The Energetics of Sociality in the Molerats (Bathyergidae)

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Abstract

Primarily, this thesis attempts to resolve the debate concerning the factors selecting for the characteristic physiological traits of subterranean rodents. It also isolates the the probable causes of eusociality within the molerats (Bathyergidae). The bathyergids display the widest range of sociality of all mammals, from strictly solitary genera (*Bathyergus, Georychus, Heliophobius*), to social and eusocial genera (*Cryptomys* and *Heterocephalus*). Sufficient ecological data on key species (e.g. *Cryptomys damarensis*) were obtained to confirm trends in resource distributions associated with an aridity gradient and increasing sociality. This included data on resource characteristics, seasonal soil and burrow temperature regimes, burrow structures, colony structures, and the activity patterns of *C. damarensis*. Thermoregulation, including measurements of body temperature (T_b) and resting metabolic rates (RMR), was investigated for *Bathyergus, Cryptomys*, and *Georychus*, and compared with data from other workers obtained for *Heterocephalus* and *Heliophobius*. The cost of burrowing was measured for *C. damarensis* and *H. glaber*. A model was constructed which investigated the probabilities (risks) of successful foraging as a function of resource dispersion patterns and group size.

The ecological data confirmed a trend of increasing food specialisation (geophytes) with increasing sociality, as habitats become more arid and geophytes become increasingly larger and more widely distributed. The physiological data showed that all bathyergids have T_bs and RMRs significantly lower than those of aboveground rodents and some subterranean rodents. Importantly, the bathyergids tend to scale RMR virtually independently of mass (termed here Risk-Sensitive Metabolism). Soil moisture played an important role in the cost of burrowing. The bathyergids have the largest metabolic scope for burrowing (*ca.* 5 x RMR) of all subterranean rodents and insectivores studied. The model showed that the low probabilities and high energetic demands of locating food, are the most important causes of sociality, and that the physiological traits can best be explained as a means of a) reducing the costs of burrowing and daily energy expenditures of individuals and whole colonies, b) facilitating worker differentiation and polyethism, and c) achieving an optimal group size related to resource characteristics. Little support was found for physiological traits selected for by hyperthermia constraints.

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Table of contents

CHAPTER ONE

Introduction

Introduction

The class Rodentia is represented by seven families of rodents which have radiated underground (Ellerman 1956, Nevo 1979). These are the pocket gophers (Geomyidae) of North America, the voles (Cricetidae) of Asia, the bamboo rats (Rhizomyidae) of Asia and east Africa, the octodonts (Octodontidae) and tuco-tucos (Ctenomyidae) of South America, and the molerats (Spalacidae and Bathyergidae) of Asia, parts of Europe, and Africa. Most aspects of these subterranean rodents have been comprehensively reviewed by Nevo (1979). In defining terms, Nevo (1979) differentiates between "fossorial" species, those subterranean rodents which spend most of their lives in sealed burrows coming to the surface only incidently, or to feed, and completely subterranean rodents which seldom, if ever, venture to the surface.

The following is a short overview from Nevo (1979). The predictability and constancy of the microclimatic features of sealed burrow systems, such as temperature, relative humidity and darkness, are consistently greater than those for aboveground habitats. Furthermore, although less reliable data are available, it has also been suggested that biotic pressures, such as food supply, low predation and parapatry, are also very predictable. In short, the subterranean ecotope can be considered as simple, stable, highly specialised, and predictable. These features have selected for a high degree of convergence determined primarily by specialisation, competition and isolation both within and between subterranean species. The morphological specialisations adaptive to living and burrowing underground include structural developments of the incisors, forelimbs, pectoral girdle, claws, sense organs and pineal gland, as well as structural reductions of limbs, tail, eyes and external ears.

