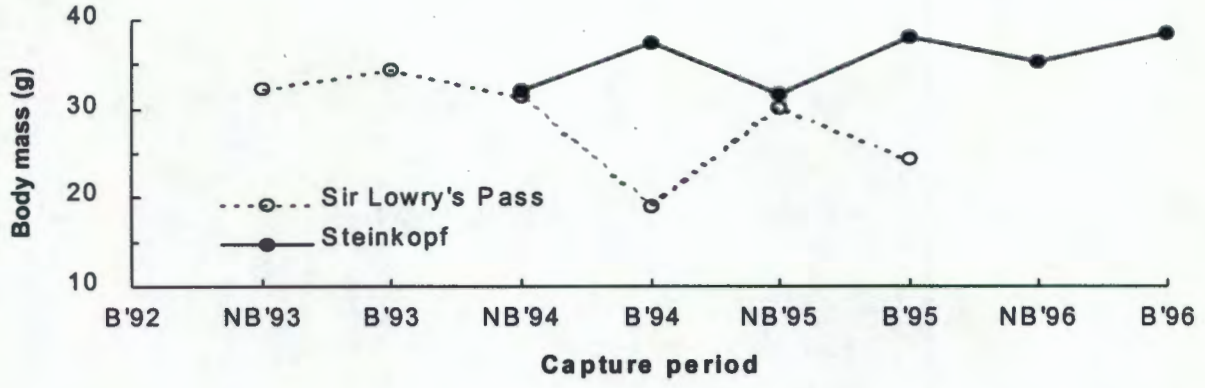


Figure 7.5: Using data for first captures only, average body mass for juvenile, non-reproductive female (NRF), non-reproductive male (NRM), reproductive female (RF) and reproductive male (RM) *C. h. hottentotus* captured at Sir Lowry's Pass and Steinkopf. a-i = significantly different groups, any groups sharing a single letter in common are significantly different (see text for details). Data presented as means ± SE. The criteria used to assign individuals to different age/sex-status classes are outlined in the materials and methods.

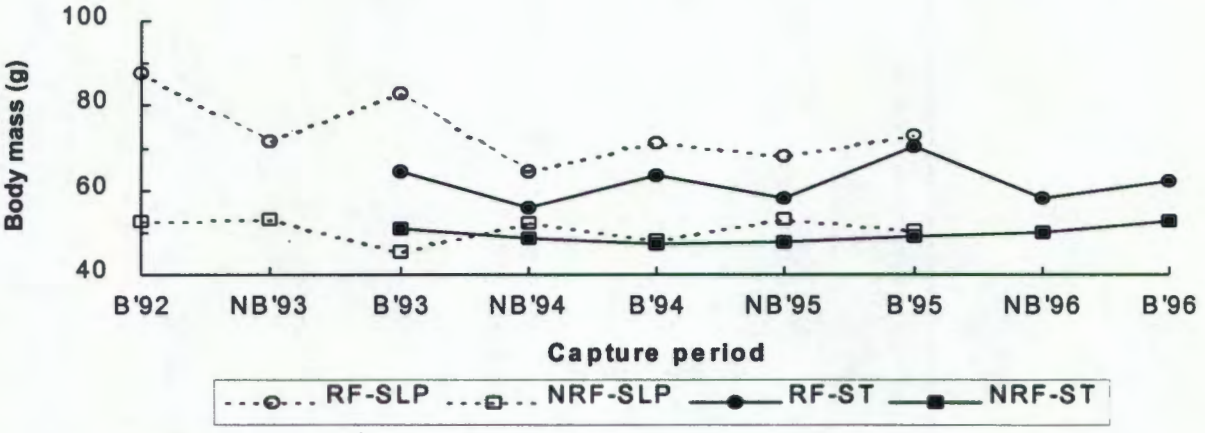
In addition to inter-site within category differences, there were significant intra-site differences between different age/sex-status categories. Irrespective of whether all captures or only first captures were used, non-reproductive males from both Steinkopf and Sir Lowry's Pass were significantly larger than non-reproductive females from the same site (SLP all captures: Mann-Whitney U-test, $U = 10.93$, $p < 0.00001$; first capture: Mann-Whitney U-test, $U = 8.04$, $p < 0.00001$; ST all captures: Mann-Whitney U-test, $U = 8.88$, $p < 0.00001$; first capture: Mann-Whitney U-test, $U = 4.67$, $p < 0.00001$; Figures 7.4 & 7.5). Similarly, reproductive males from both Steinkopf and Sir Lowry's Pass were significantly larger than reproductive females from the same site (SLP all captures: Mann-Whitney U-test, $U = 13.95$, $p < 0.00001$; first capture: Mann-Whitney U-test, $U = 8.83$, $p < 0.00001$; ST all captures: Mann-Whitney U-test, $U = 12.30$, $p < 0.00001$; first capture: Mann-Whitney U-test, $U = 7.76$, $p < 0.00001$; Figures 7.4 & 7.5).

Longitudinal data on the average body mass of juveniles, non-reproductive males and females and reproductive males and females are presented in Figure 7.6. There was substantial variation in average juvenile mass at both sites (Figure 7.6a), however, temporal patterns of juvenile mass must be interpreted with caution as average mass is strongly affected by whether the population was actively recruiting or not during or just before the capture period. For all capture periods reproductive females from Sir Lowry's Pass exhibited a greater average body mass than those from Steinkopf (Figure 7.6b). By comparison non-reproductive females from both localities revealed similar body masses for all capture periods (Figure 7.6b). Distinct periodicity was evident in the average body mass of reproductive females from both the arid and mesic sites. Body mass reached a maximum during the breeding periods and a minimum during the non-breeding periods (Figure 7.6b). For all capture periods, reproductive and non-reproductive males from Sir Lowry's Pass were on average larger than reproductive and non-reproductive males, respectively, from Steinkopf (Figure 7.6c). Notably, as with the reproductive females, reproductive males from

a) Juveniles



b) Females



c) Males

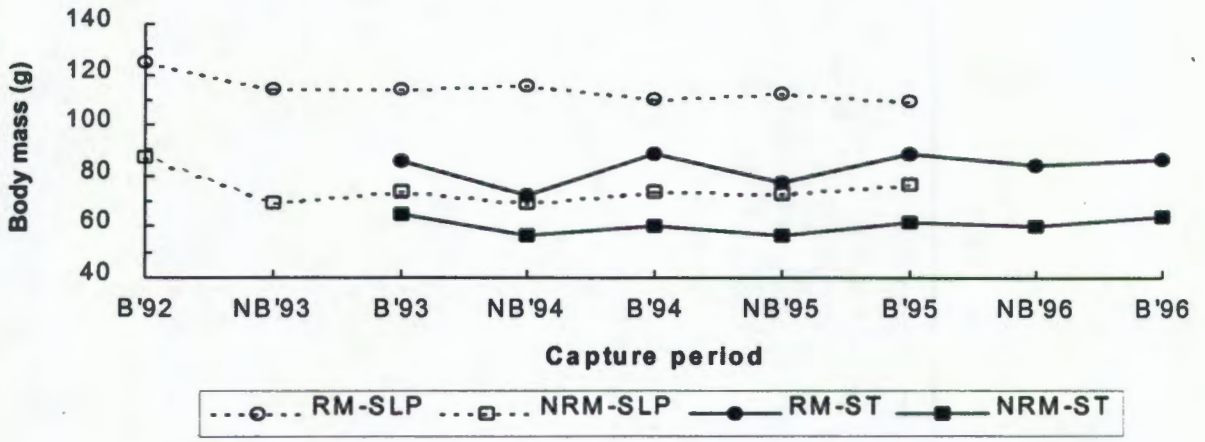


Figure 7.6: Temporal variation in the average individual body mass of *C. h hottentotus* caught at Sir Lowry's Pass and Steinkopf: (a) juveniles; (b) females; (c) males. The criteria used to assign individuals to different age/sex classes are outlined in the materials and methods. RF = reproductive female, NRF = non-reproductive female, RM = reproductive male, NRM = non-reproductive male, SLP = Sir Lowry's Pass, ST = Steinkopf. For the capture periods each label gives the year and whether the data are for the breeding period (B) or non-breeding period (NB).

the arid site exhibited cyclicity in mean body mass, which peaked during the breeding periods and bottomed during the non-breeding periods (Figure 7.6c).

Colony biomass

Mean colony biomass was significantly smaller at Steinkopf than at Sir Lowry's Pass, irrespective of whether all captures or only first captures were used (all captures SLP: 382.6 ± 15.7 g [139], ST: 286.9 ± 12.3 g [115], Mann-Whitney U-test, U = -4.56, $p < 0.00001$; first capture SLP: 384.7 ± 28.7 g [62], ST: 238.6 ± 15.0 g [50], Mann-Whitney U-test, U = -4.14, p = 0.00003). Longitudinal data on average colony biomass (Figure 7.7) revealed that for all capture periods average colony biomass at Sir Lowry's Pass was greater than that at Steinkopf. Figure 7.7 also shows that the average colony biomass at Steinkopf increased from the 1993 breeding period to 1995 non-breeding period, after which it appeared to level-off. In contrast, although there was some variation in average colony biomass at Sir Lowry's Pass, it remained more or less at a consistent level throughout the study (Figure 7.7).

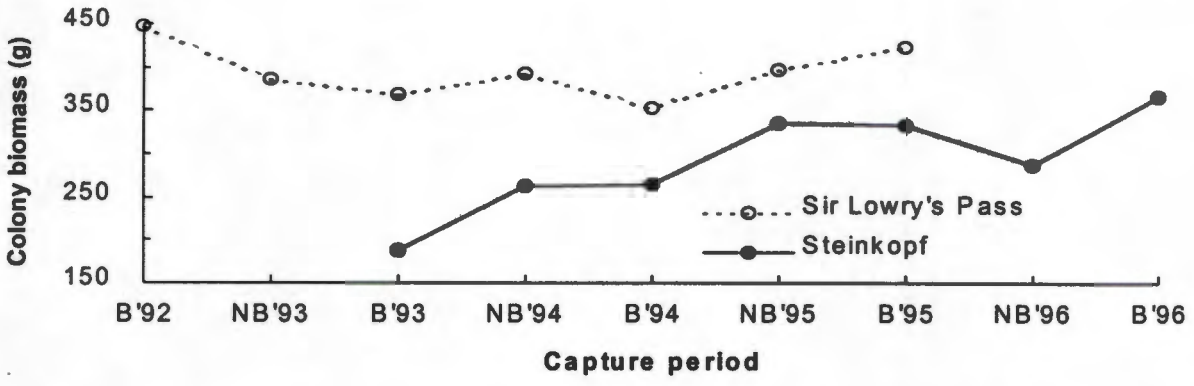


Figure 7.7: Temporal variation in mean colony biomass for complete *C. h. hottentotus* colonies captured at Sir Lowry's Pass and Steinkopf. For the capture periods each label gives the year and whether the data are for the breeding period (B) or non-breeding period (NB).

Litter size

Average litter size was similar for Sir Lowry's Pass (2.3 ± 0.2 [26]) and Steinkopf (2.6 ± 0.2 [19]; Mann-Whitney U-test, $U = -1.42$, $p = 0.2$). Figure 7.8 shows the frequency with which litters of different size occurred at Steinkopf and Sir Lowry's Pass. The frequency distributions were not significantly different (Fisher exact test, $p \geq 0.4$ for litter sizes), although litter sizes of one and two pups occurred comparatively more frequently at Sir Lowry's Pass, and litter sizes of three pups occurred comparatively more frequently at Steinkopf.

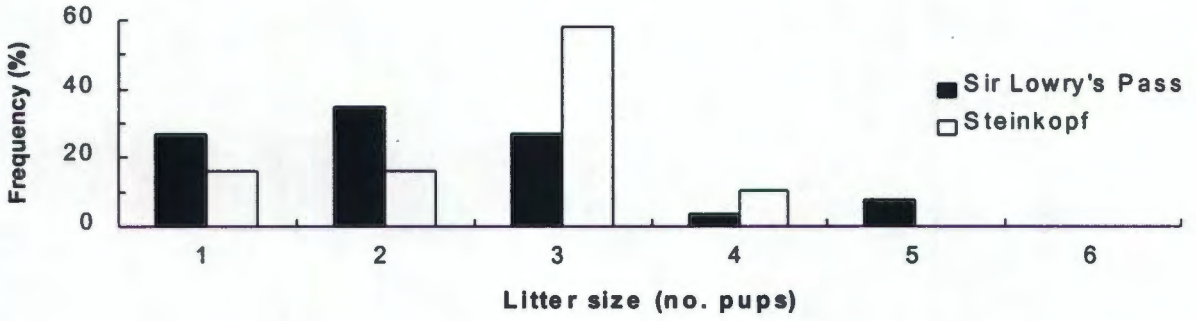


Figure 7.8: The frequency of different litter sizes of *C. h. hottentotus* at Sir Lowry's Pass and Steinkopf.

Data from sacrificed pregnant animals and from females who gave birth whilst in captivity suggest that the average litter sizes obtained from this demographic study may have been an underestimate. Of four litters from females from Steinkopf, three consisted of five pups and one of six pups, whilst of seven litters from females from Sir Lowry's Pass two contained pairs, two contained four pups, one contained five pups and two contained six pups. Given that litters in the wild were not caught immediately after birth it is likely that pup mortality between birth and capture would account for this discrepancy.

Population density

Mean densities of common mole-rats at Sir Lowry's Pass were an order of magnitude greater than those at Steinkopf (SLP: 18.7 ± 1.2 [8], ST: 1.8 ± 0.2 [8]; Mann-Whitney U-test,

$U = 3.31$, $p = 0.0009$). Figure 7.9 shows the temporal variation in population densities at Sir Lowry's Pass and Steinkopf over the study period. Although there was considerably more longitudinal variability in the estimated population size at Sir Lowry's Pass, for all capture periods densities there were markedly greater than at Steinkopf (Figure 7.9).

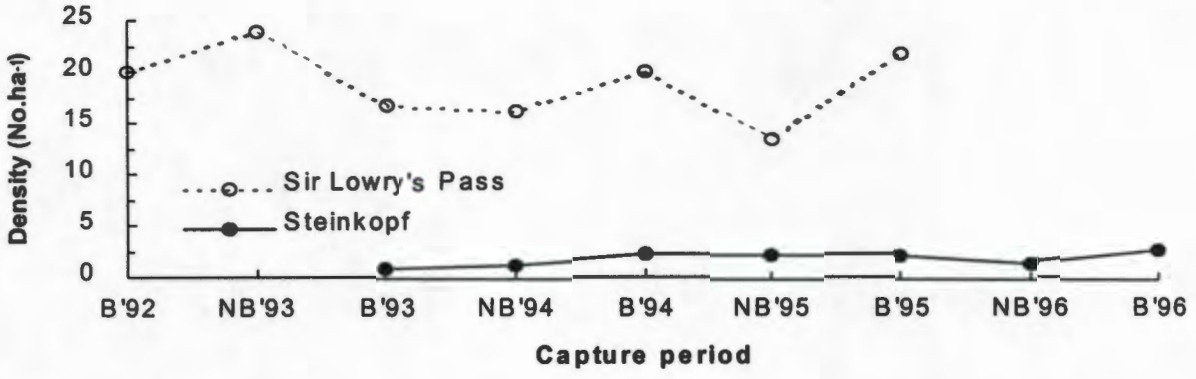


Figure 7.9. Temporal variation in population densities for *C. h. hottentotus* caught at Sir Lowry's Pass and Steinkopf. Density estimates are based on the minimum number alive. For the capture periods each label gives the year and whether the data are for the breeding period (B) or non-breeding period (NB).

DISCUSSION

To predict the long- or short-term effects of different combinations of environmental factors on the life history of a species it is critical to establish the link between habitat and demography (Van Horne *et al.* 1997). Despite the difficulty of this task, several workers have shown the influence of abiotic and habitat conditions on species demography and hence fundamental life history traits like social behaviour (Myers *et al.* 1985; Adler & Wilson 1987; Gurnell 1996; McCarthy 1996; Van Horne *et al.* 1997; Wolff 1997). Thus in examining the advent of bathyergid sociality, and in particular the validity of the AFDH, we need to appreciate the biological consequences of the environmental correlates of aridity (Chapters 2 to 5) on the basic demography and related socio-biology of mole-rats.

The AFDH asserts that cooperative foraging reduces the risks of unproductive foraging and represents a stable long-term behaviour in arid habitats where food resources are widely dispersed and foraging costs are high (Lovegrove & Wissel 1988; Lovegrove

1991; Jarvis *et al.* 1994; Lacey & Sherman 1997; Chapter 1). Consequently it predicts that, associated with the decrease in geophyte density and increase in energetic costs of foraging, colony size should be greater in arid areas (Lovegrove & Knight-Eloff 1988). Lovegrove and Wissel (1988) and Lovegrove's (1991) stochastic foraging model, the Risk Sensitivity Hypothesis, provides theoretical corroboration of this prediction. Moreover, the limited empirical evidence available (summarised in Table 7.1) seems to confirm this contention: naked mole-rats, *Heterocephalus glaber*, which occur in the most arid areas, with the lowest resource densities have the largest colony sizes, whilst the Cape mole-rat, *Georychus capensis*, which occurs in the most mesic habitats is solitary. *Cryptomys h. hottentotus* and *C. damarensis* lie between these extremes.

Table 7.1: Variation in average group size relative to food resource density in four species of bathyergid mole-rat.

Species	Resource density (# geophytes.m^{-2})	Mean group size (maximum)
Georychus capensis[a,b,c,d]	100 - 1000+*	1 (1)
C. h. hottentotus[d]	76 -1000+	5 (16)
C. damarensis[e,f,g,h]	0.03 - 160	10-25 (41)
Heterocephalus glaber[i,j]	0.06	70-80 (300)

* although *G. capensis* was not specifically investigated in this study, it did occur sympatrically with *C. h. hottentotus* at the Sir Lowry's Pass study site.
[a] Bennett 1988; [b] Du Toit *et al.* 1985; [c] J.U.M. Jarvis & B.G. Lovegrove unpublished data; [d] this study; [e] Lovegrove 1988; [f] Lovegrove & Knight-Eloff 1988; [g] Jarvis *et al.* 1998; [h] J.U.M Jarvis & N.C. Bennett unpublished data; [i] Brett 1986; [j] Brett 1991.

Given the aforementioned findings, common mole-rats at the arid locality (Steinkopf) would be predicted to occur in larger colonies than those at the mesic locality (Sir Lowry's Pass). The results from this investigation, however, do not support this expectation, both study populations exhibited an average group size of about five animals, with more than 85% of all colonies examined (irrespective of study site) containing two to eight individuals. Despite their contradiction to the expected trends, these findings do not necessarily refute

the AFDH. Instead, they may highlight the problems associated with trying to assess inter-population differences in the social development of the common mole-rat .

Models of the evolution of vertebrate sociality are typically ahistorical, variation in social behaviour being viewed as a consequence of adaptive individual plasticity moulded by current ecological conditions and social selection pressures (Krebs & Davies 1993; Prum 1994). However, evolutionary biologists are becoming increasingly cognisant of the need to consider historical information when examining questions of social evolution (Peterson & Burt 1992; Prum 1994). Hence, although adaptive plasticity may have been the proximate mechanism of social change in the bathyergids, ultimately complex social behaviour is likely to have evolved through longitudinal selection on genetic variation in behaviour, in response to the historical selective regime imposed by aridity. It is believed that the bathyergids speciated along an arid corridor extending from the present locality of *H. glaber* populations in arid East Africa, to the mesic localities of the solitary genera in the Western Cape of South Africa (Honeycutt *et al.* 1987; Nevo *et al.* 1987; Lovegrove 1991). This corridor has been opened and closed several times through fluctuating mesic and arid periods since the Miocene (Verdcourt 1969). The AFDH predicts that survival within these arid zones was dependent on the abandonment of a solitary existence and an increase in group size. The ancestor to the extant mesic-occurring *C. h. hottentotus* population may initially have been arid-adapted and was subsequently exposed to a mesic environment as the arid corridor retreated. Given this historical scenario, the question we perhaps need to ask is why have the mesic-occurring common mole-rats populations retained their social ancestry. There are several likely explanations for this apparent enigma.

(1) Divergence and evolutionary time: As outlined in Chapter 1 the two populations used in this investigation exhibit relatively little genetic divergence, sequence variation between the two populations for 1140 sequenced basepairs of the cytochrome b gene being just 2.4% (C.G. Faulkes unpublished data). This suggests that allopatry between the Steinkopf and Sir Lowry's

Pass *C. h. hottentotus* populations is a relatively recent phenomenon. Consequently the apparent absence of a breakdown in group size in the mesic-occurring common mole-rat population may simply reflect that insufficient time has elapsed to facilitate evolutionary divergence in social behaviour between it and the arid population.

The lack of genetic divergence between the two study populations further suggests that measures like absolute group size may be too coarse to reveal subtle inter-habitat deviation in social behaviour. More refined and hence discriminating measures of ethological differentiation *e.g.* divergence in the patterns of natal philopatry and dispersal (Chapter 8), are probably more appropriate.

(2) Phylogenetic constraints: Prum (1994; pp 1667) notes that "the evolution of vertebrate social behavior may have historical consequences that can limit subsequent opportunities for behavioral adaptation". Such phylogenetic constraints (Prum 1994) or lineage effects (Arnold 1994) are a consequence of events in the phylogenetic history of an organism which limit its adaptive capacity, and range from constraints due to changes in developmental capacities to constraints due to changes in selective regimes (Maynard-Smith *et al.* 1985; Arnold 1994). For example, lekking behaviour in manakins is suggested to be phylogenetically constrained via the mechanisms of sexual selection (Prum 1994). Lineage effects appear to be especially relevant to the loss of specific traits *e.g.* loss of lekking behaviour in manakins (Prum 1994). Thus although the requisite selective regime may exist in mesic habitats, the evolution of common mole-rat solitariness may be constrained phylogenetically. This contention is supported by the observation that mole-rats exhibit little flexibility in social organisation; social mole-rats are seldom encountered alone, except when dispersing, and solitary species are rarely encountered in groups, except when mating (Jarvis & Bennett 1990; 1991). These observations emphasise that a comprehensive understanding of the behavioural evolution of any group requires an historical perspective of the behavioural diversification of that group (Peterson & Burt 1992; Prum 1994).

(3) Altered selective regime: In discussing social evolution within the *Aphelocoma* jays Peterson and Burt (1992) propose that the invasion of environments in which the former social system is not strongly selected against will lead to the retention of that social system in a new ecological context. Consequently, the preservation of group-living in the Sir Lowry's Pass common mole-rat population suggests that the selective regime driving solitary evolution in mesic habitats is not as strong as that promoting social evolution in arid areas. The apparently weak selection against coloniality in mesic environments may reflect the absence of substantial fitness costs associated with the maintenance of sociality. The major fitness cost in most communally breeding birds and mammals relates to missed reproductive opportunities in subordinate group members (West Eberhard 1975; Brown 1978; Creel & Waser 1991; Keane *et al.* 1994). Wasser and Barash's (1983) Reproductive Suppression Model argues that females can optimise their lifetime reproductive success by curtailing reproduction when future reproductive potential transcends present reproductive potential, so as to exceed the costs of reproductive restraint itself. Although the constraints on independent reproduction in arid occurring mole-rats are well established (Chapters 1 to 5), there may be comparable reproductive limitations in mesic areas. Densities of mole-rats at Sir Lowry's Pass were an order of magnitude greater that those at Steinkopf. These higher densities will reduce available space, and hence opportunities for dispersal and independent reproduction may be limited. Consequently it may pay subordinate individuals to remain within their natal colonies, curtailing reproduction until suitable opportunities occur.

Sociality may be retained in mesic-occurring *C. h. hottentotus* due to the selective benefits it imparts to group members. These benefits are less obvious in mesic areas than in arid areas, but may relate to improved territory and hence resource defence. This will be especially important given the high densities of mole-rats and concomitant competition for resources in mesic areas (see above). Thus although solitariness represents an Evolutionarily Stable Strategy (ESS, *sensu* Maynard-Smith 1972) in mesic environments, thereby maximising individual inclusive fitness, group-living may impart alternative fitness

benefits and consequently represent a substitute ESS to a solitary existence. Considerations like these suggest that there may in fact be strong selection for group-living in mesic environments, and this will be explored more fully in the thesis synthesis (Chapter 10).

Individually or in combination, these factors may account for the observed maintenance of sociality in common mole-rats from Sir Lowry's Pass, and hence the similarity in colony size between the arid and mesic populations. They also suggest that more refined and hence discriminating measurements of ethological differentiation are appropriate in assessing differences in the level of social elaboration between the *C. h. hottentotus* populations at Steinkopf and Sir Lowry's Pass.

The mean colony sizes obtained for *C. h. hottentotus* in this study are fairly small in comparison to *C. damarensis* [mean group size of *ca.* 10 animals (J.U.M. Jarvis & N.C. Bennett unpublished data)]. Given that increased group size may severely curtail foraging costs (Lovegrove & Wissel 1988; Lovegrove 1991; Jarvis *et al.* 1994), it is surprising that colony sizes are not larger at Steinkopf, and this suggests that there may be upper limits to colony size. As outlined below, increases in group size may be constrained by the need to minimise colony energy expenditure. The addition of new members increases the colony's energetic costs, thereby heightening the risks of starvation for all group members. Alternatively, the small group sizes, at both sites, may simply reflect the low recruitment rates prevalent there (see below). As a consequence large groups will take a long time to form, and may rarely form if attrition rates, due to mortality and dispersal, are high enough. This latter explanation seems more parsimonious given that large colonies of ≥ 10 individuals (maximum = 13 animals) have been captured at the arid site on six occasions (= 5% of all complete colonies caught at Steinkopf).

It has been suggested that for the benefits accrued from cooperative foraging to be fully realised by social mole-rats, the energetic requirements of all colony members must be

satisfied (Jarvis & Bennett 1991). This will be particularly important in arid environments where resource encounters are infrequent and foraging costs are high. There are two components to meeting colony energetic demands: (1) maximising encounters with food items; and (2) minimising the total energy expenditure of the colony (Jarvis 1978; Lovegrove & Wissel 1988; Jarvis & Bennett 1991). Adaptations to maximise encounters with food resources, which include coloniality and pertinent foraging strategies, have been discussed in some detail in Chapters 3 to 5. The efficiency of encounters with resources can, however, only be enhanced to a limited degree and consequently adaptations that minimise total colony energy expenditure will be of crucial importance. These energetic considerations are especially relevant where they define the upper-limits to adaptations that improve foraging efficiency; for example increases in group size are constrained by the added energetic costs associated with the addition of new colony members.

Adaptations that may reduce colony energy costs include, amongst others, reduced colony size and reduced individual body size (Jarvis & Bennett 1991). However, Jarvis (1985) suggests that in the naked mole-rat, when food is limiting it is individual body size rather than the number of animals in a colony that is reduced. Consequently, it was predicted that individual body size, as reflected by body mass[5], would be smaller for common mole-rats from the arid locality than those from the mesic locality. The results from this investigation support this contention; individuals from Sir Lowry's Pass were significantly heavier than those from Steinkopf. As a consequence, average colony biomass was also significantly smaller for colonies captured at Steinkopf, relative to those captured at Sir Lowry's Pass. This reduced individual and colony biomass will translate into substantial energetic savings and ultimately diminished total colony energy expenditure in arid environments, thereby enhancing group, and hence individual, survival.

[5] Braude (1991) and Brett (1986) have shown that body mass is a good indicator of body size in naked mole-rats.

It could be argued that the smaller body size of arid-occurring mole-rats is purely a consequence of their obtaining insufficient nourishment, rather than a dietary adaptation to reduce colony energy expenditure. Whilst it is difficult to separate cause and effect in this case, this would seem unlikely. If animals at Steinkopf had insufficient access to food, and hence were effectively starving, we would expect this to be reflected in their physical condition. However, although smaller in size, animals from the arid site were qualitatively in no worse physical condition than those from Sir Lowry's Pass. Moreover, studies of several mammalian species have demonstrated that individuals respond to nutritional stress by reducing their metabolic energy requirements (*e.g.* Buffenstein 1984; McCarter & McGee 1989; Markussen *et al.* 1992; Boily & Lavigne 1995). Consequently, even if restricted access to food limits growth rates in arid-occurring *C. h. hottentotus*, the resultant reduced individual body size and accompanying diminished energetic requirements would still be adaptive as they would curtail colony energetic costs.

Analysis of inter-populational differences in body mass revealed two interesting patterns. First, reproductive males and females from Steinkopf and reproductive females from Sir Lowry's Pass appear to exhibit seasonal cyclicity in body mass, reproductive individuals showing a notable reduction in body mass during the non-breeding period. Whilst this probably reflects the onset of pregnancy in reproductive females, it possibly represents an energy saving strategy in reproductive males. Consequently, reproductive males may put on weight during the breeding period in order to aggressively defend their reproductive position, but lose weight during the non-breeding period, thereby curtailing individual, and ultimately colony, energy expenditure. Second, for both study populations, adult males were larger than adult females, and reproductive males were larger than reproductive females. Thus despite that inter-habitat divergence in absolute body mass, the sex and status-related patterns of mass distribution are comparable for the two sites.

Related to energetic constraints, it was also predicted that colony recruitment should be lower in arid environments, and this could be reflected in a reduced average litter size.

The findings from this investigation do not support this contention, average litter sizes being comparable for the two study populations. As outlined in Chapter 1 common mole-rats from both study populations are seasonal breeders, typically producing a single litter each year. This together with their small litter sizes (average of just over two pups per litter) means that recruitment in this species is already very low. By comparison, Brants' whistling rat, *Parotomys brantsii*, a seasonally breeding murid rodent occurring sympatrically with *C. h. hottentotus*, produces three to four litters of three to four pups (*i.e.* 9 - 16 young) during each breeding season (Jackson submitted). Given that mole-rats occurring in arid areas need to recruit colony members to cooperate in foraging, they may not be able to curtail colony recruitment any further as this would impact negatively on colony foraging success. Jarvis *et al.* (1998) have demonstrated that in Damaraland mole-rats the size of a colony is a crucial determinant of its persistence, partly as a consequence of the size of the colony work force available to locate food in times of environmental stress. Alternatively, the lack of inter-habitat divergence in litter sizes may merely indicate that the low rates of recruitment in both study populations have severely limited the scope for inter-habitat differentiation in the patterns of recruitment.

In conclusion, the demographic variables investigated in this chapter reveal conflicting results with respect to inter-site variation in the degree of social elaboration/regression. Predicted inter-site differences in colony size were not apparent. Moreover, study populations revealed no differences with respect to litter sizes and concomitant recruitment rates. However, common mole-rats from Steinkopf did exhibit a reduced individual and colony biomass relative to those from Sir Lowry's Pass, probably as an adaptation to reduce total colony energy expenditure given the elevated foraging constraints in arid environments. This finding may suggest a heightened degree of social specialisation in the arid-occurring common mole-rat population, related to the energetic constraints prevalent in arid areas.

Chapter 8

Comparative colony dynamics: dispersal and philopatry

ABSTRACT

The differential patterns of dispersal and philopatry, in the two study populations were investigated. Four predictions, derived from the Aridity Food-Distribution Hypothesis (AFDH) and current dispersal theory, were evaluated: (1) rates of dispersal should be reduced in arid relative to mesic areas; (2) rates of dispersal will be a function of colony size; (3) neither of the study populations will exhibit sex-biased dispersal; and (4) dispersing animals will exhibit better body condition than their non-dispersing colony mates, and this will be expressed as a greater body mass. The results from this investigation provided support for predictions (1) and (2), mixed support for prediction (3) and no support for prediction (4). Rates of immigration and emigration were markedly lower in the arid study locality relative to the mesic site, probably reflecting divergence in the ecological constraints on dispersal. The rates of dispersal at both sites increased as a function of group size. However, at Sir Lowry's Pass colony attrition as a function of group size increased more rapidly than at Steinkopf, and it is suggested that this reflects the relaxation of dispersal constraints in mesic areas. Whilst there was no sex-biased dispersal at Steinkopf, dispersal at Sir Lowry's Pass was significantly skewed towards males, though this may simply reflect male-biased adult sex ratios at this site. Dispersing individuals at both study sites were comparable in mass to their non-dispersing colony mates. This lack of morphological differentiation between dispersers and non-dispersers may be a consequence of either the sampling protocol or the life history traits and breeding strategy of the common mole-rat. The results reveal distinct differences between the two study localities in both the quantitative and qualitative nature of dispersal. These may reflect adaptive variation in social behaviour between the regions, and the results suggest that delayed dispersal and cooperation may be more crucial to individual survival in arid than in mesic areas. As such these findings provide support for the underlying contention of the AFDH that ecological constraints on foraging in arid areas have promoted a greater degree of social elaboration.

INTRODUCTION

The influence of dispersal on animal demography, spatial distribution and social organisation is well established (Greenwood 1980; 1984; Sherman & Morton 1984;

Johnson & Gaines 1990; Brandt 1992; Stenseth & Lidicker 1992; Alberts & Altmann 1995; Doolan & MacDonald 1996). Dispersal, and the opportunity for independent reproduction it embodies, plays a crucial role in shaping mating systems and life-history tactics (Greenwood 1980; 1984; Stenseth & Lidicker 1992). This should be especially pertinent in outbred *singularly breeding* (*sensu* Brown 1987; French 1997) cooperative breeders, such as the social bathyergids. Subordinate colony members of social mole-rat species experience an interplay between the need to secure acceptable breeding opportunities and ecological constraints on dispersal (see Chapter 9). Conflict between these factors must ultimately shape life-history traits, including social behaviour. Consequently, investigations of dispersal may be crucially important for understanding the evolution and adaptive significance of sociality in the Bathyergidae. By investigating inter-populational divergence in patterns of dispersal and philopatry, researchers may gain key insights into regional differences in the levels of social development. Accordingly, this chapter investigates the differential patterns of dispersal and philopatry in the two study populations. To achieve this end I evaluate four crucial predictions which follow from the AFDH and current dispersal theory:

(1) The AFDH asserts that the ecological constraints imposed by (a) the energetic costs of burrowing, and (b) the distribution of crucial food resources in arid environments, substantially increase the risks associated with foraging and effectively curb opportunities for successful emigration of individuals from the natal burrow system (Bennett 1988; Lovegrove & Wissel 1988; Lovegrove 1991; Jarvis *et al.* 1994; Lacey & Sherman 1997). Consequently, I predict that dispersal within arid areas will be lower relative to mesic areas, due to these ecological constraints. This should be expressed as reduced rates of immigration and emigration within colonies in the arid population. Furthermore, as a result of the curtailed pace of dispersal, colonies of arid-occurring common mole-rats should exhibit greater temporal stability[1], with more predictable group membership over time.

[1] This presumes similar rates of mortality within colonies from the two study localities.

(2) In social organisms, an individual's inclusive fitness will vary as a function of group size (Pulliam & Caraco 1984). The AFDH predicts that increased group size maximises *per capita* consumption rates, and hence individual fitness, by reducing foraging risks (Bennett 1988; Lovegrove & Wissel 1988; Lovegrove 1991; Jarvis *et al.* 1994; Lacey & Sherman 1997). However, in very large mole-rat colonies there may be distinct costs to individual group-members, for the following reasons: (a) above an optimal group size, *per capita* food consumption rates will decrease and extra colony members will negate the benefits of social foraging (Pulliam & Caraco 1984; Krebs & Davies 1993); and (b) larger groups may be more susceptible to predation as a result of their increased conspicuousness[2] (Pulliam & Caraco 1984; Krebs & Davies 1993). Consequently, as colony size increases there may be some group size above which individual inclusive fitness is no longer being maximised and it pays individuals to risk dispersal. Therefore, I predict that beyond some "optimal group size", rates of disappearance (either via dispersal or mortality) from colonies will increase as a function of increased colony size.

(3) Male-biased dispersal is typical of mammals, and Greenwood (1980) suggests that the prevalence of polygyny as a mating system, with its associated intense intrasexual competition between males for mates, has led to elevated male dispersal, as they are compelled to leave their natal area in search of females. However, several workers have argued that in monogamous species competition for mates should be equally distributed between the sexes, and accordingly males and females should disperse in equal proportions (Greenwood 1980; Dobson 1982; Liberg & Von Schantz 1985; Pusey 1987; Wolff 1993). As outlined in Chapter 1, *C. h. hottentotus* is rare amongst group-living mammals in exhibiting behavioural monogamy.

[2] Although the subterranean ecotope is generally buffered against massive predation (Nevo 1982; Jarvis & Bennett 1990), predation does occur and burrowing activities of larger mole-rat colonies should attract more attention from predators than those of smaller colonies.

Consequently, I predict that neither study population will exhibit sex-biased patterns of dispersal.

(4) Body mass, body size and body condition have all been implicated in the temporal patterns of natal dispersal in various mammals (Holekamp 1984; 1986; Nunes & Holekamp 1996). For example Nunes and Holekamp (1996) have shown that the body mass and body fat of juvenile Belding's ground squirrels, *Spermophilus beldingi*, influence the timing of dispersal behaviour. Similarly, O'Riain *et al.* (1996) and O'Riain (1996) have demonstrated that potential disperser naked mole-rats, *Heterocephalus glaber*, are significantly heavier and have a higher percentage of body fat than non-dispersers of the same age. Consequently, I predict that dispersing common mole-rats should be in better body condition than their non-dispersing colony mates, and that this will be expressed as a greater body mass.

At the outset it is important to recognise that the process of dispersal in the cryptomids, and mole-rats as a whole, is poorly understood, as the subterranean life-style of mole-rats makes dispersal difficult to observe and document. Dispersal occurs when an individual or subgroup leaves the natal burrow system in response to the appropriate social and ecological cues. Evidence exist to support both below-ground and above-ground dispersal.

Definition of terms

Any discussion of dispersal is fraught with problems of terminology (Greenwood 1980), resulting in an inconsistent and often equivocal use of terms. To avoid this confusion the terms used in this chapter are defined below. The most widely used definition of dispersal, and the definition used in this chapter, is that of Howard (1960): "the permanent movement an individual makes from its birth site to the place where it reproduces or would have reproduced had it survived and found a mate". Greenwood (1980) observed that this applies

exclusively to young permanently vacating their birth site and moving to their first breeding or potential breeding site, and thus is more suitably termed *natal dispersal*. Natal dispersal is distinct from *breeding dispersal*, or the movement of an individual from one territory to another, between breeding attempts, irrespective of whether reproduction was successful (Greenwood 1980; 1984; Greenwood & Harvey 1982; Johnson & Gaines 1990). No minimum distance requirement for dispersal is specified in these definitions, either in actual distance of home range diameters, as Johnson and Gaines (1990) observe that such *a priori* limitations are arbitrary.

MATERIALS AND METHODS

Methods used to capture and process animals, and the capture periods are detailed in the previous demography chapter (Chapter 7). Data from all field-trips were combined and used to assess the comparative colony dynamics of the two study populations.

Dispersing animals were identified in two ways: (1) animals which were previously marked and released within one colony and subsequently recaptured within another colony. These were referred to as known dispersers, and their pre-dispersal details (*i.e.* mass and reproductive status) were known; (2) large adult and previously unmarked animals newly captured within a colony. Their pre-dispersal details were unknown. It was not possible to capture all dispersers as many would have left the study area, and consequently this represents a subset of the total pool of dispersers within the population.

Data analysis

Using the methods of Braude (1991), the overall loss and addition of individuals from and to colonies was assessed by measuring colony attrition and recruitment rates respectively;

$$\text{attrition} = \frac{\text{no. of individuals lost from colony between successive capture periods A and (A + 1)}}{\text{colony size at capture period A}}$$

$$\text{recruitment} = \frac{\text{no. of individuals gained by colony between successive capture periods A and (A + 1)}}{\text{colony size at capture period A}}$$

attrition rates are expressed as the number of animals lost per original group member per year, and the recruitment rates as the number of new individuals per original group member per year.