Most interspecific variation of these specialisations are a consequence of phylogenetically determined burrowing styles. For instance, some subterranean rodents shear soil loose exclusively with the incisors (Spalacidae and Bathyergidae, except *Bathyergus*), whereas the others use a combination of the forefeet and the incisors. Excavated soil is either pushed along the burrow with the head and snout (Spalacidae) and forefeet (Geomyidae), or is pushed backwards with sweeping motions of both the hind- and forefeet (Bathyergidae). Molehills are constructed in the same way. The subterranean rodents are all herbivorous, and are forced to burrow to locate food. They eat a variety of subterranean corms, bulbs, tubers and roots, as well as aerial stems, leaves, flowers and grasses. Most are apparently food generalists, particularly in habitats where production and food quality is low, with limited food specialisation occurring in habitats where resources have a higher abundance and nutritional rank.

Generally, subterranean rodents are solitary, parapatric, and highly territorial, defending home ranges of up to 1000 m^2. Male/female sex ratios are in favour of females ranging from 0.25 - 0.5, and population densities range from 1 - 60 animals.0.4ha^{-1}. A few species are colonial (*Ctenomys peruanus, C. minitus* and *Spalacopus cyanus*), whereas two genera (*Cryptomys* and *Heterocephalus*) are highly social and display caste structures (see also Bennett & Jarvis 1987). In this respect *Heterocephalus glaber* is a fascinating animal (Jarvis 1978, 1981, 1985; Brett 1986). It represents the sole species of one of the five genera of the family Bathyergidae, and has a colony size of approximately 60 animals, although as many as 296 animals have been recorded in one colony (Jarvis 1985, Brett 1986). Jarvis (1981) has identified two worker castes in the colony. The "worker" caste consists of the smaller animals (mean mass = 28 g) in the colony, whereas the "infrequent workers" are significantly larger (mean mass = 35 g). The infrequent workers include the single breeding female, the largest molerat in the colony (*ca.* 53 g), that never partakes in worker duties or foraging. Those molerats destined to remain in the worker caste permanantly have very slow growth rates, whereas other workers display polyethism in that they are capable of suddenly commencing a change of caste accompanied by a progressive increase in growth rate (Jarvis 1981). Jarvis (1981) has proposed that the eusociality displayed by *H. glaber*, the most conclusive case amongst the mammals, is analagous to that of the eusocial diploid termites (Isoptera).

Interestingly, it has very recently been suggested (Bennett & Jarvis 1987) that *Cryptomys damarensis* displays many social features analagous to those of *H. glaber*. With the exception of *C. hottentotus* which is also social, and possibly also a few other cryptomyids about which little is known, the other bathyergids are all strictly solitary. The Bathyergidae is comprised of five genera, namely *Heterocephalus*, *Cryptomys* (*ca.* 10 species, but taxonomy confusing), *Bathyergus* (two species), *Georychus* (one species), and *Heliophobius* (three species) (Nevo 1979, De Graaff 1981). Generally, the solitary genera are the largest (150 - 1500 g), whereas the two social genera tend to be small (28 - 200 g). As such, the bathyergids are an interesting family in that they display the greatest range of body sizes, and complexity of social organisation of all the subterranean rodents.

Undoubtedly one of the most controversial topics concerning the subterranean rodents is their physiology (e.g. McNab 1966, 1979a; Jarvis 1978; Vleck 1979, 1981; Withers & Jarvis 1980; Contreras 1986). Subterranean rodents display mass-specific resting metabolic rates (RMR) and body temperatures (T_b) that are lower than those of aboveground rodents (see McNab 1979a for review). McNab (1979a) also insists that all subterranean rodents display a higher than normal thermal conductance (C_m), particularly if they inhabit warm burrows. Not surprisingly, *H. glaber* exemplifies the extremes of these traits. With the exception of a few scattered, tactile, sinusoidal hairs, it is completely hairless (Thigpen 1940). It has a body temperature of 31 - 32°C at thermoneutrality, a RMR which is 43 % of that predicted for a rodent of its size, an extremely high thermal conductance, and is virtually incapable of maintaining homeothermy below ambient temperatures of 20°C (McNab 1966, Jarvis 1978, Withers & Jarvis 1980).