As noted by Gaines and McClenaghan (1980) disappearance of individuals from a population may be due to mortality *in situ* or dispersal, and it is usually impossible to distinguish between these sources of loss without direct observation. Consequently the attrition presented here is a composite estimate of loss from the colony due to both death and emigration. Similarly recruitment represents a complex estimate of addition to the colony via both natality and immigration. Attrition and recruitment rates were only determined for complete (fully trapped-out) colonies. Where a colony was captured several times, each recruitment and attrition rate between successive capture periods was treated as a separate data point. Attrition and recruitment rates for all colonies and all capture periods were averaged to give a mean colony attrition and recruitment rate for each study locality. Any deviations from parity (1:1) in the sex ratio of disappeared mole-rats were tested using the chi-square goodness-of-fit test (Zar 1984).

Inter-habitat differences in colony attrition and recruitment rates, as well as intra-habitat differences in recruitment rate between the breeding and non-breeding periods were tested using the Mann-Whitney U-test (Zar 1984). Correlations between colony attrition rate and colony size for both study sites were investigated using the Spearman rank correlation (Zar 1984). Furthermore, inter-site differences in the regression parameters for attrition rate versus colony size were examined by Analysis of Co-variance (ANCOVA). The F-max test was used to test for homogeneity of variance between the sample groups and revealed that

the variances were equivalent for the two study populations (F-max test, $F\text{-}max_{(2;\,73)} = 1.63$, $p > 0.05$) .

Intra-site differences in mean body mass between males and females, prior to and after dispersal, were tested using the Mann-Whitney U-test (Zar 1984). For assessing inter-sex differences in pre-dispersal mass, only known dispersers were used, whilst for assessing inter-sex differences in post-dispersal mass all dispersers were used. Intra-habitat differences in mean body mass between known dispersers at last capture prior to dispersal and their non-dispersing colony mates[3] were assessed using the Mann-Whitney U-test (Zar 1984). Disperser body mass on last capture prior to dispersal was used for the known disperser mass. The body mass of all non-dispersing colony mates (excluding the reproductive animals) on the last capture of the colony prior to the known disperser emigrating, was used for non-dispersing animal mass. To determine whether disperser sex ratio deviated significantly from parity, the chi-square goodness-of-fit test was used (Zar 1984).

Information on juvenile and adult sex ratios are included as they are of relevance in interpreting the observed patterns of movement. As for the analyses of demographic data in Chapter 7, the analyses of sex ratio data in this investigation was complicated by the same animals being captured in several capture periods, and the concomitant problem of pseudoreplication (*sensu* Hurlbert 1984). This problem was addressed by analysing data in two ways: (1) at first capture only; and (2) for all captures combined (in this latter case tests may not be statistically valid but are used as an indication of the degree of differences between the study populations). The conclusions drawn were not significantly influenced by whether only first capture data or all capture data combined, were used. To test whether juvenile and adult sex ratios deviated significantly from parity, the chi-square goodness-of-fit test was used (Zar 1984). Using the criteria outlined in Chapter 7 juveniles were considered as the previous season's young, and were identified as unmarked animals, usually first

[3] Only adult (see Chapter 6) animals were used

caught during the non-breeding period, weighing less than 40 g. By contrast adults were all ≥ 40 g in mass. Juvenile sex ratio represents a best-guess estimate of the sex ratio at birth. Any intra-site differences in sex ratio between capture periods, as well as differences between disperser and adult sex ratios were examined using the chi-square goodness-of-fit test (Zar 1984).

RESULTS

Colony attrition and recruitment

Colony attrition rates were significantly higher at Sir Lowry's Pass than at Steinkopf (Sir Lowry's Pass [SLP]: 0.64 ± 0.07 animals lost per original group member per year [n=75], Steinkopf [ST]: 0.24 ± 0.06 [63]; Mann Whitney U-test, $U = -4.50$, $p < 0.00001$).

At both sites the rate of attrition was significantly correlated with the original colony size (Figures 8.1 & 8.2), although the wide scatter of points at Sir Lowry's Pass suggests a tenuous relationship at this site. The regression equations revealed a positive relationship between attrition and group size (Figures 8.1 & 8.2), although the slopes of the regression lines were very shallow. Whilst the regression coefficients for Steinkopf and Sir Lowry's Pass were comparable (ANCOVA, $F_{(1;\ 134)} = 3.00$, $p > 0.05$), the regression elevation at the mesic site was significantly higher than at the arid site (ANCOVA, $F_{(1;\ 135)} = 24.24$, $p < 0.001$).

At Sir Lowry's Pass the sex ratio for departed (dispersed or dead) common mole-rats deviated significantly from parity and was markedly skewed towards males [Sex ratio (m/f) = 1.7 (104); chi-square goodness-of-fit test, $\chi^2_{(1)} = 6.5$, $p = 0.01$]. Although the sex ratio of departed animals at Steinkopf was also skewed towards males, it did not deviate significantly from parity [Sex ratio (m/f) = 1.5 (45); chi-square goodness-of-fit test, $\chi^2_{(1)} = 1.8$, $p = 0.2$].

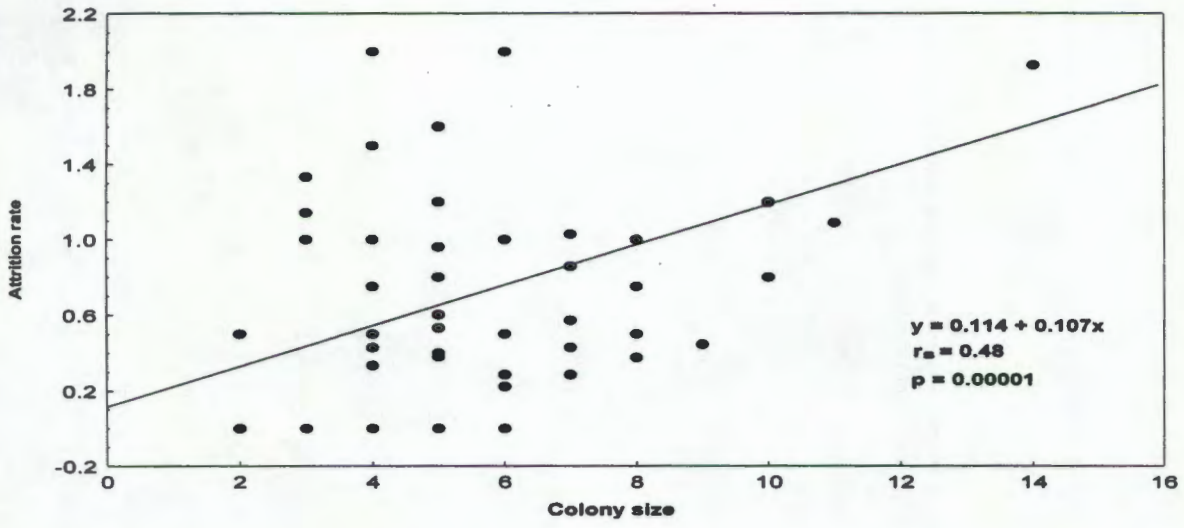


Figure 8.1: The relationship between attrition rates (no. of animals lost per original group member per year) and colony size for *C. h. hottentotus* colonies caught at Sir Lowry's Pass. The Spearman rank correlation (r_s) was used to assess the relationship statistically. Regression line equation, r_s value and significance level given on figure.

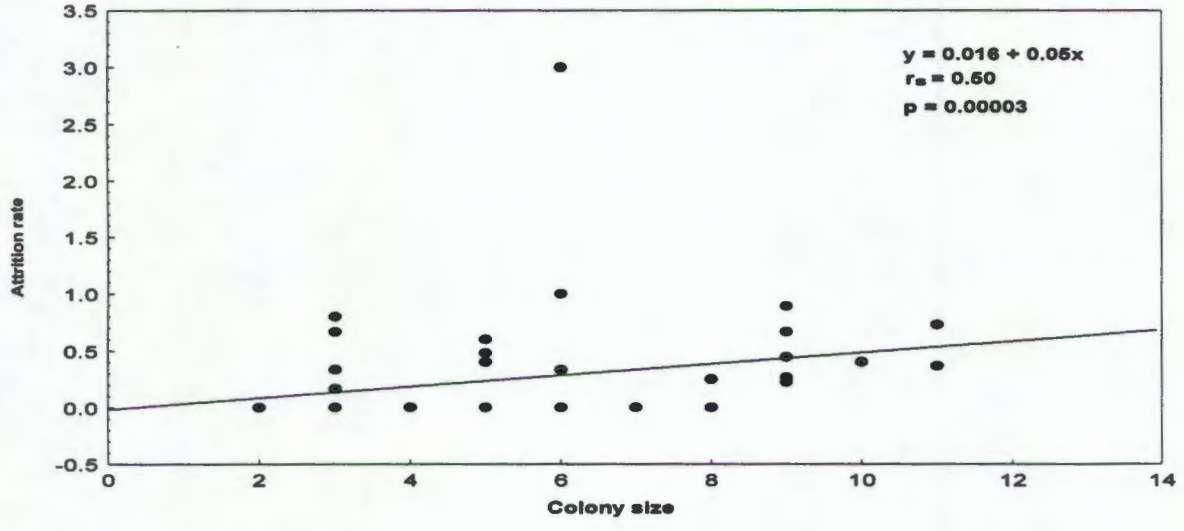


Figure 8.2: The relationship between attrition rates (no. of animals lost per original group member per year) and colony size for *C. h. hottentotus* colonies caught at Steinkopf. The Spearman rank correlation (r_s) was used to assess the relationship statistically. Regression line equation, r_s value and significance level given on figure.

The mean rate of colony recruitment was significantly greater at Sir Lowry's Pass than at Steinkopf (SLP: 1.27 ± 0.22 new animals per original group member per year [n=75], ST: 0.89 ± 0.20 [63]; Mann-Whitney U-test, U = -2.16, p = 0.03). At Sir Lowry's Pass recruitment rates were similar during and outside the breeding period (Breeding period [BP]: 1.42 ± 0.29 [54], Non breeding period [NBP]: 0.89 ± 0.24 [21]; Mann-Whitney U-test,

Mesic

a) Colony F

ID	Sex	1	2	3	4	5	6	7
4701	m	R	—	—	—	—	—	?
3009	f	R	—	R	—	?		
4402	f		—	R	—	?		
4404	m			—	—	—	—	R' →
4420	m		d+	—	—	—	—	R' →
4440	f				d+/R	—	?	
4410	f						d+/R	→
4470	m							→

b) Colony HIV

ID	Sex	1	2	3	4	5	6	7	8
7003	m		R	—	?				
1277	f		R	—	—	—	—	?	
1300	m			—	—	—	—	?	
1301	f			—	—	—	—	R —	?
1101	m			d+	—	?			
1320	m			d+/R	—	—	—	?	
1302	f					—	—	R	→
1304	f					—	—	?	
1307	m						d+/R	—	→
1310	m								→
1340	f								→

c) Colony KSV

ID	Sex	1	2	3	4	5	6	7	8
3090	f	R	—	—	?				
3001	m	R	—	—	—	—	—	?	
3027	m		—	—	—	—	?		
3041	m		—	—	?				
3042	m		—	—	—	—	—	R	→
3044	m		—	—	—	?			
3047	m		—	?					
3077	f		—	—	—	?			
3018	f			—	?				
3019	m			—	—	—	—	—	?
3023	m			—	—	?			
3026	m				d+	—	—	—	→
3028	m				—	—	—	—	→
3037	m				—	?			
7207	m				d+	—	d-		
3701	f						d+/R	—	→
3207	m							d+	— ?
3200	m								→
3201	m								→
3202	m							d+	— ?
3420	m							d+	— ?
3204	f							—	?
****	f								→
****	m								→
****	m								d+ →
****	f								→
****	m								→
****	f								→
****	f								→
****	m								→

Figure 8.3 Changes in colony composition for three colonies collected at Sir Lowry's Pass: a) F; b) HIV and c) KSV. Key: 1-8 = capture periods (1 = '92 breeding period, 2 = intermediate between end '92 breeding period and start '93 non-breeding period[4], 3 = '93 non-breeding period, 4 = '93 breeding period, 5 = '94 non-breeding period, 6 = '94 breeding period, 7 = '95 non-breeding period, 8 = '95 breeding period); m = male; f = female; R = reproductive animal; R' = possible reproductive animal; X = known death; d- = dispersed out of colony; d+ = dispersed into colony; ? = fate unknown; → = still alive and resident in colony at end of study.

[4] Additional field-trip undertaken to Sir Lowry's Pass at onset of study to increase the number of marked individuals within the study population

Arid

a) Colony 800's

ID	Sex	1	2	3	4	5	6	7	8
844	m	R	—	—	—	—	—	?	
874	f	R	—	—	—	—	?		
877	f	—	—	—	?				
4099	m	—	—	—	—	?			
4074	f	—	?						
801	m		—	—	—	—	—	?	
802	m		—	—	—	—	—	—	→
804	f		—	—	—	—	—	—	→
4001	f		—	—	—	—	—	—	→
4277	f			—	—	—	?		
811	f				—	—	—	—	→
807	f					—	—	—	→
810	f					—	—	—	→
820	m					—	—	—	→

b) Colony 1000's

ID	Sex	1	2	3	4	5	6	7	8
1007	f	R	—	—	—	—	—	—	→
1001	m		R	—	—	—	—	—	→
1004	m		—	—	—	—	—	—	→
1010	f		—	—	—	—	?		
1002	m		—	—	—	—	?		
1020	f		—	?					
1040	f		—	—	—	—	—	—	→
1070	m		—	—	—	—	?		
1003	m		—	—	—	—	—	—	→
1005	m					—	—	—	→
1006	m					—	—	—	?
1008	m					—	?		
1101	m						d+	—	?
1011	m							—	→
1012	m							—	→

c) Colony 2000's

ID	Sex	1	2	3	4	5	6
2074	f	R	—	—	—	—	→
2077	m	R	—	—	—	—	→
2001	f		—	—	—	—	?
2002	m		—	—	—	—	→
2004	m		—	—	—	—	?
3007	f		—	—	—	—	→
2007	f					—	→
2010	f					—	→
2020	m					—	→

Figure 8.4 Changes in colony composition for three colonies collected at Steinkopf: a) 800's; b) 1000's; and c) 2000's. Key: 1-8 = capture periods (1 = '93 breeding period, 2 = start '94 non-breeding period[5], 3 = mid-'94 non-breeding period, 4 = '94 breeding period, 5 = '95 non-breeding period, 6 = '95 breeding period, 7 = '96 non-breeding period, 8 = '96 breeding period); m = male; f = female; R = reproductive animal; X = known death; d- = dispersed out of colony; d+ = dispersed into colony; ? = fate unknown; → = still alive and resident in colony at end of study.

[5] Additional field-trip undertaken to Steinkopf at onset of study to increase the number of marked individuals within the study population

U = -0.28, p = 0.8). In contrast, however, at Steinkopf recruitment rates were significantly higher during the breeding period than during the non-breeding period (BP: 1.25 ± 0.29 [39], NBP: 0.31 ± 0.21 [24]; Mann-Whitney U-test, U = -3.20, p = 0.001).

Colony histories

Temporal changes in colony composition and form for six selected colonies from Sir Lowry's Pass and Steinkopf (three colonies from each site) are summarised graphically to aid the understanding of colony dynamics (Figures 8.3 & 8.4). These provide a qualitative insight into colony dynamics and several important points are immediately apparent from these figures:

(1) The basic colony unit, consisting of a reproductive pair and non-breeding colony members (usually related offspring), was similar for the two study populations.

(2) As suggested by the higher attrition rates, the period of residence of colony members within their natal colony was markedly lower at Sir Lowry's Pass than at Steinkopf.

(3) At both study sites the fate of departed individuals was usually difficult to ascertain.

(4) Recruitment to the colony via the immigration of foreign animals seems to occur far more frequently at Sir Lowry's Pass than at Steinkopf, and this is corroborated by the higher recruitment rates. In addition, multiple dispersal (*i.e.* successive dispersal events by the same individual) was recorded at Sir Lowry's Pass (*e.g.* animal # 7207, Figure 8.3c) but not at Steinkopf.

(5) The longevity of reproductive tenure within colonies at Steinkopf appeared to be substantially longer than that at Sir Lowry's Pass. Reproductive animals disappeared fairly frequently at this mesic site. Furthermore, reproductive replacement following the disappearance of the reproductive animals, occurred readily at Sir Lowry's Pass. By comparison, reproductive replacement may occur less readily at Steinkopf, as

evident for colony 800's (Figure 8.4a), although the available data is too superficial to be unequivocal.

(6) At Sir Lowry's Pass, following the loss of reproductive individuals, the colony did not fragment, but remained intact and replacement reproductives assumed the dominant positions. This is particularly apparent for Colony KSV (Figure 8.3c). During capture periods four and five this colony was without any female members, including a reproductive female, but remained intact until capture period six when a foreign immigrant, # 3701, became the new reproductive female. Comparative data were not available for Steinkopf due to the infrequent loss of reproductive animals throughout the period of study.

(7) As evident in Figure 8.3, replacement reproductives at Sir Lowry's Pass never came from within the natal colony, but in all cases were foreign immigrants. This provides further support for the contention that *C. h. hottentotus* is an obligate outbreeder.

(8) On several occasions the occurrence of multiple reproductive females within a colony was observed at Sir Lowry's Pass (*e.g.* reproductive females # 3009 & # 4402, Figure 8.3a), but not at Steinkopf. In the case of colony F (Figure 8.3a), # 3009 was the original reproductive female when the colony was first caught during capture period one. At capture period two, two females, # 3009 and # 4402, were pregnant on capture. By capture period three, # 3009 had disappeared and # 4402 was the sole reproductive female. By capture period four, # 4402 had also disappeared and a foreign immigrant, # 4440, was the new reproductive female. During all these capture periods, it appears that # 4701 remained the sole reproductive male.

Dispersing animals

All of the known dispersing mole-rats (Total n = 75, SLP n = 52, ST n = 23) were adult animals, weighing ≥ 40 g (see Chapter 7), on their last capture prior to dispersal. For both study populations, on the last capture prior to dispersal, known dispersing mole-rats were not significantly heavier than their non-dispersing colony mates (SLP: *known dispersers:* 67.7 ± 4.7 g [24], *non-dispersers:* 68.2 ± 3.3 g [52]; Mann-Whitney U-test, $U = 0.11$, $p = 0.9$; ST: *known dispersers:* 55.0 ± 3.2 g [12], *non-dispersers:* 48.5 ± 2.9 g [26]; Mann-Whitney U-test, $U = -1.29$, $p = 0.2$). At Sir Lowry's Pass, known dispersing males were significantly larger than known dispersing females on their last capture prior to dispersal (females 47.6 ± 4.4 g [8], males 83.5 ± 4.9 g [21]; Mann-Whitney U-test, $U = 3.5$, $p = 0.0004$). In contrast, known male and female dispersers at Steinkopf were of comparable mass (females: 50.4 ± 5.2 g [5], males: 62.2 ± 4.2 g [9]; Mann-Whitney U-test, $U = 1.27$, $p = 0.2$). At both study localities, on the first capture after dispersal, dispersing males were on average significantly larger than dispersing females (SLP - females: 71.3 ± 5.5 g [11], males: 94.5 ± 2.8 g [41]; Mann-Whitney U-test, $U = 3.36$, $p = 0.0008$; ST - females: 55.7 ± 2.4 g [13], males: 77.2 ± 3.1 g [10]; Mann-Whitney U-test, $U = 3.95$, $p = 0.00008$).

At Sir Lowry's Pass all known dispersing females shortly became reproductives within their new colony, whereas only 56% of known dispersing males appeared to immediately became breeders in their new colony. For known dispersers at Steinkopf, 77% of females and 60% of males appeared to assume the reproductive roles within their new colony.

The sex ratio of dispersers at Sir Lowry's Pass deviated significantly from parity, and was strongly biased towards males [Sex ratio (m/f) = 3.7; chi-square goodness-of-fit test, $\chi^2_{(1)} = 17.31$, $p = 0.0003$]. By contrast the sex ratio of dispersers at Steinkopf was close to parity [Sex ratio (m/f) = 0.8; chi-square goodness-of-fit test, $\chi^2_{(1)} = 0.39$, $p = 0.5$]. If data from first captures only are used, the sex ratio of dispersers deviates significantly from the adult sex ratio (chi-square goodness-of-fit test, $\chi^2_{(1)} = 5.31$, $p = 0.02$). However, if all

captured data combined are used, the sex ratio of dispersers does not deviate significantly from the adult sex ratio (chi-square goodness-of-fit test, $\chi^2_{(1)} = 2.26$, $p = 0.13$).

Juvenile and adult sex ratios

For both study populations the sex ratio of juveniles did not deviate significantly from parity (Table 8.1). Furthermore, adult sex ratios at Steinkopf did not differ significantly from parity, irrespective of whether all capture or only first captures were used (Table 8.1). In contrast, at Sir Lowry's Pass, adult sex ratios were significantly skewed towards males, irrespective of whether all capture data combined, or only first capture data were used (Table 8.1).

Longitudinal (temporal) changes in adult sex ratio are summarised graphically in Figure 8.5. Adult sex ratios did not differ between capture periods at the mesic site and were highly skewed towards males (Figure 8.5; chi-squared goodness of fit test, $\chi^2_{(13)} = 1.50$, $p = 0.99$). Similarly, at the arid site, adult sex ratios were comparable for all capture periods, but in contrast to Sir Lowry's Pass were close to parity (Figure 8.5; chi-squared goodness of fit test, $\chi^2_{(13)} = 1.80$, $p = 0.99$). For all the comparable capture periods, adult sex ratios were markedly higher at Sir Lowry's Pass than Steinkopf, indicating the heavy skew towards males at the former study site.

Table 8.1: Number of adult male and female *C. h. hottentotus* captured at Sir Lowry's Pass and Steinkopf over the eight capture periods at each site. The chi-square goodness-of-fit test was used to determine whether adult sex ratios deviated significantly from parity

	Sir Lowry's Pass				Steinkopf			
Age class	males	females	χ^2	p	males	females	χ^2	p
Juveniles	24	33	1.42	0.2	24	26	0.32	0.6
Adults								
First capture‡	301	174	33.96	<0.00001	194	174	1.09	0.3
All captures†	510	228	107.76	<0.00001	323	281	2.92	0.1

‡ only using data from animals at first capture; † using data for all captures combined.

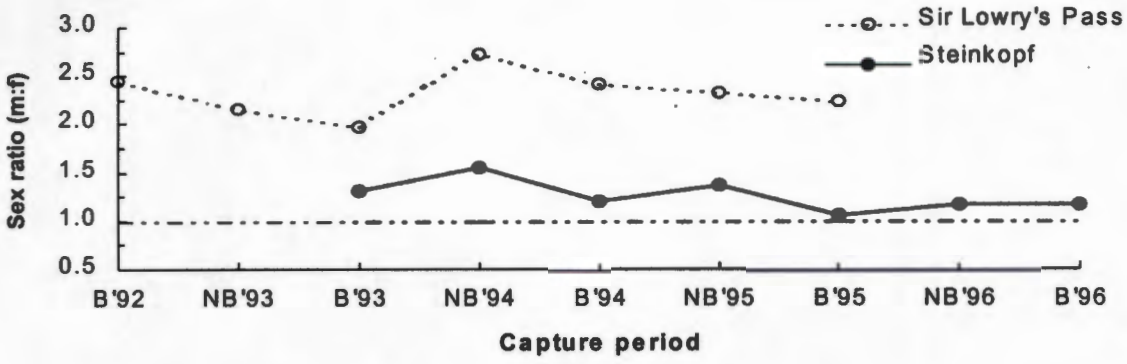


Figure 8.5: Temporal variation in adult sex ratio for *C. h. hottentotus* caught at Sir Lowry's Pass and Steinkopf. The horizontal dotted/dashed line at a sex ratio of one indicates parity. For the capture periods each label gives the year and whether the data are for the breeding period (B) or non-breeding period (NB).

DISCUSSION

In studying dispersal in small mammal populations there is a fundamental problem in distinguishing individuals that are dispersing or have dispersed from animals making routine exploratory movements or animals that have suffered mortality (Gaines & McClenaghan 1980). The dilemma of detecting dispersing individuals is most acute for small, nocturnal or crepuscular species that occupy habitats precluding direct observation, such as mole-rats (Gaines & McClenaghan 1980). For these species dispersal must be studied using indirect techniques *e.g.* live-trapping programs. Consequently this severely curtails the rigour of data which can be collected, and therefore the level of insight into crucial biological processes which may be surmised.

Dispersal carries with it significant risks, most importantly an increased risk of mortality (Gaines & McClenaghan 1980; Horne 1984; Getz *et al.* 1994; Alberts & Altmann 1995). Gaines and McClenaghan (1980) observe that the probability of a given individual dispersing successfully is highly unpredictable, depending on both individual attributes as well as range of environmental factors. Nevertheless, dispersal may have crucial ramifications for the lifetime reproductive success (LRS) of group-members in singularly

cooperatively breeding mammals. In these species, philopatric non-reproductive subordinate group members benefit from increases in the indirect component of their inclusive fitness (as reviewed in Koenig *et al.* 1992). However, realisation of the direct components of their inclusive fitness and the concomitant maximisation of LRS are dependent upon successful dispersal from the natal group (Doolan & MacDonald 1996). Consequently, given (1) incest avoidance and (2) that the social unit consists of a familial group, there will be potent selection for timely dispersal of subordinate colony members in the social cryptomids. Therefore, the aim of the hypotheses generated in the introduction to this chapter was to investigate dispersal in the common mole-rat in more detail.

The results from this investigation provide support for hypothesis 1 (introduction to this chapter), that dispersal appears to occur more readily at Sir Lowry's Pass than at Steinkopf. Colony attrition rates at the mesic site were more than twice those at the arid site, indicating that far more animals were disappearing from colonies at Sir Lowry's Pass. As mentioned previously, Gaines and McClenaghan (1980) note that the disappearance of individuals from a population may be due to either mortality or emigration, and that the two are often indistinguishable. However, it seems unlikely that the elevated attrition at Sir Lowry's Pass is due to increased predation pressure: (1) Nevo (1982) and Jarvis and Bennett (1990) observe that the subterranean environment is buffered against massive predation pressure[6], and (2) Jarvis *et al.* (1994) note that there is no evidence of qualitative regional differences in the types or abundance of predators. Consequently, these differences are probably related to inter-site divergence in the rate of emigration.

The overall recruitment to colonies at Sir Lowry's Pass was significantly greater than at Steinkopf. In Chapter 7 it was shown that litter sizes and litter frequencies (*i.e.* natality) were similar for the two sites. This suggests that the difference in recruitment must be due to the immigration of adult individuals into the colony, thereby corroborating the results for

[6] Although the subterranean niche is buffered against massive predation, dispersing mole-rats will be more prone to predation than non-dispersers conspecifics, as a consequence of their increased conspicuousness whilst burrowing.

attrition and indicating greater rates of dispersal at the mesic site. This contention is supported by the seasonal patterns of recruitment observed in the two populations. At Sir Lowry's Pass recruitment rates were similar during both the breeding and non-breeding periods, whilst at Steinkopf the recruitment rates were significantly higher during the breeding period. As alluded to previously, recruitment is a consequence of natality (and subsequent philopatry) and immigration. Recruitment during the breeding period is mostly a product of natality, whilst recruitment during the non-breeding period is the result of immigration only. As outlined in Chapter 6, the non-breeding season at both sites coincides with the period of maximal rainfall, and thus optimal dispersal opportunities (see also Chapters 1 & 2). The fact that dispersal during the non-breeding period at Sir Lowry's Pass is equivalent to that during the breeding period suggests that a substantial amount of immigration occurs during this season. By contrast, the significant drop-off in recruitment during the non-breeding period at Steinkopf, suggests a fairly modest rate of immigration, and that most dispersing animals form new colonies rather than join existing colonies (*cf.* the large number of pairs at Steinkopf). As the non-breeding season coincides with the optimal dispersal period at both sites, these findings indicate that immigration, and hence natal dispersal occur with greater frequency at Sir Lowry's Pass.

Qualitative support for regional differences in dispersal is also provided by the colony tenure patterns (Figures 8.3 & 8.4), with tenure periods (*i.e.* residence within colony) of colony members being markedly lower at Sir Lowry's Pass than at Steinkopf. This supports the higher attrition rates at the mesic site and suggests that there is a more regular turnover of group membership in colonies from Sir Lowry's Pass. Additions to the colony via the immigration of foreign animals appeared to occur with considerably greater regularity at Sir Lowry's Pass than at Steinkopf. This further supports the high overall and non-breeding season recruitment rates, and the postulated greater rates of dispersal at the mesic site. These findings suggest that colonies from Steinkopf exhibit greater temporal stability, with

more predictable group membership over time. Moreover, this stability would appear to be indicative of lower rates of dispersal in the arid locality.

The findings of greater dispersal rates at the mesic site are congruent with AFDH predictions (see hypothesis 1 in the introduction to this chapter), and probably reflect adaptive variation in social behaviour between the study populations. The ecological constraints on successful foraging at Steinkopf (outlined in Chapters 2 to 5) will curb opportunities for dispersal and promote cooperation in the common mole-rats occurring there. Colony members should subsequently maximise their inclusive fitness by natal philopatry and forage cooperatively until dispersal opportunities (see Chapter 1 & 2) arise. By contrast, the relaxation of ecological constraints at Sir Lowry's Pass (Chapters 2 to 5) provides regular opportunities for dispersal and independent reproduction. Whilst mole-rats occurring in this mesic site may exhibit philopatry due to the increased population density and accompanying reduction in available "breeding sites" (see Chapter 7), individuals may be able to maximise their inclusive fitness and LRS by dispersing earlier than conspecifics in arid areas. These fitness predictions agree with the observed regional divergence in patterns of dispersal and philopatry.

In their delayed dispersal threshold model Koenig *et al.* (1992) suggest four factors that may influence the decision to disperse: (1) risks associated with dispersal; (2) probability of successful establishment in a suitable territory; (3) the probability of securing a mate; and (4) the probability of successful independent reproduction (see also Emlen 1982a). For common mole-rats these factors must all play a crucial role in dispersal decisions. However, for mesic occurring *C. h. hottentotus* populations the probabilities of securing a territory, finding a mate and successful independent reproduction might be more important than the risks of dispersal *per se*. This follows from the relaxation of ecological constraints (Chapters 2 to 5) and the high population densities (Chapter 7) prevalent in mesic areas.

All documented dispersal events at Steinkopf were in the form of natal dispersal. Given the dispersal costs faced by mole-rats in arid areas there can be little selective

advantage to breeding dispersal, except perhaps in the event of mate mortality. By contrast, both natal and breeding dispersal were documented at Sir Lowry's Pass, and probably reflect a relaxation of ecological restrictions. Besides differences in the constraints on immigration/emigration, such regional divergence in the types of dispersal may also reflect inter-site differences in the patterns of colony dynamics. At Steinkopf nascent colonies typically formed from pairs, and consequently, when recaptured, emigrants had usually paired with a foreign conspecific. By comparison, although nascent colonies formed from pairs occurred at Sir Lowry's Pass, foreign individuals were frequently observed moving into already established colonies. If the foreign immigrant did not assume the reproductive position within the colony (*i.e.* reproductive replacement), they sometimes then underwent breeding dispersal. An interesting corollary follows from this observation. In Chapter 9 I suggest that in mesic areas, dominant animals may provide "staying incentives" (*sensu* Keller & Reeve 1994) to subordinate colony members to encourage natal philopatry. The movement of sexually mature foreign animals into established colonies may reflect this proposition, as it provides resident animals with an opportunity to mate with foreign conspecifics (*cf.* Chapter 9). This contention is further supported by the presence of multiple reproductive females in colony F at Sir Lowry's Pass (Figure 8.3a). By comparison immigration into established colonies at Steinkopf occurred very rarely, and multiple reproductive females were never encountered.

As outlined in the introduction to this chapter, two of the most important costs of group-living are increased competition for food and increased conspicuousness to predators (Krebs & Davies 1993). Consequently I postulated (hypothesis 2 in the introduction to this chapter) that there may be distinct fitness costs associated with group-living in the bathyergids, and hence there may be some group size above which individual inclusive fitness is no longer being maximised and it pays individuals to risk dispersal. The findings from this investigation support this hypothesis; at both Steinkopf and Sir Lowry's Pass attrition was positively correlated with colony size. These results suggest that as group sizes

increases the rate at which individuals disappear from the colony, either via emigration or mortality, increases accordingly. In addition, the regression elevation at Sir Lowry's Pass was significantly greater than at Steinkopf. This finding indicates that, although colony attrition rates at both sites increase with increasing colony size, for equivalent group sizes far greater losses occur at the mesic site than at the arid site. These differences may reflect regional divergence in the costs of dispersal. As previously suggested, greater attrition at Sir Lowry's Pass relative to Steinkopf is more likely to reflect inter-site divergence in emigration rates rather than in mortality within the colony. Given the heightened dispersal constraints in arid areas relative to mesic areas, the risks associated with dispersal at Steinkopf are substantially greater than those at Sir Lowry's Pass. Consequently, faced with these constraints *C. h. hottentotus* at Steinkopf may be compelled to remain in large colonies, delaying dispersal and tolerating reduced fitness gains and potential fitness costs. By comparison animals at Sir Lowry's Pass will be able to disperse earlier without incurring as high fitness costs. The greater regression elevation for the mesic site relative to the arid site may reflect these regional differences.

Due to the occurrence of monogamy in the common mole-rat, it was predicted that there would be no sex-biased dispersal at either study locality. The results from this investigation provide mixed support for this prediction. At Steinkopf the sex-ratio of dispersed animals did not deviate significantly from parity, supporting the prediction and indicating an absence of sex-biased dispersal. By contrast the sex ratio of dispersed individuals at Sir Lowry's Pass deviated markedly from parity, and was heavily skewed towards males. However, this result does not necessarily reflect male-biased dispersal in the mesic population. As evident from the sex ratio results, the adult sex ratio at Sir Lowry's Pass was heavily skewed towards males. Given that all dispersing individuals captured at Sir Lowry's Pass were adults, the skewed sex ratio of dispersers may simply reflect that males and females dispersed in proportion to their relative abundance within the population,

hence the pattern of male-biased dispersal. This obviously raises the question; why is the adult sex ratio at Sir Lowry's Pass so radically skewed towards males?

Sex allocation theory maintains that parents may increase their fitness by varying the sex ratio of their progeny in response to differences in the costs and benefits of producing sons and daughters (Clutton-Brock & Iason 1986; Packer & Pusey 1987; Dickman 1988; Frank 1990; Krackow 1995; Wright *et al.* 1995). Consequently, it may be hypothesised that the skew in adult sex ratios at Sir Lowry's Pass is purely the product of adaptive variation in offspring or juvenile sex ratios. However, an equivalent number of male and female offspring were produced at the mesic site, negating maternal manipulation of offspring sex ratios. Alternatively, the skew towards males at Sir Lowry's Pass may reflect heightened rates of dispersal or mortality for females relative to males. Dispersal related events are unlikely to be important given that: (1) female emigration should be balanced by immigration; and (2) dispersal is male-biased. Consequently, this leaves differential mortality as the only viable explanation for male-biased adult sex ratio. However, unless there are as yet unknown behavioural differences between males and females, it is improbable that gender differences in mortality will account for the dramatic bias in adult sex ratio at Sir Lowry's Pass. As yet the explanation for the male-biased sex ratio at the mesic site remains an enigma.

Body mass, body size and body condition have been implicated in the temporal patterns of natal dispersal in various mammals (Holekamp 1984; 1986; Nunes & Holekamp 1996). O'Riain *et al.* (1996) and O'Riain (1996) demonstrated that dispersing naked mole-rats are morphologically distinct from other same-aged colony members, dispersers being laden with additional deposits of body fat. They suggest that these fat reserves may serve as nutritional surety against the risks of starvation during dispersal and colony foundation, in a manner similar to the fatty tissues of the winged alates of termites. Consequently, it was hypothesised that at both study sites, dispersing common mole-rats would be larger than equivalently aged, non-dispersing counterparts. Although few studies have directly

may reflect the sampling protocol employed in this investigation. The wide spacing of capture sessions at both study sites may have resulted in a substantial temporal delay between the last capture of known dispersers and their actual dispersal event. Consequently, the capture of known dispersers prior to dispersing may have occurred too long before they dispersed to reflect differences in body mass between them and their non-dispersing colony mates.

In conclusion the results from this chapter reveal distinct differences in the nature of dispersal between Steinkopf and Sir Lowry's Pass. Most notably, dispersal occurred less frequently at Steinkopf and colonies demonstrated greater temporal stability, with more predictable group membership over time. The regional differences in dispersal patterns revealed in this investigation may reflect adaptive variation in social behaviour between the study populations, and the results suggest that delayed dispersal and cooperation may be more crucial to individual survival in arid than in mesic areas. As such these findings provide support for the underlying contention of the AFDH that ecological constraints on foraging in arid areas have promoted a greater degree of social elaboration.

Chapter 9

Inter-colonial encounters and xenophobia: the effects of aridity, sex and reproductive status.

ABSTRACT

The ecological constraints prevalent in arid environments have promoted the evolution of social groups with a high reproductive skew in the mole-rat species occurring there. Outbred social bathyergids face conflict between maintaining colony integrity to enhance personal foraging success and hence survival, and dispersal to maximise individual lifetime reproductive success (LRS). This conflict will be a crucial determinant of the response of colony members to the presence of foreign conspecifics. Here I investigate how ecological constraints, sex and reproductive status influence the outcome of meetings between foreign common mole-rats, in a series of dyadic encounters. Individuals from Steinkopf and Sir Lowry's Pass, were used to assess the effects of aridity. The effects of sex and reproductive status were investigated by trials between individuals of differing sex and status. The arid population revealed substantially higher levels of rejection than the mesic population. Sex and status played a significant role in moderating individual response. For both populations, encounters between different-sexed individuals produced lower levels of rejection than those between same-sexed individuals. For the mesic site, rejection was greatest for encounters between reproductive animals. Conversely, for the arid site, the levels of rejection were comparatively high, and comparable for all combinations of reproductive status. Ecological constraints, sex and reproductive status are significant factors in interactions between foreign common mole-rats, ultimately influencing individual survival, colony integrity and the differential LRS of all colony members. The results provide insight into the evolution and maintenance of family groups within the bathyergids.

INTRODUCTION

Social elaboration, to the degree evident in the African mole-rats (Bathyergidae), is unparalleled amongst subterranean mammals. Most subterranean mammals are solitary, and strongly xenophobic to conspecifics (Nevo 1979; 1982; Jarvis & Bennett 1990; Lacey & Sherman 1997). Bathyergid sociality is thought to have evolved via natal philopatry, as an adaptation to high foraging and dispersal risks in arid environments (Jarvis 1985; Lovegrove & Wissel 1988; Lovegrove 1991; Jarvis *et al.* 1994; Chapter 1). As detailed in

measured the relative proportion of fat in same aged dispersing versus non-dispersing vertebrates, it is frequently assumed that the heavier body masses of dispersers reflects the amount of energy stored as fat (O'Riain 1996). Consequently, in this study it was considered unnecessary to measure differences in fat content directly and that divergence in body mass would suffice. The findings from this investigation do not support the prediction, in both study sites dispersing individuals were of comparable mass to their non-dispersing colony mates[7]. The presence of morphological divergence between dispersing and non-dispersing naked mole-rats, and its absence in common mole-rats may reflect interspecific differences in life-history traits and mating strategies. In the facultatively inbred naked mole-rat, life-long natal philopatry is the norm, and dispersal apparently occurs infrequently (O'Riain *et al.* 1996). Consequently, given the disparate life history traits of dispersing individuals relative to philopatric individuals, morphological divergence between these phenotypes should be readily apparent in *H. glaber*. By contrast, in the outbred common mole-rat all subordinate colony members must disperse to maximise their LRS. Therefore all non-dispersers in *C. h. hottentotus* colonies are potential dispersers who have delayed dispersal longer than the dispersers. Moreover, given the ecological constraints on dispersal (Chapters 2 to 5), optimal dispersal conditions may (1) only occur sporadically and (2) exhibit large individual variation, making it necessary for subordinates to be perpetually primed for dispersal. Consequently dispersal readiness in all subordinates would nullify any morphological differences, and account for the similarity in mass between dispersers and "non-dispersers" revealed in this study. The contention that subordinate colony members are perpetually primed for dispersal may be supported by the fact that reproductive activity is maintained throughout the year in non-reproductive males and females (Chapter 6). Alternatively, the absence of differences in mass between dispersers and non-dispersers

[7] Age in wild caught mole-rats is difficult to establish accurately, but all animals used were adult animals. The lack of mass difference between dispersers and non-dispersers is unlikely to be an age effect: (1) dispersers and non-dispersers were taken from similar cohorts in the colony; and (2) age differences should create a discontinuity in body mass rather than the observed similarity.