The controversy, mentioned earlier, concerns the factors selecting for these traits and their adaptive significance. There are two main viewpoints. McNab (1966, 1979a) published two definitive papers in which he argues that the traits displayed by subterranean rodents are primarily a consequence of the need to reduce the likelihood of "overheating", or hyperthermia, in warm, closed burrows. He maintains that "...basal metabolic rate is modified to assure an appropriate balance between heat production and loss, and that if these requirements extend over some appreciable range in mass, the power of the metabolism-mass function will be adjusted to that of the conductance-mass function". He also states that "...the interaction of body mass, rate of metabolism, and thermal conductance is dictated by the necessity to prevent overheating in a closed burrow...".

These papers have been criticised (e.g. Jarvis 1978; Vleck 1979, 1981) primarily for failing to consider the energetic constraints of foraging faced by subterranean rodents. This is ironical in one sense, because McNab (1969, 1974, 1978a, 1978b, 1984, 1986) is also an ardent advocate of the hypothesis that food habits are important in selecting for the RMRs of aboveground animals. McNab's critics argue that selection for low RMRs can be better explained as a means of reducing energy expenditure, given the various energetic constraints of subterranean foraging. Having measured the cost of burrowing in *Thomomys bottae*, Vleck (1979) suggested that "...a low metabolic rate and a low conductance are useful adaptations because they combine to reduce energy expenditure for maintenance activities...", and that they "...may not be primarily a result of thermoregulatory adaptations but may be mandated by the high cost-benefit ratio of their mode of foraging and the resulting pressure of energy conservation". Vleck (1979) concluded that "...the energy constraints imposed by the fossorial niche provide a better explanation of the body size and energy metabolism than do possible thermoregulatory reasons". In a similar argument, Jarvis (1978) cautioned that "...both temperature and food resources must be considered when seeking an explanation for the unique features found in *Heterocephalus*". She has proposed that in the arid habitats of Kenya, food is limiting to *H. glaber*, and that consequently there has been selection for physiological and social parameters which ensure a low energy expenditure of the whole colony. Furthermore, Jarvis (1985) points out that within the family Bathyergidae sociality appears to increase with aridity, and suggests that some answers as to why *H. glaber* is so highly social will probably be found through studying other genera of molerats living in both mesic and xeric regions of southern Africa. Brett (1986) has recently completed a field study on *H. glaber*, and although he did not undertake physiological studies, he supports the arguments presented by those advocating the "energy conservation" hypothesis.

The purpose of this thesis was primarily to attempt to resolve this debate, and at the same time to isolate the factors influencing sociality and the physiological traits of the bathyergids. The trend of increasing sociality with aridity noted by Jarvis (1985) is quite obvious. The largest, solitary genera, *Bathyergus* and *Georychus*, occur within the winter rainfall mediterranean region of the Cape Province, South Africa (De Graaff 1981). *Cryptomys*, the genus intermediate in sociality between the solitary species and *H. glaber*, occurs in both mesic (Cape Province) and arid

(Kalahari Desert, South Africa, Namibia and Botswana) regions (De Graaff 1981). *H. glaber* occurs in Kenya, in arid regions with an annual rainfall less than 400 mm (Jarvis 1985, Brett 1986). Although some ecological data is available for *H. glaber* (Brett 1986) and for the solitary species *Bathyergus suillus* (Davies & Jarvis 1986) and *Georychus capensis* (Du Toit *et al.* 1985, Lovegrove & Jarvis 1986), very little information is available on the species of intermediate sociality. Consequently, I concentrated my ecological studies on *Cryptomys damarensis* (Chapters Two - Four). I regard this species to be the 'key intermediate species' in establishing the causes of sociality in the bathyergids. It is a social species with a structured colony of 15 - 25 animals (Bennett & Jarvis 1987). It has a body size of 100 - 200 g (*op. cit.*) and occurs throughout the extent of the Kalahari Desert.