Chapter 1, low and sporadic rainfall and the low density and highly dispersed nature of food resources in arid habitats will increase foraging costs, thereby constraining dispersal and promoting cooperative foraging (Lovegrove 1991; Jarvis *et al.* 1994). As a consequence of these constraints, the colony burrow system and the resources it contains represent critical assets for the continued survival of all colony members (Bennett 1988; Jarvis *et al.* 1994; O'Riain & Jarvis 1997). O'Riain and Jarvis (1997) suggest that, in naked mole-rats (*Heterocephalus glaber*), the importance of protecting these resources has selected for a highly efficient defence system and a reliable mechanism of colony member recognition, whereby all foreigners are vigorously excluded from the natal burrow system. This explains the intensive degree of xenophobia evident in this species (O'Riain & Jarvis 1997).

As outlined in Chapter 6, reproduction within mole-rat colonies is highly skewed. However, whereas naked mole-rats routinely inbreed (Faulkes *et al.* 1990b; Reeve *et al.* 1990; Honeycutt *et al.* 1991b; Jarvis 1991a; O'Riain *et al.* 1996), the remaining social bathyergids appear to be obligate outbreeders, and non-breeding colony members can only maximise their lifetime reproductive success (LRS) by leaving the natal colony and mating with foreigners (Jarvis *et al.* 1994; Burda 1995; Bennett *et al.* 1997; Rickard & Bennett 1997). Consequently, inter-colony encounters in these outbred mole-rats cannot merely be assessed in the context of resource defence, but must also be viewed in relation to the outbreeding opportunities that they may represent. Acceptance or rejection of foreigners during such encounters will have significant ramifications for the direct fitness of the interactants. Consequently, I predict a diminished xenophobic response in outbred social mole-rat colonies, relative to the inbred *H. glaber*, to facilitate pair-bond formation and outbreeding.

In this investigation I examined the outcome of meetings between foreign common mole-rats in a series of dyadic encounters. I predict that the reaction of individuals during encounters between foreign conspecifics will be influenced by ecological constraints and the sex and reproductive status of interactants, such that: (1) the fitness penalties for failing to

exclude foreigners should be substantially more severe in populations from arid, relative to mesic areas and I expect this will heighten xenophobia in the former; (2) opposite sexed interactants should be more willing to accept one another to facilitate outbreeding; and (3) animals of both reproductive and non-reproductive status should be equally likely to reject foreigners as these may represent a dilution of reproductive output and kin relatedness. Clearly, the effects of sex and status on the outcome of encounters between foreign conspecifics should be moderated by the overriding ecological constraints.

MATERIALS AND METHODS

Study animals

Animals from both Steinkopf and Sir Lowry's Pass were investigated in this study. The mole-rats were captured using modified Hickman live-traps (Hickman 1979a), and only animals from colonies which had been completely trapped-out were used (see Chapter 7). I used a total of 86 individuals from 26 colonies in this investigation: (1) 25 individuals from six colonies at Steinkopf; and (2) 61 individuals from 20 colonies at Sir Lowry's Pass. Although exact age could not be established without sacrificing the study animals, all the individuals used in this study were sexually mature adults, males weighing between 57 and 132 g and females between 43 and 87 g (Chapters 6, 7 & 8).

Complete colonies were transferred to the laboratory, and were housed in transparent acrylic plastic burrow systems, with wood shavings and paper towelling provided as nesting material (Jarvis 1991b). The mole-rats were fed, *ad libitum*, on a variety of vegetables, supplemented with a high protein cereal (Pronutro®).

Behavioural tests were conducted in November/December 1995 for the Sir Lowry's Pass population and in November 1995 and October 1996 for the Steinkopf population. The period of September to December coincides with the breeding season for both populations.

Behavioural trials

The experimental apparatus (Figure 9.1) consisted of two plastic containers (16 x 12 x 8.5 cm) containing woodshavings, connected by a one metre long acrylic plastic tunnel (5 x 5 cm). This design was chosen to simulate a below-ground encounter between mole-rats from neighbouring colonies. Three expanded metal gates were fitted to the tunnel. One gate, situated in the middle of the tunnel, enabled the apparatus to be separated into two (Figure 9.1). The other gates, one at the entrance to each chamber, allowed the interactants to be confined to their respective chambers (Figure 9.1).

Figure 9.1: Experimental apparatus. A and B represent plastic containers used to house the interactants, and are connected by an acrylic plastic tunnel. Arrows indicate position of mid-tunnel and chamber-entrance gates. Scale bar = 14 cm.

Behavioural trials were conducted in the laboratory and consisted of dyadic encounters. Initially interactants were confined to their respective chambers for a five minute period of habituation to the apparatus. Trials were then initiated by first lifting the chamber entrance gates and, after both interactants had entered the tunnel, lifting the mid-tunnel gate. Each encounter lasted 10 minutes. The outcome of each trial was scored as a categorical variable with two mutually exclusive states, accept or reject. Trial outcome was scored as accept if both interactants exhibited non-aggressive interactions (*i.e.* sniffing and ignoring). The trial was scored as reject if (1) one or both of the interactants displayed aggressive behaviours (*i.e.* biting and tooth-fencing), or (2) one or both of the interactants exhibited overt avoidance behaviour (*i.e.* interactant actively avoided contact with its dyadic "competitor" by retreating from it). All encounters were terminated before the interactants sustained any physical injury. The apparatus was thoroughly washed, with chlorinated water, between trials to remove previous odours.

I conducted a total of 206 trials, including 51 controls. Experimental trials consisted of dyadic encounters between individuals from different colonies collected at the same study site. Controls consisted of encounters between individuals from the same colony. Individuals were assigned to locality, gender and status groups, and trials were then chosen deliberately to test the effects of locality, sex and reproductive status. Within any treatment, selection of individuals was randomised to control for inter-colony variation affecting trial outcome. The effects of aridity were explored through dyadic encounters between individuals from different colonies captured at the same site; either Steinkopf (arid) or Sir Lowry's Pass (mesic). To assess the effects of sex and reproductive status, encounters between all combinations of sex and status from each study site, were conducted. Reproductive females could readily be identified by their perforate vaginas and prominent teats. The heaviest male in each colony was identified as the reproductive male (criteria Bennett 1989; 1992; Rosenthal *et al.* 1992). Wherever possible animals were only used in a single trial. Where individuals were used more than once they were immediately returned to their natal colony after the initial trial, and a minimum of three hours was allowed to elapse before they were used in any subsequent trial. On reintroduction to their natal colony individuals settled down very rapidly, there were no aggressive interactions with colony-mates, no physical injuries were sustained by any individuals, and within 10 minutes colony activity and individual behaviour had returned to normal. Consequently, where an animal was used in more than a single trial three hours was considered more than sufficient time to ensure independence of trial outcomes.

As outlined in the introduction to this chapter, in this study I investigated the conflict between maintaining colony integrity to enhance personal foraging success and hence survival, and dispersal to maximise individual lifetime reproductive success. Conflict between these factors should be maximal when conditions are not suitable for dispersal, and consequently most insight will be gained by investigating aggression when the interactants have not experienced appropriate dispersal cues. Accordingly, the animals used in this

investigation were not primed for dispersal by the pertinent triggers *i.e.* precipitation. Furthermore, laboratory trials were conducted between October and December, a period coincident with the dry summer period in the field.

Data Analysis

Acceptance or rejection in dyadic encounters was recorded as a categorical variable with two states, accept or reject. It was not possible to accurately record the intensity of aggression due to ethical considerations requiring that no physical harm be experienced by any of the interactants. This necessitated that the observer intervene whenever the potential for serious injury existed, effectively preventing an assessment of the aggression rate.

Bivariate logistic regression analysis (Hosmer & Lemeshow 1989) was used to find the best fitting model to describe the relationship between the dyadic behavioural outcome (a binary response variable), and the set of independent covariates (body weight, locality, status and sex). Body weight was expressed in terms of the size difference between pairwise interactants. A given difference in body weight between two interactants could influence the outcome of an encounter in a manner that depended on the absolute value of their respective size. To control for such a scaling effect, a dimensionless ratio, similar to that used by Beacham (1988) and Beaugrand *et al.* (1991), was calculated. The size differential between contestants in each dyadic encounter was expressed as a percentage of the body weight of the smaller individual;

$$\text{size differential} = \frac{\text{larger body weight - smaller body weight}}{\text{smaller body weight}} \times 100\%$$

Size differential was coded as a continuous variable (size differential, Table 9.1), and locality as a binary variable (locality, Table 9.1) in the logistic regression model. Design (dummy) variables were used to parameterise the threefold permutations of both

reproductive status and sex in dyadic encounters between individuals (status$_{(1)}$ and status$_{(2)}$, and sex$_{(1)}$ and sex$_{(2)}$ respectively, Table 9.1). An interaction term between the sex and status variables was similarly coded. All logistic regression analyses were run on Statistica software using the non-linear estimation module (Statistica 1995). In addition I examined the interaction between reproductive status and locality *post-hoc* using a chi-square goodness-of-fit test (Zar 1984).

To control for the effects of the experimental apparatus, the results from control trials were tested against results from experimental trials, using a chi-square goodness-of-fit test (Zar 1984). The control trial results differed significantly from the experimental trial results (0% rejection in control trials versus 52.9% rejection in experimental trials; $\chi^2_{(1)} = 47.61$, $p < 0.0001$). This effectively excludes experimental apparatus design as a determinant of experimental trial outcome.

RESULTS

Maximum likelihood estimates of the covariates in the subset model are provided in Table 9.1. The null hypothesis that the estimated covariate coefficients in the model were equal to zero was tested against a chi-square distribution with six degrees of freedom. The results reveal a significant model fit ($\chi^2_{(6)} = 57.951$, $p < 0.0001$). In a saturated model (where all independent variables had been included), the maximum likelihood estimate of the interaction term was non-significant (coefficient $\pm$ SE = 0.8334 ± 0.845, t-stat = 0.987, $p = 0.325$). However, the predictive power of the model including the interaction term did not differ significantly from the model presented here ($\chi^2_{(6)} = 58.912$, $p < 0.0001$). Hence, the interaction between sex and reproductive status was excluded from the model selection.

The results indicate a significant effect of locality, sex combination, and reproductive status combination on the outcome of experimental trials. In contrast, the size differential had no significant impact. To aid interpretation the pattern of rejection for dyadic encounters

between individuals from different localities, of different sex and of differing reproductive status are presented graphically in Figures 9.2 to 9.4 respectively, and are detailed below.

Table 9.1: Results of the bivariate logistic regression analysis between four independent variables and experimental trial outcome. Maximum likelihood estimates (coefficients) are indicated for each variable. Standard error measurements (SE) and significance levels (p) for each estimate are provided.

Variable	Estimate	SE	t-stat	p
Locality	1.239	0.418	2.961	<0.0001
Size differential	0.009	0.008	1.058	0.291
$Sex_{(1)}$†	1.796	0.507	3.554	0.001
$Sex_{(2)}$ †	-0.304	0.505	-0.603	0.547
$Status_{(1)}$ †	1.880	0.500	3.761	<0.0001
$Status_{(2)}$ †	1.197	0.520	2.300	0.023
Constant	-2.778	0.600	-4.636	<0.0001

† Design (dummy) variables used to parameterise the threefold permutations of reproductive status and sex in dyadic encounters between individuals

Locality

Locality was identified in the model as being a significant variable in accounting for variation in the level of rejection (Table 9.1). Levels of rejection were substantially higher for trials between mole-rats from the arid site than between those from the mesic site (Figure 9.2).

Sex combination

The sex combination of dyadic interactants had a marked effect on the pattern of rejection (Table 9.1; Figure 9.3). For both arid and mesic populations, encounters between different sexed individuals produced lower levels of rejection than those between same sexed individuals (Figure 9.3). Consistent with the locality results, the percentage of rejection was higher for the arid site than the mesic site, for all combinations of sex.

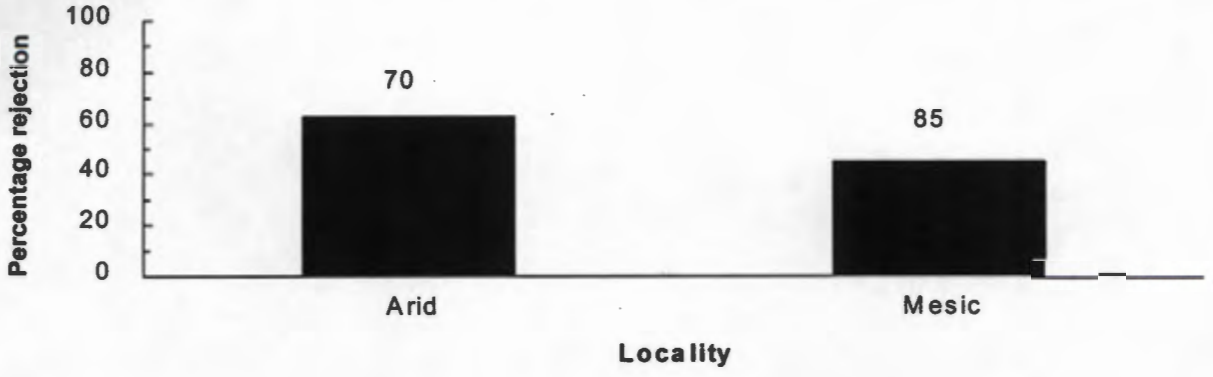


Figure 9.2: Percentage rejection for encounters between *C. h. hottentotus* dyads from arid and mesic localities. Numbers of trials for each category shown above each bar.

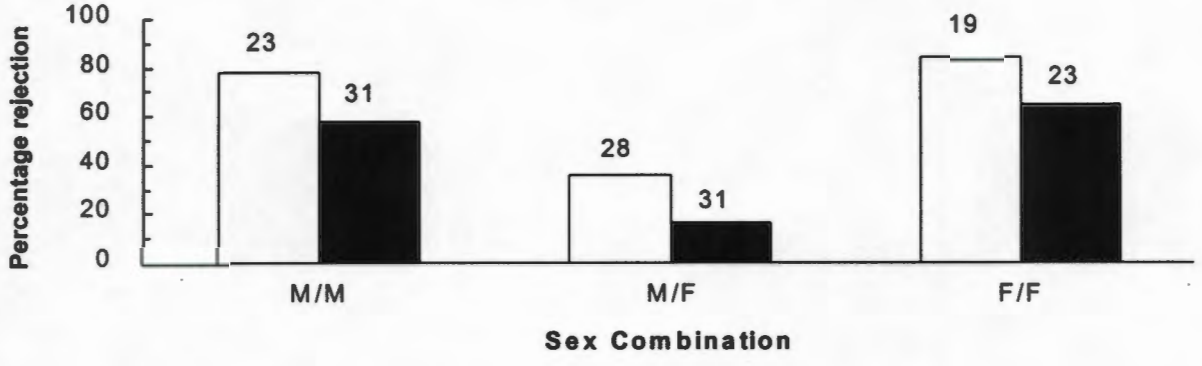


Figure 9.3: Percentage rejection for dyadic encounters between different sex combinations of *C. h. hottentotus* from arid (□) and mesic (■) localities. Numbers of trials for each category shown above each bar. For sex combination; M/M = male versus male, M/F = male versus female, F/F = female versus female

Reproductive status combination

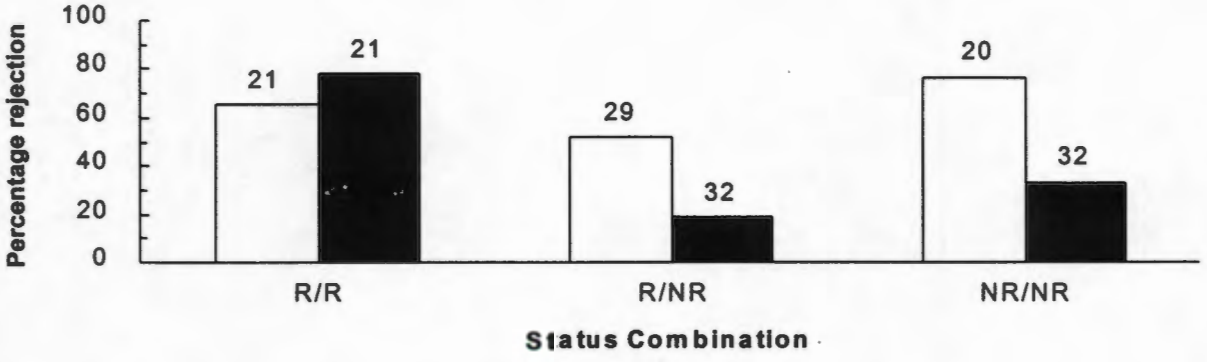


Figure 9.4: Percentage rejection for dyadic encounters between different reproductive status combinations of *C. h. hottentotus* from arid (□) and mesic (■) localities. Numbers of trials for each category shown above each bar. For status combination; R/R = reproductive animals versus reproductive animal, R/NR = reproductive animal versus non-reproductive animal, NR/NR = non-reproductive animal versus non-reproductive animal.

Although the model revealed that reproductive status combination was an important determinant of trial outcome (Table 9.1), trends in the level of rejection for different combinations of reproductive status were equivocal (Figure 9.4). There was a significant interaction between reproductive status and locality (post-hoc chi-square goodness-of-fit test: $\chi^2_{(2)} = 22.04$, $p < 0.001$), suggesting that the pattern of rejection differed between the arid and mesic populations, and this is evident in Figure 9.4. In trials between individuals from the mesic site, rejection was greatest for encounters between reproductive animals (Figure 9.4). Furthermore, encounters between reproductive and non-reproductive animals, and between non-reproductive dyads from the mesic population, produced a relatively low level of rejection. In contrast, for individuals from the arid site, the levels of rejection were comparatively high, and comparable for all combinations of reproductive status (Figure 9.4).

DISCUSSION

The key to understanding the evolution of family groups lies in understanding the causes of delayed dispersal (Koenig *et al.* 1992; Emlen 1994; 1995). In mole-rats the hypothesised selective advantages for familial group formation are well-known (Jarvis 1985; Bennett 1988; Lovegrove & Wissel 1988; Lovegrove 1991; Jarvis *et al.* 1994). Emlen (1995) postulated that family groupings will be unstable, and disintegrate when acceptable reproductive opportunities materialise elsewhere. This would appear to be true for outbred mole-rat families, in which dispersal and outbreeding typically occur when rainfall provides optimal digging conditions (Jarvis & Bennett 1990; 1991; 1993; Lovegrove 1991; Jarvis *et al.* 1994). For the majority of the time, however, conditions are unfavourable for dispersal, and social mole-rats may satisfy their inclusive fitness requirements indirectly by helping closely related kin within the familial group (Jarvis *et al.* 1994). During this non-dispersal period the survival of all colony members will ultimately depend on maintaining colony integrity, and protecting the burrow system and its associated resources against foreigners. Thus, conflict between

maintaining group cohesion and outbreeding must arise when foreigners, encountered in the natal burrow system, provide an opportunity for the maximisation of the LRS requirements of the non-breeding colony members.

As predicted, *C. h. hottentotus* individuals from the arid area revealed significantly higher levels of rejection in dyadic encounters, than those from the mesic area. As previously suggested, the costs of foraging in arid habitats are higher than in mesic ones (Jarvis & Bennett 1990; 1991; Lovegrove 1991; Jarvis *et al.* 1994). Given the restrictions on foraging, there should thus be a strong selection to reduce these costs in arid environments. Foreign animals may elevate costs, threatening colony, and hence individual, survival by: (1) increasing pressure on limited food resources; and (2) parasitising the colony workforce, *i.e.* consuming colony food resources but not assisting in their location. In addition, foreign animals may disrupt colony integrity, through the breeding opportunities they present to the subordinate members of the colony they invade. Consequently, adaptation to arid environments may have selected for high levels of kin discrimination and the rejection of foreigners. In mesic areas, reliable precipitation translates into improved foraging predictability, and consequently the penalties for failing to exclude foreign conspecifics should be reduced. Individuals from mesic areas are thus more likely to accept foreign conspecifics, and the opportunities for independent reproduction that they represent.

It could be argued that inter-habitat differences in aggression are a consequence of differences in predation pressure rather than aridity. Higher rates of predation in arid areas may, theoretically, select for individuals which are more aggressive towards predators and as a by-product toward foreigners. Predation rates are difficult to assess, as predation is never directly observed and it is difficult to distinguish between disappearance due to mortality, predation or dispersal. However evidence available from long-term demographic studies (Chapters 7 & 8) suggests that individuals from the arid site remain resident within their natal colony for a substantially longer time period than those from the mesic site, indicating that the rates of predation are not higher in the arid area. Moreover, Nevo (1979;

1982) suggests that the subterranean niche is well buffered against high levels of predation. These considerations mitigate against there being substantial inter-habitat differences in predation rates, and consequently against predation pressure as an explanation for inter-habitat divergence in aggression.

In their investigation of aggression in the solitary Israeli mole-rat, *Spalax ehrenbergi*, Nevo *et al.* (1986; 1992) and Ganem and Nevo (1996) suggest that, due to physiological constraints, aggression is curtailed in arid areas. They go on to propose that ecological constraints may have been a major proximate determinant of the evolution towards pacifism, and subsequently sociality, observed in bathyergids inhabiting harsh environments. Although aggression rates were not measured in our study, the results do suggest that, for the common mole-rat, levels of aggression are in fact higher in arid areas. Once sociality has evolved one may expect differentiation in agonistic behaviour. Selection should favour colony members which are highly aggressive to foreigners, who threaten colony integrity and colony resources, but unaggressive towards colony members, thereby promoting the cooperative behaviours essential to survival in arid regions. Clearly aggression towards both foreigners and colony-mates will be moderated by the selfish desire to maximise LRS and the concomitant need to outbreed.

The effect of sex on the outcome of dyadic encounters was unequivocal. For both localities, levels of rejection were, as predicted, lowest in encounters between individuals of different sex. In the Damaraland mole-rat Jacobs *et al.* (submitted) have shown that resident colony members will readily accept foreigners of the opposite sex. Similarly Jarvis *et al.* (1994) note that foreign conspecific male and female *C. damarensis* could be paired with little or no aggression. In encounters between mole-rats of the opposite sex, interactants are probably influenced by the desire to outbreed and maximise personal LRS. Indeed in several instances animals were observed attempting to copulate during the behavioural trials. It is noteworthy that even encounters between opposite sex interactants from the arid locality revealed relatively low levels of rejection. It must be remembered that in arid areas,

even when dispersal conditions are favourable, there are overwhelming odds against successful outbreeding. These relate to the low probability of finding a dispersing mate of the opposite sex. Consequently, when faced with a concrete opportunity to maximise their LRS, foreign conspecifics may accept one another, even when the risks to colony integrity and resources are high. In encounters between same sexed individuals, few fitness benefits will accrue if combatants accept their competitors, and in fact, as previously discussed, considerable fitness costs may result. This may explain the high levels of rejection observed for encounters between same sexed individuals at both localities.

The existence of fundamental asymmetries in the distribution of lifetime reproductive success amongst group members of social mammals, is well established (Vehrencamp 1983a; 1983b; Keller & Reeve 1994). For example dwarf mongoose, *Helogale parvula* (Rasa 1973; Rood 1980), slender-tailed meerkat, *Suricata suricatta* (Doolan & MacDonald 1996), spotted hyaena, *Crocuta crocuta* (Frank 1986), wild dog, *Lycaon pictus* (Frame *et al.* 1979; Malcolm & Marten 1982; Creel *et al.* 1997), common marmoset, *Callithrix jacchus jacchus* (Abbott 1984; Rothe 1975) and cotton-top tamarin, *Saguinius oedipus oedipus* (French *et al.* 1984; Hampton *et al.* 1966) exhibit a marked reproductive skew, with dominant individuals monopolising reproduction. The same is true of social mole-rats (Jarvis & Bennett 1990; 1991; 1993; Jarvis *et al.* 1994). Consequently, dominance/reproductive status will have a substantial impact on realised LRS, and should be an important motivational determinant of decisions during meetings between outbred social mole-rats. The results from the present study are however, enigmatic and consequently, were difficult to interpret within the context of our predictions. The consistently high levels of rejection for all combinations of reproductive status, in trials between animals from Steinkopf, reflects the fact that foreign animals, irrespective of their status, represent a substantial threat to colony integrity and resources in arid areas. Although, by contrast, the penalties for failing to reject foreign conspecifics should tend to be rather negligible in mesic areas, the exact fitness cost will depend on the dominance status of the alien animal. In encounters between dominants, the

competitors are likely to recognise the threat posed by the foreigner to their reproductive position, hence the high level of rejection. In encounters between dominants and subordinates and between subordinate dyads, the subordinate status of at least one interactant will immediately eliminate the perceived threat to reproductive position.

A crucial feature of cooperatively breeding animal societies is the variation in the distribution of LRS amongst group members, or the degree of reproductive skew[1] (Vehrencamp 1983a; 1983b; Reeve & Keller 1995). A critical assumption of models of skew is that dominant members of the group control reproduction of the subordinates (Vehrencamp 1983a; 1983b; Keller & Reeve 1994). If dominants benefit from the retention of subordinates, it may pay the dominant to allow some subordinate reproduction as an inducement to remain in the colony, or "staying incentive" (Keller & Reeve 1994). Optimal skew theory predicts that the degree of reproductive skew and concomitant magnitude of staying incentives, will be influenced by both intrinsic and extrinsic factors, the most significant being extrinsic (Keller & Reeve 1994). Consequently, where ecological constraints on independent reproduction are strong, a higher reproductive skew should result (Keller & Reeve 1994). Staying incentives will decrease as subordinates can expect only small, if any, fitness payoffs for leaving the colony. Conversely, where ecological constraints are more moderate staying incentives will increase to encourage social fidelity. For example, Creel and Waser (1991) and Keane *et al.* (1994) suggest that dominant dwarf mongooses may concede their monopoly on reproduction in order to retain helpers. Constraints on dispersal of mole-rats occurring in mesic regions, are few, and there may be little long-term advantage, to subordinates in natal philopatry. However, dominant animals are likely to gain significant fitness benefits by retaining helpers. Therefore, it is possible that dominants may permit some reproduction in subordinates as a staying incentive. Although it remains to be properly tested, the low levels of rejection in trials between dominant and

[1] Vehrencamp (1983b) defines reproductive skew as the difference in fitness amongst members of a group, due to usurpation of subordinates by dominants.

subordinate animals from Sir Lowry's Pass, may provide support for the notion that dominants entice subordinate philopatry by offering staying incentives. Further supported is furnished by the results from the demographic studies, which revealed the frequent immigration of foreign adults into colonies at Sir Lowry's Pass (Chapter 8).

Dispersal, and the opportunities for independent reproduction it embodies, plays a significant role in mating systems and life-history tactics (Greenwood 1980). This should be especially true of obligate outbreeding cooperative breeders with a high reproductive skew, like the social bathyergids. As previously suggested, subordinates of social mole-rat species experience an interplay between the need to secure acceptable breeding opportunities and constraints on dispersal. Conflict between these factors must ultimately moderate life-history traits. The majority of social bathyergids are outbred, the exception being the naked mole-rat, which is a facultative inbreeder (Faulkes *et al.* 1990b; Reeve *et al.* 1990; Honeycutt *et al.* 1991b; Jarvis 1991a; O'Riain *et al.* 1996). Jarvis *et al.* (1994) report that dispersal success in the habitats occupied by naked mole-rats, is very low (<0.1%). Facing such odds against successful outbreeding, selection may favour the evolution of inbred groups, where individuals can occasionally satisfy direct fitness by attaining a dominant position within the family (Faulkes *et al.*, 1990b; Reeve *et al.*, 1990). Within such inbred groups inclusive fitness gains will be maximised by (1) helping closely related kin and (2) attaining reproductive dominance. It is interesting that, in vertebrate terms, naked mole-rat colonies are relatively large (mean = 79 individuals, max. = 300 individuals) and consequently access to reproduction is greatly restricted, many individuals living their entire lives without breeding (Brett 1986; Jarvis *et al.* 1994). Although subordinates still satisfy their fitness requirements indirectly, this may explain why a few individuals still risk dispersal to outbreed (O'Riain *et al.* 1996).

In the other social bathyergids, dispersal success, although not high, is substantially greater than for the naked mole-rat (*e.g.* C. damarensis = 8-14%, Jarvis & Bennett 1993; Jarvis *et al.* 1994). Under these conditions, it may be even better for individuals to risk

dispersal for the considerable fitness rewards a success represents. Somewhere, between the 0.1% level of success found in naked mole-rats and the 8% success of other social bathyergids, there may be a threshold frequency where the inclusive fitness benefits of dispersal and outbreeding, outweigh those of extended natal philopatry and inbreeding.

In conclusion, the results from this study reveal a significant departure from the patterns found in the naked mole-rat (O'Riain & Jarvis 1997). This disparity is probably linked to deviations in mating strategy. In social mole-rat species in general (including *H. glaber*), protection of the natal burrow system and its associated resources may have substantial implications for the survival of all colony members. However, in outbred social species like *C. h. hottentotus*, this may clash with the selfish desire to maximise LRS, especially during meetings between foreign conspecifics. Conflict between these fitness components is regulated to some degree by the sex and reproductive status of interactants, but especially by ecological constraints. For arid-occurring populations, the penalties for failing to exclude foreigners will be substantially more severe than for mesic-occurring populations, resulting in elevated levels of xenophobia. Results from this type of study provide keen insight into understanding the evolution and maintenance of familial groups.

Chapter 10

Synthesis and conclusions

Cooperative breeding presents biologists with challenging evolutionary questions (Mumme 1997). Natural selection favours individuals that "strive" to maximise their own fitness. Consequently social systems in which cooperating organisms forgo their own selfish "aspirations" in the interest of group cohesion, demand explanation in terms of current evolutionary theory. The aim of this thesis was to address the origin and evolution of sociality in the African mole-rats. Specifically, the common mole-rat, was used as a model to assess the Aridity Food-Distribution Hypothesis (AFDH; outlined in Chapter 1) as an explanation for the evolution of bathyergid sociality. Solomon and Getz (1997) propose that important insights into social evolution will be gained by evaluating the effects of habitat variables on cooperative breeding, in particular they suggest that the effect of habitat variables should be examined intraspecifically in optimal and sub-optimal habitats. In this thesis I have endeavoured to achieve this end by an intraspecific investigation of the common mole-rat in a mesic and an arid habitat, representing relatively favourable and unfavourable habitats respectively.

Since the inception of this thesis a more fundamental question, than the validity of the AFDH, has arisen with regard to the origin of sociality in the Bathyergidae. In the past, studies of social behaviour have been dominated by an *a priori* assumption that eusociality represents an evolutionary endpoint, *i.e.* the evolution of eusociality is irreversible (Wcislo & Danforth 1997). However, recent phylogenetic studies of insect taxa have revealed evidence of apparent evolutionary transitions from eusocial to solitary behaviour, challenging the traditional view that social evolution is unidirectional (Wcislo & Danforth 1997). Similarly, H. Burda (pers. comm.) has questioned Jarvis and Bennett's (1991) suggestion that the first

Bathyergidae were solitary, and that the evolutionary shift was from solitariness to sociality. H. Burda (pers. comm.) proposed that the common ancestor to the extant members of the Bathyergidae was in fact social, a trait derived from their hystrigognath ancestors, and that the extant solitary species are secondarily solitary. Indeed, the most recent bathyergid phylogeny (Faulkes *et al.* 1997a; see Figure 1.4) suggests that assumptions of ancestral solitariness or sociality are equally parsimonious.

Wcislo and Danforth (1997) maintain that this realisation has implications for our understanding of the evolution of social behaviour. However, I believe that the functional questions, and in particular the validity of explanations for the evolution of mole-rat sociality are not influenced by the social status of the bathyergid common ancestor. Irrespective of their ancestry the question remains, why are some mole-rat species solitary whilst others are social? In terms of evolutionary theory, group-living poses more of an evolutionary dilemma than solitariness; the latter is expected as a consequence of individuals maximising their personal fitness requirements. Thus irrespective of whether mole-rats are derived from a social or solitary ancestor the crucial question remains why has advanced social behaviour evolved in two bathyergid genera (see Chapter 1), but does not occur in any other completely subterranean mammalian taxa (see also Lacey & Sherman 1997). Wcislo and Danforth (1997) recognised the evolutionary significance of sociality versus solitariness when they remarked that "Studies of the conditions that lead to the suppression or loss of social behavior can help to illuminate those factors that lead to its origins and maintenance.".

This thesis, however, was not designed to test phylogenetic arguments about the social status of the bathyergid ancestors, but rather to examine the role of aridity in maintaining and/or strengthening the social behaviour we observe in an extant mole-rat species. The results thereby obtained also giving insight into the origins of sociality in the African mole-rats as a whole. Moreover, the experimental design of this thesis, *viz.* the use of an intraspecific comparison, controls for any phylogenetic effects in the interpretation of the results.

THE ARIDITY FOOD-DISTRIBUTION HYPOTHESIS AND BATHYERGID SOCIALITY

Two simple, yet critical, questions underlie the corroboration of the AFDH[1] as a valid explanation for the evolution of sociality within *C. h. hottentotus*: (1) do the assumptions of the AFDH hold true *i.e.* do arid and mesic habitats exhibit ecological differences, specifically with regard to the pattern of resource dispersion and the energetic costs of foraging, which influence foraging risks and consequently the costs of dispersal? and (2) do these inter-habitat differences have ramifications for bathyergid social evolution *i.e.* do the common mole-rat populations inhabiting arid and mesic areas exhibit regional differentiation in social behaviour?

Substantial inter-site divergence in ecological characteristics, notably climate and resource attributes, were revealed in this study. Although both study localities exhibit identical patterns of seasonality in climatic variables, rainfall at the arid site was markedly lower and more sporadic and evaporation levels significantly higher than at the mesic site. Moreover, thermal constraints were more limiting at the arid site. These features should greatly elevate the costs of soil excavation and the risks of hyperthermia, severely restricting the occurrence of suitable burrowing opportunities at the arid locality. Consequently, foraging will be severely constrained in this area. At the mesic site, high, predictable rainfall, low evaporation rates and reduced thermal constraints will translate into more suitable burrowing opportunities for most, if not all, of the year.

Regional differentiation was also evident in the resource characteristics. Although resources were clumped at both study localities, the density of geophytes was lower and the distance between resource clumps concomitantly greater at the arid relative to the mesic site. Differences in resource dispersion in turn influenced the patterns of foraging, as

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[1] At this point it is important to recognise that the rigorous evaluation of the AFDH is hampered by a lack of viable alternative hypotheses for the evolution of bathyergid sociality. This absence of realistic alternatives against which to contrast the AFDH makes an objective evaluation of its underlying assumptions and associated predictions very difficult.

evident from the patterns of burrow excavation at the two sites (Chapter 4). Furthermore, food storage and *in situ* harvesting were essential components of cooperative foraging in *C. h. hottentotus* as they minimised the risks of starvation, particularly in arid habitats. Thus resource characteristics together with the climatic restrictions on burrowing in arid areas may have a marked impact on foraging behaviour, imposing heavy constraints on the mole-rats occurring there and ultimately shaping their foraging responses. Together, these factors satisfactorily account for the first underlying premise of the AFDH, that arid and mesic habitats exhibit ecological differences with regards to the pattern of resource dispersion and the energetic costs of foraging, which are likely to influence foraging risks and the costs of dispersal.

In evaluating the AFDH, the second question which needs to be addressed is whether the study populations revealed divergence in their social behaviour. As outlined in Chapter 1 the common mole-rat populations used in this investigation exhibit relatively minor genetic divergence (C.G. Faulkes unpublished data). This suggests that allopatry between the arid and mesic populations is a relatively recent phenomenon. Consequently, there should be only modest inter-site differentiation in social behaviour. The results from this thesis support this contention. Study populations revealed no differences in absolute group size or in reproductive characteristics which were related to the effects of aridity *per se*. However, distinct inter-population divergence was apparent in phenotypically plastic traits such as dispersal behaviour and xenophobia. Clear differences were evident between the arid and mesic sites in both the quantitative and qualitative nature of dispersal; most notably dispersal was markedly constrained at the arid site and colonies demonstrated greater temporal stability, with more predictable temporal group membership. The ecological constraints on successful foraging at the arid site (see above) will curb opportunities for dispersal and promote cooperation in the common mole-rats occurring there. Colony members should therefore maximise their inclusive fitness by natal philopatry, delay dispersal and engage in cooperative foraging.

Inter-site differences were also apparent in the response of colony members to foreign conspecifics. Common mole-rats from the arid site were substantially more xenophobic than those from the mesic site, and aggressively rejected foreigners. For arid-occurring populations, the fitness penalties for failing to exclude foreigners from the colony burrow system and associated resources, will be substantially more severe than for mesic-occurring populations, resulting in elevated levels of xenophobia. Again colony cohesion and cooperation in arid areas are essential to individual survival and inclusive fitness. The regional differences in dispersal patterns and xenophobia revealed in this investigation may reflect adaptive variation in social behaviour between the study populations, and the results suggest that delayed dispersal and cooperation may be more crucial to individual survival in arid than in mesic areas. As such these findings provide support for the underlying contention of the AFDH that ecological constraints on foraging in arid areas have promoted a greater degree of social elaboration in mole-rats occurring there.

This thesis provides persuasive support for the AFDH as an explanation for the adaptive significance of social behaviour and cooperation in the common mole-rat, and together with Bennett (1988) and Faulkes *et al.*'s (1997a) interspecific investigations, suggests that the AFDH provides a valid explanation for the evolution of group-living in the Bathyergidae. However, several important considerations were highlighted during the course of this study:

(1) It is the pattern of resource distribution and density, not the total available energy, which differs between arid and mesic sites, ultimately constraining foraging efficiency and promoting group-living in the bathyergids (see also Jarvis *et al.* 1994).

(2) Too much emphasis has been placed on inter-habitat divergence in the pattern of resource dispersion *i.e.* whether resources exhibit a random, a clumped or a uniform spatial distribution in different habitats (*e.g.* Brett 1986; 1991; Lovegrove & Wissel 1988; Jarvis & Bennett 1991; Jarvis *et al.* 1994). I believe that this should be considered as a branch of the AFDH, rather than a main focus (see Chapter 4).

Geophyte density and the concomitant scale of clumping will be more important determinants of differential foraging risks in different habitats, rather than the pattern of dispersion *per se*.

(3) Models of social evolution in the Bathyergidae, including the AFDH, emphasise the role of resource characteristics, often at the expense of climatic considerations (*e.g.* Lovegrove & Wissel 1988; Lovegrove 1991; Lacey & Sherman 1997). Patterns of precipitation and evaporation have direct implications with regards to differences in foraging risks in arid and mesic environments, and consequently are a crucial determinant of dispersal constraints and the evolution of group-living (see Chapter 2).

(4) It is interesting to speculate about the significance of group-living in mesic-occurring common mole-rat populations. In Chapter 6 I conjectured that the similarity in group size between arid and mesic sites may reflect that there is strong selection for group-living in mesic environments. The results from this thesis suggest that sociality in mole-rats is an adaptation to the unpredictability of arid environments, and is associated with the climatic and food-resource characteristics prevalent in these habitats. Although, by comparison mesic areas are far more stable and predictable, even these areas are exposed to sporadic variation in climatic patterns. For example, global circulation patterns associated with the *El Niño* Southern Oscillation (ENSO) may result in prolonged droughts in traditionally mesic areas of southern Africa. Such unpredictable shifts in weather patterns may occur frequently enough for selection to favour adaptations which enhance species survival during these climatically aberrant periods. This seems a plausible suggestion given: (1) the two to ten year ENSO cycle (Cane 1983); and (2) the established ENSO effects on avian and mammalian population demography, reproductive biology and behaviour (*e.g.* Zabel & Taggart 1989; Clark *et al.* 1990; Wilson 1991; Massey *et al.* 1992; Meserve *et al.* 1995). Thus, although the evolutionary inception of mole-rat sociality appears to have been a consequence of aridity, selection may have maintained group-living in

common mole-rats subsequently exposed to mesic conditions, as an adaptation to long-term unpredictability in climatic patterns.