The approach taken in this study represents an attempt to amalgamate physiological data with ecological trends and to integrate both sets of data with habitat-specific constraints of foraging, such as the probabilities of locating subterranean food resources. I have investigated the physiology of the three unstudied genera, *Bathyergus*, *Georychus* and *Cryptomys* (Chapters Five - Seven), and together with data from *H. glaber* (McNab 1979a, Withers & Jarvis 1980) and *Heliophobius argenteocinereus* (McNab 1979a), have evaluated the metabolic allometry for the whole family. Considering the importance of the cost of burrowing in the debate, I have investigated the burrowing energetics of *C. damarensis* and *H. glaber*, and have compared these data with those for *G. capensis* (Du Toit *et al.* 1985) in Chapter Eight. Finally, I have developed a model which investigates the probabilities of successful foraging, given particular resource distribution characteristics (Chapter Nine), and have used this model to evaluate the survivorship potential, or fitness, of molerats as a function of sociality (group size), RMR, resource distribution characteristics, and the thermal regime of closed burrows (Chapter Eleven).

CHAPTER TWO

Food Resources of *Cryptomys damarensis*: Abundance, Quality and Spatial Distribution.

Introduction

The choice of *C. damarensis* as "key intermediate species" has highlighted the paucity of information on the ecology and natural history of this species. De Graaff (1972) provides an account of the most basic ecological information, whereas Bennett & Jarvis (1987) have very recently reported on the the colony structure and reproduction of this species. Fortunately, considerably more ecological and dietary data are available for those molerat species which represent the two extremes of bathyergid sociality, namely for the eusocial *H. glaber* (Jarvis 1978, 1985; Brett 1986), and for solitary species such as *G. capensis* (Du Toit *et al.* 1985, Lovegrove & Jarvis 1986) and *B. suillus* (Davies & Jarvis 1986). The following three chapters report on various field studies on *C. damarensis* undertaken in the Kalahari Gemsbok National Park (KGNP), South Africa. I have attempted to provide sufficient ecological data on *C. damarensis* to establish whether any meaningful patterns and trends exist which may assist in explaining the trend towards sociality with increasing aridity (Jarvis 1985). These chapters are not intended to provide a comprehensive overview of the ecology of this molerat, but merely to provide sufficient data with which to address the debate outlined in Chapter One.

This chapter examines the resource characteristics of *C. damarensis* in the southern Kalahari. Primarily it concerns food abundance, quality, and the nature of the spatial distribution of the resource. During the course of the field work, many interesting and unusual aspects of the ecology of this species emerged, but for the purposes of this thesis they can not be pursued here.

Methods

Field work was undertaken at two sites near Nossob camp (25°S, 20°E), KGNP, during January 1986. Molerat colonies were located by driving transects approximately 10 km east and west of the Nossob camp. Two study sites were selected. The first (Nossob site) was situated on the east bank of the Nossob River, approximately 0.3 km from the riverbed. The second site (Dune site), was situated in the sand dunes approximately 9.5 km west of the Nossob camp.

The Nossob site was generally flat, bordered in the east by red sand dunes, and in the east by the riverine *Rhigozum* plant communities. The vegetation at this site is well described by Leistner (1967) for "compact pink and white sands". The dominance of *Dipcadi gracillimum* Bak., together with the marked lack of grasses (Fig. 1), suggest that the site is subject to heavy overgrazing (Leistner 1967). The characteristic plants at this site were *Acacia erioloba* E.

Fig. 1. The stems and seed-pods of *Dipcadi gracillimum* at the Nossob site. Note the lack of grasses possibly suggesting overgrazing.

Mey., *Rhigozum trichotomum* Burch., *Acacia mellifera* (Vahl) Benth. and *Monechma incanum* (Nees)C.B. CL. The 'good' December 1985 rainfall of 51.9 mm (M. Knight pers. comm.) had stimulated the growth and seeding of *D. gracillium* (Fig. 1), thereby providing a clear indication of the potential densities of the bulbs of this species.

To sample areas that appeared to have the highest and lowest densities of *D. gracilimum* bulbs, two transects were subjectively selected in close proximity to one burrow system. Ten 1 x 1 m quadrats were dug to a depth of 0.3 m at 3 m intervals along each transect (Fig. 2). The sand from each quadrat was sieved with a 5 mm sieve, and all geophytes collected were immediately placed in labelled plastic bags to reduce dessication. All samples were analysed later the same day at Nossob camp. Therefore, a total of 6 m^3 of sand with an estimated mass of 12000 kg was sampled. All bulbs collected from each quadrat were subjectively separated into four size classes. Each size class was counted and weighed (0.01 g).