Investigations of sociality and cooperative breeding in birds and mammals have distinguished between ecological-constraints (extrinsic constraints) and benefits-of-philopatry (intrinsic benefits) explanations for delayed dispersal (Emlen 1982a; Stacey & Ligon 1987; 1991; Heinsohn *et al.* 1990; Zack 1990; Koenig *et al.* 1992; Jennions & MacDonald 1994). Recently, Emlen (1994; 1995) has argued that these explanations represent semantic sides of the same coin and accordingly suggests that the distinction is of little heuristic value However, Heinsohn *et al.* (1990) originally emphasised that a detailed consideration of both extrinsic constraints and intrinsic benefits is essential for a comprehensive approach to investigations of social behaviour. Koenig *et al.* (1992) went on to note that the distinction between intrinsic benefits and extrinsic constraints can only be applied at the level of current utility, and not at the level of evolutionary origin. Thus for example, individuals may glean intrinsic benefits even when a population is forced into group living by extrinsic constraints. The findings from this thesis suggest that sociality has evolved in the mole-rats due to the costs of dispersal and concomitant constraints on independent reproduction in arid environments. Cooperative foraging is simply the logical by-product of constrained dispersal, as once individuals are forced to remain within their natal group, they will enhance their personal fitness by cooperating with their parents and siblings. I suggest that although cooperative foraging is an intrinsic benefit of sociality in mole-rats, its occurrence is driven by constraints on dispersal and solitary foraging. Thus, dispersal constraints rather than the benefits of group-living *per se* appear to have promoted bathyergid sociality. O'Riain (1996) observed that the role of cooperation and altruism in mole-rat social behaviour is often over-emphasised. Although mole-rat colonies appear to exhibit numerous cooperative behaviours that may be construed as altruistic, it is in fact more realistic to think of each colony member as exploiting the colony for food and shelter until conditions are suitable for dispersal (in

outbred species) and independent reproduction. Consequently, sociality in the bathyergids would be better perceived from the viewpoint of frustrated dispersers rather than content families.

CLOSING REMARK

> "A general theory of social evolution must transcend the phylogenetic limitations and taxonomic biases of the biologists who build it." (Mumme 1997, pp 382)

Studies of vertebrate and invertebrate sociality have proceeded more or less independently (Lacey & Sherman 1997). Mumme (1997) recognised that a comprehensive understanding of social evolution will best be attained by overcoming such taxonomic boundaries. A major advance towards this unity has been the recognition of the ubiquity of ecological parameters as determinants of sociality in vertebrates and invertebrates alike. Consequently, studies which improve our understanding of the proximate and ultimate basis of ecological determinants of group living in any species, *viz.* the AFDH and bathyergid sociality, promise to play a pivotal role in efforts to unite the occurrences of eusociality and cooperative breeding under a single theoretical umbrella, and bring us closer to a synergy in sociobiological thinking.

Chapter 11

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Appendix I

Foraging simulation model

The basic code for the foraging model used in Chapter 5 is outlined below. The model given here is the version for Steinkopf. The basic code for the Sir Lowry's Pass model was identical, however, corresponding empirical variables for the mesic site were inserted were appropriate. The model was written in True BASIC (True BASIC Inc., 39 South Main Street, Hanover, NH 03755, U.S.A.)

```
REM MOLE-RAT MODEL
! STEINKOPF VERSION
! by Éva Plagányi and Andrew Spinks

RANDOMIZE
CLEAR

!*** SET MAXSIM (no. of sims), TDAY (sim length) & NUMOLES (no. moles)
!*** before each run

LET MAXSIM = 1
LET TDAY = 90          ! TOTAL NO. OF DAYS
LET NUMOLES = 1

LET MOLMASS = 65       ! ** AVE MOLE MASS IN GRAMS - CAN CHANGE!!
LET L = 200            ! LENGTH OF MODEL AREA (m)
LET P = 0.25           ! LENGTH OF CELL
! AREA = 200X200; TO CONVERT TO VOLUME, NEED DEPTH OF SEARCH AREA:
! BURROW DIAM = 6CM + MODAL BULB DIAM = 5.6 MM
! SET DEPTH = 8 CM = 0.08 M
TOTVOL = 3200          ! TOTAL VOLUME
! STEINKPF - BULB DENS = 76 PER M2 = 6 PER 0.08 M3
! LOWRY - DENS = 1424 PER M2 = 114 PER 0.08 M3
LET DENS = 76          ! BULB DENSITY PER M3
LET D = DENS * TOTVOL  ! / 0.018
PRINT 'NO. OF BULBS PER MODEL AREA = ";D

LET MXD = 2            ! METRES: MAX. DAILY EXTENSION OF BURROW BY ONE MR
!LET MXD = MDIST/P     ! MODEL CELLS: MAX. DAILY EXTENSION OF BURROW BY ONE
MR
LET MAXCELLS = (MXD/P)

LET MXT = 360          !ACTIVE DAILY TIME LIMIT PER MOLE - IN MINUTES

! TIME TO DIG ONE CELL - NOTE: PARAMETER CHANGED DAILY DEP. ON RAIN ETC.
```

```
LET DIGTIME = 50        !50 MINS FOR 0.25 M FROM DATA: 0.3M PER HR

LET P11 = 0.80          ! PROBABILITIES OF TRAVELLING IN 4 DIRECTIONS
LET P22 = 0.10
LET P33 = 0.10
LET P44 = 0
DIM PROB(4,4)
MAT READ PROB
DATA 0.8,0.1,0.1,0
DATA 0,0.8,0.1,0.1
DATA 0.1,0,0.8,0.1
DATA 0.1,0.1,0,0.8
MAT PRINT PROB

LET CELL = INT(L/P)    !NO. OF MODEL CELLS = 800

DIM BR(50),BC(50)    !CO-ORDS OF BRANCH ENDPOINTS
DIM BD(50)           !DIRN OF BRANCH : VALUES 1 - 4
DIM BZ(50)           !DISTANCE ALONG BRANCH - IN UNITS OF CELLS
DIM BH(50)           !DISTANCE BETWEEN NEST AND BRANCHPOINT
DIM BF(50)           !FLAG TO SEE IF BRANCHING HAS OCCURRED

DIM PATHR(1000),PATHC(1000)
DIM CELLS(8000)

DIM EAT(100)         !BIOMASS OF BULBS EATEN EACH DAY
DIM STORE(100)       !BIOMASS STORED EACH DAY
DIM DGAIN(100)       !DAILY ENERGETIC GAIN PER MOLE

DIM HANDLE(100)
DIM NESTTRIP(100)
DIM DIG(100)

OPEN #1:NAME "C:\MOLES\PATH.OUT",ORGANIZATION TEXT
SET #1: POINTER BEGIN
ERASE #1

DIM RAIN(90)
OPEN #11:NAME "C:\TBASIC\MOLES\RAINSTF.DAT",ORGANIZATION TEXT
SET #11: POINTER BEGIN
LET j = 0
DO WHILE MORE #11
  LET j = j + 1
  INPUT #11: RAIN(j)
LOOP
!MAT PRINT RAIN;
!INPUT TT
CLOSE #11

OPEN #333:NAME "C:\MOLES\ENET.OUT",ORGANIZATION TEXT
SET #333: POINTER BEGIN
ERASE #333

FOR sim = 1 TO MAXSIM
```

```
CLEAR
PRINT SIM-1,ENETAVE

! Initialise branch co-ords
MAT BH = 0
LET BH(1) = 0        !BRANCH 1 IS MAIN BRANCH
MAT BR = 0
MAT BC = 0
MAT BD = 0
MAT BZ = 0
MAT BF = 0

let tz = 0

LET DIR = 1
LET BRANCH = 1       !Keeps track of different branches
LET TBRANCH = 1      !Counts total no. of branches
LET BRDIS = 7 / P    !Min. dist. between branches
LET ZBR = BRDIS

LET FINDS = 0        ! NO. OF BULBS FOUND BY MOLERAT
LET Z = 0
LET CHK = 0

!Initialise matrices
MAT PATHR = 0
MAT PATHC = 0
MAT CELLS = 0
MAT HANDLE = 0
MAT NESTTRIP = 0
MAT DIG = 0
MAT EAT = 0
MAT STORE = 0

!SET WINDOW 200,600,200,600
SET WINDOW 1,800,1,800

FOR DAYS = 1 TO TDAY      !****** LOOP FOR DAYS

LET MAXDIST = MXD * NUMOLES
LET MAXCELLS = MAXDIST/P
LET MAXTIME = MXT * NUMOLES

!RAIN: CODES 1 = WET SOIL; 0 = DRY
IF RAIN(DAYS) = 1 THEN
  LET DIGTIME = 50
ELSE
  LET DIGTIME = 200
END IF

LET DIST = 0
LET FLAGZ = 0    !Used to calc. distance moved along main branch
PRINT tab(2,2); "DAY ";DAYS
```

```
LET ATIME = 0          !TIME COUNTER FOR EACH DAY
LET DIGT = 0           !TIME SPENT DIGGING EACH DAY

! MOLERAT COORDS
! MR ALWAYS STARTS AT THE NEST = MIDDLE OF MODEL AREA
IF DAYS = 1 THEN
  LET R = 400
  LET C = 400
  LET PATHR(1) = 400
  LET PATHC(1) = 400
ELSE
  ! NO BRANCHES WITHIN BRDIS (=6m) OF NEST
  IF Z < BRDIS THEN   !OR TBRANCH > Z/84
   LET R = BR(1)
   LET C = BC(1)
   LET DIR = BD(1)
  ELSE
   LET MAINDIST = BZ(1) - ZOLD
   LET ZOLD = BZ(1)
   IF PRIM < INT(Z/84)+1 THEN
    LET PRIMPROB = 1
   ELSE
    LET PRIMPROB = (MAINDIST/84)*(BZ(1)/350)  !**EXPLAIN
   END IF
   !PRINT TAB(15,2);"PROB  ";PRIMPROB
   !PAUSE 0.5
   LET X = RND

   ! CHOOSES A BRANCH END TO START THE DAY AT
   IF X >= PRIMPROB OR Z < (ZBR+1) THEN
    DO
     LET X = INT(RND*TBRANCH)+1
     !IF BF(X) = 2 THEN PRINT "BRANCH FLAG = 2 "
    LOOP UNTIL X=1 OR BF(X) <> 2
     LET BRANCH = X
     LET R = BR(X)
     LET C = BC(X)
     LET DIR = BD(X)

     ! SECONDARY BRANCH   ****CHK XX PROB
     LET XX = RND
     IF XX < 1 AND BZ(X) > BRDIS AND BF(X) = 0 THEN
       CALL SECONDARY(BD, X, DD, TBRANCH, SEC, BFF)
       BF(X) = BFF
       LET DIR = DD
       BRANCH = TBRANCH
       LET BD(BRANCH) = DD
       LET BF(BRANCH) = 3     !MARKS AS A SEC. BRANCH
     END IF

   ELSE
    ! START A NEW PRIMARY BRANCH
    LET TBRANCH = TBRANCH + 1
    LET PRIM = PRIM + 1
```

```
      PRINT TAB(7,2);"PRIMARIES ";PRIM
      BRANCH = TBRANCH
      CALL PRIMARY
      ! DISTANCE OF BRANCHPOINT FROM NEST
      LET BH(BRANCH) = X
      PRINT TAB(19,2);"BRANCH,BZ  ";BRANCH,BH(BRANCH)
      LET BD(BRANCH) = DIR
      !PRINT "NEW BRANCH NO, DIRN, tot branches  ";BRANCH,DIR,tbranch

      ! ZBR is min. distance main branch must be extended
      !   before another branch
      LET ZBR = X + BRDIS

    END IF
   END IF
END IF
PRINT TAB(4,2);"BRANCHES ";TBRANCH

DO WHILE DIST < MAXDIST AND ATIME < MAXTIME
  IF R = 1 OR R = 800 OR C = 1 OR C = 800 THEN
    PRINT "MR HITS BOUNDARY - MOVEMENT TOO FAST"
    LET DIST = 10000
    LET DAYS = 100
  END IF

  ! *** STARTING DIRN ***
  IF DAYS = 1 AND CHK = 0 THEN
    LET CHK = 1

    LET X = RND
    IF X < 0.25 THEN
      LET DIR = 1
      LET P1 = P11
      LET P2 = P22
      LET P3 = P33
      LET P4 = P44
    ELSE IF X < 0.5 THEN
      LET DIR = 2
      LET P1 = P22
      LET P2 = P11
      LET P3 = P33
      LET P4 = P44
    ELSE IF X < 0.75 THEN
      LET DIR = 3
      LET P1 = P33
      LET P2 = P44
      LET P3 = P11
      LET P4 = P22
    ELSE
      LET DIR = 4
      LET P1 = P44
      LET P2 = P33
      LET P3 = P22
      LET P4 = P11
```

```
    END IF
    !PRINT X,P1,P2,P3,P4
    LET BD(1) = DIR
    PRINT TAB(5,2);"MAIN BRANCH DIRN = ";BD(1)
  END IF

PRINT "DAY, DIR = ";SIM,DAYS,DIR
  LET P1 = PROB(DIR,1)
  LET P2 = PROB(DIR,2)
  LET P3 = PROB(DIR,3)
  LET P4 = PROB(DIR,4)

  LET X = RND
  IF X < P1 THEN
    LET R = R+1
    LET C = C
  ELSE IF X < (P1+P2) THEN
    LET R = R-1
    LET C = C
  ELSE IF X < (P1+P2+P3) THEN
    LET R = R
    LET C = C + 1
  ELSE
    LET R=R
    LET C = C - 1
  END IF

  IF BRANCH = 1 THEN
   ! Z COUNTS CELL NO.
    LET Z = Z + 1
    IF FLAGZ = 0 THEN
      LET ZOLD = BZ(1)
      LET FLAGZ = 1
    END IF
    LET BZ(1) = Z
    LET BH(1) = Z
    LET PATHR(Z) = R
    LET PATHC(Z) = C
  ELSE
    !DISTANCE ALONG A BRANCH
    LET BZ(BRANCH) = BZ(BRANCH) + 1
    !TOTAL DISTANCE FROM BRANCH END TO NEST
    LET BH(BRANCH) = BH(BRANCH) + 1

  END IF
  !print "BRANCH,DIRN  = ";BRANCH,DIR

  ! OPTIONAL TO INCLUDE - PUTS LIMIT ON LENGTH OF 2 BRANCH
  IF BF(BRANCH) = 3 AND BZ(BRANCH) > 20 THEN
    CALL PRIMARY
  END IF

  LET DIST = DIST + P
  PLOT R,C
```

```
  !PRINT DAYS,DIST,R,C,HIT
  !print tab(24,2);r;c

  PRINT #1: R,C

  LET BR(BRANCH) = R
  LET BC(BRANCH) = C

  !KEEPING TRACK OF WHICH CELLS MOLE HAS BURROWED THRU
  LET TZ = TZ + 1
  LET CELLS(TZ) = 800*(R-1)+C
  IF BRANCH > 1 THEN
  FOR i = 1 TO TZ-MAXCELLS
    IF CELLS(TZ) = CELLS(i) THEN
      !*** MOLE SENT TO MAIN BRANCH - NOTE TIME FACTOR...
      !PRINT TAB(18,2);"HITS ANOTHER BURROW"
      LET BF(BRANCH) = 2   !BRANCH FLAG = 2 IMPLIES NO FURTHER EXTN
      !MOVE MOLE BACK TO MAIN BRANCH
      LET XX = RND
      IF XX < 0.5 AND Z > 40 THEN
        CALL PRIMARY
      ELSE
        CALL MAIN
      END IF
      LET i = TZ-1
    END IF
  NEXT i
  END IF

  !****** FOOD ENVIRONMENT **********
  !**** CHK AMT OF FOOD IN CELL R,C
  !*** CALC. DAILY TOTAL BIOMASS EATEN AND STORED

  ! SEND TO SUB INFO. ON DIST FROM NEST
  LET NESTDIST = BH(BRANCH)
  CALL BULBS(TDAY,DAYS,EAT,STORE,NESTDIST,HANDLE,NESTTRIP)
  PRINT TAB(15,2);HANDLE(DAYS)

  !***** CHK TIME EXPENDITURE
  LET DIGT = DIGT + DIGTIME     !EVERY CELL = TIME DEP. ON SOLI CONDTN
  LET SHAND = HANDLE(DAYS)
  LET STRIP = NESTTRIP(DAYS)
  CALL LIMITS(DIGT,SHAND,STRIP,ATIME)

LOOP
IF DIST > MAXDIST THEN LET DLIM = DLIM + 1 ELSE LET TLIM = TLIM + 1
LET DIG(DAYS) = DIGT

NEXT DAYS
PRINT TAB(23,2);"NO. OF TIME LIMITED BY DIST,TIME ";DLIM;TLIM

! CALCULATING ENERGETIC GAIN TOTALS
CALL EGAIN(TDAY,NUMOLES,EAT,STORE,DGAIN,TOTGAIN)
```

```
! CALCULATING ENERGETIC EXPENDITURE TOTALS
CALL
ELOSS(TDAY,NUMOLES,MOLMASS,DIG,HANDLE,NESTTRIP,RAIN,DGAIN,TOTLOSS)

LET ENET = TOTGAIN - TOTLOSS
! NET ENERGETIC GAIN PER MOLE:
LET ENET = ENET/NUMOLES
LET ENETAVE = ENET/TDAY
PRINT "NET ENERGETIC BUDGET  ";ENET
PRINT "AVERAGE DAILY NET ENERGETIC BUDGET  ";ENETAVE

PRINT TAB(10,2);"SECOND/PRIMARY = ";SEC/PRIM

! ESTIMATING MAX. LENGTH OF BURROW
CALL BLENGTH(Z,PATHR,PATHC,BLEN)

PRINT #333: SIM,ENETAVE,BLEN

NEXT SIM

CLOSE #333
PRINT #1
PRINT #1: Z
CLOSE #1

SUB MAIN
   LET R = BR(1)
   LET C = BC(1)
   LET DIR = BD(1)
   LET BRANCH = 1
END SUB

SUB PRIMARY
   ! Z is max. distance (in cell units) along main branch
   LET X = INT(RND * (Z-BRDIS)) + BRDIS
   LET R = PATHR(X)
   LET C = PATHC(X)
   IF R = 0 OR C = 0 THEN PRINT "ZERO..";R;C;X;ZBR
   LET XX = RND
   IF BD(1) = 1 OR BD(1) = 2 THEN
      IF XX < 0.5 THEN DIR = 3 ELSE DIR = 4
   END IF
   IF BD(1) = 3 OR BD(1) = 4 THEN
      IF XX < 0.5 THEN DIR = 1 ELSE DIR = 2
   END IF
   !PRINT "NEW BRANCH NO, DIRN, tot branches  ";BRANCH,DIR,tbranch
END SUB

END

!EXTERNAL SUBROUTINES
SUB SECONDARY(BBD(),I,DD, TBRANCH, SEC, BFF)
! Chooses dirn of secondary branch
      LET X = RND
```

```
      ! DATA: 74% PROB OF SECONDARY BRANCH OFF PRIMARY BRANCH
      IF X < 0.74 THEN
       LET SEC = SEC + 1
       LET BFF = 1
       LET TBRANCH = TBRANCH + 1
       IF BBD(I) = 1 OR BBD(I) = 2 THEN
         IF X < 0.37 THEN DD = 3 ELSE DD = 4
       END IF
       IF BBD(I) = 3 OR BBD(I) = 4 THEN
         IF X < 0.37 THEN DD = 1 ELSE DD = 2
       END IF
      ELSE
       LET DD = BBD(I)
       LET BFF = 0
      END IF
      !PRINT "BD-PRIMARY, DD-SECONDARY, SECONDS = ";BBD(I);DD;SEC
      PRINT TAB(8,2);"SECONDARIES ";SEC
END SUB

SUB BLENGTH(Z,PATHR(),PATHC(),BLEN)
! FINDING BURROW LENGTH
LET MINR,MAXR = 0
LET MINC,MAXC = 0
! BUBBLE SORT TO FIND MIN AND MAX CO-ORDS
FOR j = 1 TO Z-1
  FOR k = 1 TO Z-j
    IF PATHR(K) > PATHR(k+1) THEN
      LET TEMP = PATHR(k)
      LET PATHR(k) = PATHR(k+1)
      LET PATHR(k+1) = TEMP
    END IF
  NEXT k
NEXT j
FOR j = 1 TO Z-1
  FOR k = 1 TO Z-j
    IF PATHC(K) > PATHC(k+1) THEN
      LET TEMP = PATHC(k)
      LET PATHC(k) = PATHC(k+1)
      LET PATHC(k+1) = TEMP
    END IF
  NEXT k
NEXT j
!MAT PRINT PATHR;
LET MINR = PATHR(1)
LET MAXR = PATHR(z)
LET MINC = PATHC(1)
LET MAXC = PATHC(z)
LET DIFF1 = MAXR-MINR
LET DIFF2 = MAXC-MINC
! LENGTH BY PYTHAG
LET BLEN = SQR(DIFF1^2 + DIFF2^2)
PRINT DIFF1,DIFF2,BLEN
END SUB
```

```
SUB BULBS(TDAY,DAYS, EAT(), STORE(), NESTDIST, HANDLE(), NESTTRIP())
  !ASSUME BULBS DISTRIB ACCORDING TO NEG. BINOMIAL DISTRIB -
  ! PROBS CALC. IN SUBROUTINE BINOM
  ! MAX OF 6 DIFFERENT BULB TYPES
  DIM MASS(6)
  MAT READ MASS
  DATA 1,2,3,4,5,10      !**CHK BULB MASS
  ! MAX OF 12 BULBS PER MODEL CELL
  DIM BULB(12)
  DIM BFATE(12)
  DIM HT(3)
  MAT READ HT
  ! HANDLING TIME IN MINUTES - CHK VALUES ***
  DATA 2.7,3.7,4  ! BIG BULBS NEED TO BE FREED ETC.
  CALL BINOM(BNUM)

  PRINT "BULBS IN CELL.. ",DAYS,BNUM
  MAT BULB = 0
  ! BULB FATES: 0=NO BULB, 1=EATEN, 2=STORED
  MAT BFATE = 0
  FOR i = 1 TO BNUM
    LET XX = RND
    ! 1=SMALL BULB = 1g, 2=MEDIUM,3=LARGE
    !FRQ. OF DIFFERENT BULB SIZES FROM SPINKS DATA
    IF XX < 0.71 THEN
      LET BULB(i) = 1
      LET BFATE(i) = 1
    ELSE IF XX < 0.82 THEN
      LET BULB(i) = 2
      !50% CHANCE OF EITHER FATE - CAN BE MODIFIED LATER IF REQ.
      IF XX < 0.77 THEN LET BFATE(i) = 1 ELSE BFATE(i) = 2
    ELSE IF XX < 0.86 THEN
      LET BULB(i) = 3
      !50% CHANCE OF EITHER FATE - CAN BE MODIFIED LATER IF REQ.
      IF XX < 0.84 THEN LET BFATE(i) = 1 ELSE BFATE(i) = 2
    ELSE IF XX < 0.89 THEN
      LET BULB(i) = 4
      !50% CHANCE OF EITHER FATE - CAN BE MODIFIED LATER IF REQ.
      IF XX < 0.875 THEN LET BFATE(i) = 1 ELSE BFATE(i) = 2
    ELSE IF XX < 0.9 THEN
      LET BULB(i) = 5
      !50% CHANCE OF EITHER FATE - CAN BE MODIFIED LATER IF REQ.
      IF XX < 0.895 THEN LET BFATE(i) = 1 ELSE BFATE(i) = 2
    ELSE
      LET BULB(i) = 10
      LET BFATE(i) = 2
    END IF
  NEXT i

  FOR i = 1 TO BNUM

  ! ** CLASSIFYING BULBS AS SMALL, MED. OR LARGE
    LET BB = BULB(i)
    IF BB <= 1 THEN   !SMALL
```

```
      LET BB = 1
    ELSE IF BB <= 5 THEN   !MEDIUM
      LET BB = 2
    ELSE
      LET BB = 3    !LARGE
    END IF

    IF BFATE(i) = 1 THEN
   ! CHANGE TO INCLUDE ACTUAL MASSES IN CATS ABOVE
   !   LET EAT(DAYS) = EAT(DAYS) + MASS(BB)
     LET EAT(DAYS) = EAT(DAYS) + BULB(i)
     LET HANDLE(DAYS) = HANDLE(DAYS) + HT(BB)
    ELSE
     !BULB RETURNED TO NEST AND STORED
     LET STORE(DAYS) = STORE(DAYS) + MASS(BB)
     LET NESTTRIP(DAYS) = NESTTRIP(DAYS) + 2*NESTDIST
     IF BB = 3 THEN
      !TIME TO FREE BIG BULBS
      LET HANDLE(DAYS) = HANDLE(DAYS) + HT(BB)
     END IF
    END IF
  NEXT i
  !PRINT TAB(22,40);DAYS;EAT(DAYS);STORE(DAYS)

  IF DAYS = TDAY AND PFLAG = 0 THEN
   LET PFLAG = 1
  OPEN #3:NAME "C:\MOLES\ACTIVITY.OUT",ORGANIZATION TEXT
  SET #3: POINTER BEGIN
  ERASE #3
  PRINT #3: "DAILY ACTIVITIES BY MOLES"
  PRINT #3: "DAY, TOTAL HANDLING TIME, TOTAL DISTANCE TO STORE BULBS"
    FOR i = 1 TO TDAY-1
     PRINT #3:i,HANDLE(i),NESTTRIP(i)
     !PRINT TAB(17,2);"HT...";i,HANDLE(i),NESTTRIP(i)
     LET THANDLE = THANDLE + HANDLE(i)
     LET TTRIPS = TTRIPS + NESTTRIP(i)
    NEXT i
   PRINT #3
   PRINT #3:"TOTALS ",THANDLE,TTRIPS
  CLOSE #3
  END IF

END SUB

SUB EGAIN(TDAY, NUMOLES, EAT(), STORE(),DGAIN(),TOTGAIN)
  LET EVAL = 14.3     !* STEINKOPF - BULBS = 14.3 KJ/G
                !* SL  17.3 kJ/G
  FOR i = 1 TO TDAY
    LET TOTEAT = TOTEAT + EAT(i)
    LET TOTSTORE = TOTSTORE + STORE(i)
  NEXT i
  OPEN #2:NAME "C:\MOLES\EGAIN.OUT",ORGANIZATION TEXT
  SET #2: POINTER BEGIN
  ERASE #2
```

```
  PRINT #2: "GROSS ENERGETIC GAIN BY MOLES"
! PRINT #2: "DAY, TOTAL BIOMASS EATEN, TOT BIOM STORED, TOT PER MOLE"
  PRINT #2: "DAY, TOTAL ENERGETIC GAIN PER MOLE - IN KJ"
  ! COUNTERS
  LET C50,C100,CT50,CT100 = 0
  FOR i = 1 TO TDAY
    ! PRINTING RESULT IN GRAMS
    ! PRINT #2:i,EAT(i),STORE(i),(EAT(i)+STORE(i))/NUMOLES
    ! PRINTING RESULT IN kJ
    LET DEAT = (EAT(i)*EVAL)/NUMOLES
    LET DGAIN(i) = ((EAT(i)+STORE(i))*EVAL)/NUMOLES
    IF DEAT < 50 THEN LET C50 = C50 + 1
    IF DEAT < 100 THEN LET C100 = C100 + 1
    IF DGAIN(i) < 50 THEN LET CT50 = CT50 + 1
    IF DGAIN(i) < 100 THEN LET CT100 = CT100 + 1

    PRINT #2:i,((EAT(i)+STORE(i))*EVAL)/NUMOLES

  NEXT i
  LET TOTGAIN = EVAL*(TOTEAT+TOTSTORE)
  PRINT "TOTGAIN ";TOTGAIN
  PRINT "COUNTERS C50,C100,CT50,CT100"
  PRINT C50,C100,CT50,CT100
  PRINT #2
  PRINT #2:"TOTALS ",TOTEAT*EVAL,TOTSTORE*EVAL
  PRINT #2:"TOTAL ENERGETIC GAIN (kJ) ",TOTGAIN
  PRINT #2:"TOTAL ENERGETIC GAIN (kJ) PER MOLE ",TOTGAIN/NUMOLES
  CLOSE #2
END SUB

SUB
ELOSS(TDAY,NUMOLES,MOLMASS,DIG(),HANDLE(),NESTTRIP(),RAIN(),DGAIN(),TOTLO
SS)
  DIM EMINUS(100)
  LET CONV = 0.014309       ! CONVERTING MG.O TO KILO JOULES
  LET BASAL = 0.68          ! FROM HAIM & FAIRALL 1986
  ! BASAL METABOLIC RATE IN UNITS OF JOULES.MOLERAT.HOUR
  LET BASAL = BASAL * CONV * MOLMASS
  ! *** METABOLIC RATES FOR RUNNING & HANDLING FOOD - 2XBASAL = 1.36 ***
  LET MHAND = 1.36
  LET MRUN = 1.36
  LET MHAND = MHAND * CONV * MOLMASS
  LET MRUN = MRUN * CONV * MOLMASS

  LET TOTLOSS = 0
  FOR i = 1 TO TDAY
  !** LOVEGROVES (1989) ESTIMATES FOR DIGGING IN SOFT SOIL = 5.02XBASAL = 3.41
  ! & IN DRY SOIL = 4.53XBASAL = 3.08
  ! ######## NOTE - CAN CHANGE METABOLIC RATES FOR RUNNING ETC
    IF RAIN(i) = 1 THEN
      LET MDIG = 3.41
    ELSE
      LET MDIG = 3.08
    END IF
```

```
      LET MDIG = MDIG * CONV * MOLMASS
      ! CONVERT MINUTES TO HOURS
      LET DAILYT1 = DIG(i)/60
      LET DAILYT2 = (HANDLE(i)+NESTTRIP(i))/60
      LET DAILYT = DAILYT1 + DAILYT2
      ! BALANCE OF TIME IN BASAL RESTING STATE
      LET TTIME = 24*NUMOLES
      LET BALT = TTIME-DAILYT
      LET EMINUS(i) = DAILYT1*MDIG + DAILYT2*MRUN + BALT*BASAL
      LET TOTLOSS = TOTLOSS + EMINUS(i)
!      PRINT "e LOSS ";i,EMINUS(i)
   NEXT i
   OPEN #5:NAME "C:\MOLES\ELOSS.OUT",ORGANIZATION TEXT
   SET #5: POINTER BEGIN
   ERASE #5
   PRINT #5: "GROSS ENERGETIC LOSS BY MOLES"
   PRINT #5: "DAY, TOTAL ENERGETIC EXPENDITURE, PER CAPITA EXPENDITURE"
   LET CNET = 0
   FOR i = 1 TO TDAY
      LET DLOSS = EMINUS(i)/NUMOLES
      IF DLOSS > DGAIN(i) THEN LET CNET = CNET + 1
      PRINT #5:i,EMINUS(i),EMINUS(i)/NUMOLES
   NEXT i
   PRINT "ELOSS > ENET = ";CNET
   PRINT #5
   PRINT #5:"TOTAL LOSS (IN JOULES) ",TOTLOSS
   PRINT #5:" AVE DAILY ENERGETIC EXPENDITURE ",TOTLOSS/TDAY
   CLOSE #5
END SUB

SUB LIMITS(DIGT,SHAND,STRIP,ATIME)
   LET CELLTIME = 0.01    !*** NOTE CHK VALUE = TIME TO RUN THRU 1 CELL
   LET RTIME = STRIP * CELLTIME
   ! TOTAL TIME = BURROW TIME+HT+STORAGE TRIP TIME
   LET ATIME = DIGT + SHAND + RTIME
END SUB

SUB BINOM(BNUM)
! NEG BINOMIAL - USED TO DESCRIBE SPATIAL DISTRIBUTION OF BULBS
! NOTE:  INCREASING K CHANGES DISTRIB FROM CLUMPED TO MORE EVEN
LET K = 1
LET DENS = 75
LET XBAR = 75/16    !MEAN DENS PER 0.25M2
DIM PX(12)
!CLEAR
!SET WINDOW 0,10,0,0.5
FOR X = 0 TO 11
   LET FACT1 = 1
   LET FACT2 = 1
   FOR N = 1 TO X
    LET FACT1 = FACT1 * N
    LET FACT2 = FACT2 * (K+N-1)
   NEXT N
   LET FACT3 = 1
```

```
   FOR N = 1 TO (K-1)
      let fact3 = fact3*(N)
   next n
!  PRINT X,FACT1,FACT2,FACT3
   LET M1 = (1+(XBAR/K))^(-K)
   LET M2 = FACT2/(FACT1*FACT3)
   LET M3 = (XBAR/(XBAR+K))^X
   LET PX(X+1) = M1*M2*M3
   ! ** PX IS PROBABILITY OF FINDING X BULBS IN MODEL CELL R,C
  ! PRINT X,
  ! PRINT USING "#.###":PX(x+1)
  ! PLOT X,PX(x+1);
NEXT X
DIM PCUM(12)
LET PCUM(1) = PX(1)
FOR i = 2 TO 12
   LET PCUM(i) = PCUM(i-1) + PX(i)
NEXT i
!MAT PRINT PX
!MAT PRINT PCUM

   LET XX = RND
   IF XX < PCUM(1) THEN
     LET BNUM = 0
   ELSE IF XX < PCUM(2) THEN
     LET BNUM = 1
   ELSE IF XX < PCUM(3) THEN
     LET BNUM = 2
   ELSE IF XX < PCUM(4) THEN
     LET BNUM = 3
   ELSE IF XX < PCUM(5) THEN
     LET BNUM = 4
   ELSE IF XX < PCUM(6) THEN
     LET BNUM = 5
   ELSE IF XX < PCUM(7) THEN
     LET BNUM = 6
   ELSE IF XX < PCUM(8) THEN
     LET BNUM = 7
   ELSE IF XX < PCUM(9) THEN
     LET BNUM = 8
   ELSE IF XX < PCUM(10) THEN
     LET BNUM = 9
   ELSE IF XX < PCUM(11) THEN
     LET BNUM = 10
   ELSE IF XX < PCUM(12) THEN
     LET BNUM = 11
   ELSE
     LET BNUM = 12
   END IF

END SUB
```

Appendix II

Sperm motility parameters defined

DEFINITIONS

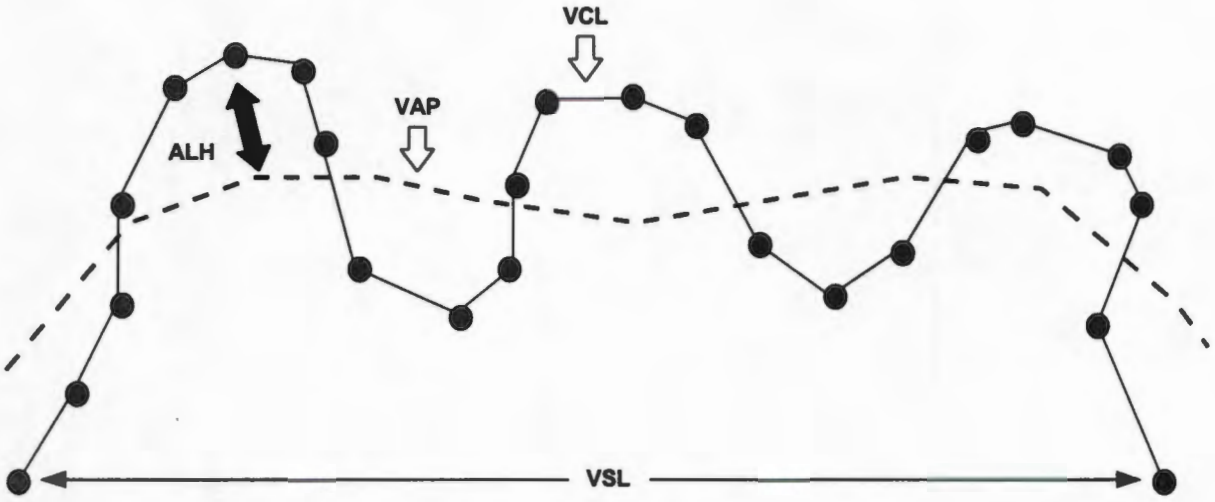

Figure II.1: Diagrammatic representation of sperm trajectory to illustrate several sperm motility parameters assessed in this thesis. The shaded grey circles indicate the points at which the sperm head position was fixed by the computer during image analysis. VCL = curvilinear velocity; VSL = straight-line velocity; VAP = average path velocity; ALH = amplitude of lateral head displacement.

The terminology used is internationally accepted and recently defined by Katz (1991) and now commonly used in the literature.

(A) Velocities

(1) Curvilinear velocity (VCL): time-averaged velocity of sperm head along its actual path or curvilinear trajectory (Figure II.1).

(2) Straight-line velocity (VSL): time-averaged velocity of sperm head as projected along the straight line between its first and final detection positions (Figure II.1).

(3) Average path velocity (VAP): time-averaged velocity of sperm head projected along its spatial average trajectory (Figure II.1).

(B) Ratios, amplitudes and frequencies

(4) Linearity (LIN): a ratio of projected length to total length of the curvilinear trajectory. The formula for LIN = VSL/VCL.

(5) Amplitude of lateral head displacement (ALH): maximum amplitude of lateral distances of the sperm head trajectory about its spatial average path (Figure II.1). Katz (1991) notes that there is no unique definition for ALH, even for a fixed definition of average path and it should be recognised that different sperm analysis systems measure it differently.

(6) Wobble (WOB): ratio of VAP to VCL and is an expression of the degree of oscillation of the curvilinear path about its spatial average path. The formula for WOB = VAP/VCL.

(7) Straightness (STR): ratio of VAP to VSL and is an expression of the straightness of the average path. The formula for STR = VAP/VSL.

(8) Dance (DNC): defined by the product of VCL and ALH, and describes sperm motion as the space occupied by the sperm head path during one second. The formula for DNC = VCL x ALH.

(9) Radian (RAD): by using the radian, which is the radius of the circle of which the total curvilinear track is an arc, circling sperm can be detected. When the average angle of curvature is 180° the RAD is 3.14 and 6.28 when the average angle of curvature is

360°. The formula for RAD = (Radius/π) x 180°. This parameter gives information on the average angle at which sperm turn when motile.

(10) Curvature (CURV): reflects progressiveness of movement and is reflected in the curve 0-1. The smaller the curve 0-1, the straighter the sperm path and the higher its progressiveness. This parameter also gives information on the mode of movement and a value > 0.5 will indicate sperm swim in a circular mode. The formula for CURV = 1 - (VSLpath/VCLpath). Both RAD and CURV are new parameters and have previously been used in semi-automatic analysis by Samuels & Van der Horst (1986). CURV helps to assess the form of the sperm path whereas RAD assess how sperm attain this. Virtually no research is available on these parameters and they seem to have great potential.

(C) <u>Percentage groupings</u>

(11) Percentage motile sperm (PM): percent motility of sperm population in field of view and represents all forms of motility from wiggling sperm to fast and highly progressively motile sperm.

(12) Percentage progressively motile sperm (PPM): only sperm that swim in a progressively forward direction with a LIN > 30%, VAP > 20 $\mu m.s^{-1}$, VCL > 30 $\mu m.s^{-1}$.

Sections (A) and (B) represent swimming characteristics of each individual sperm in a given field, whereas (C) represents an overall view of the motile status of the sperm population in a given field. The above 12 parameters can also be divided into different classes based on functionality:

(1) *Vigour of motility*: VCL; VSL; and VAP.

(2) *Pattern of motion*: LIN; STR; WOB; ALH; DNC; CURV; and RAD.

(3) *Overall population motility*: PM and PPM.

(4) *Progressiveness of sperm movement*: LIN; STR; CURV; and RAD.