The vegetation at the Dune site is described by Leistner (1967) for "non-calcereous red sands and dune slopes". On a large scale the area is characterised by parallel ridges of sand dunes lying in a north-westerly orientation (Leistner 1967) on average 229 m apart and 31 m high (Lewis 1936). The dunes are separated by sandy dune valleys or *strate*

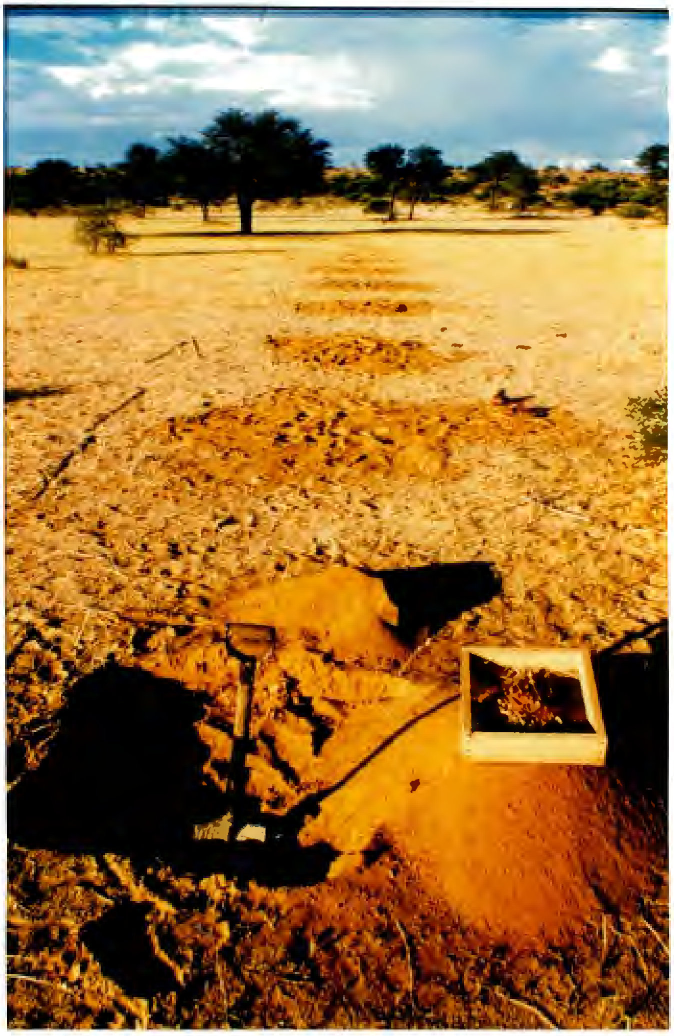


Fig. 2. Transect A at the Nossob site, showing the evenly spaced 1 x 1 m quadrats dug to a depth of 0.3 m and sieved.

(Leistner 1967). Typically, the dune slopes are vegetated with *Stipagrostis* and *Eragrostis* grasses, whereas the dune valleys tend to support microphanerophytes and nanophanerophytes such as *A. mellifera*, *A. haematoxylon* Willd. and *Boscia albitrunca* (Burch.) Gilg et Benedict (Fig. 3). The tubers of the Gemsbok cucumber *Acanthosicyos naudinianus* (Sond.) C. Jeffrey (Fig. 4), were by far the most common geophytes at this site. The subterranean presence of individual tubers of *A. naudinianus* could easily be established by the long surface 'runners' characteristic of this plant (Leistner 1967).

In three dune valleys in close proximity to each other (< 1 km), which showed abundant signs of molerat colonies, stratified sampling was conducted. Two sampling procedures were used. The objective of the first procedure was to measure the dispersion pattern and abundance of *A. naudinianus* tubers. Each dune valley was divided into seven distinct zones according to aspect and slope, similar to those used by Nel & Rautenbach (1975). These zones represented the dune crests (C zone), the east- and west-facing steep slopes (SSE and SSW zones), the east- and west-facing gentle slopes (GSE and GSW zones), and the flat zone in the trough of the dune valley (F zone). Because of the relatively widely dispersed nature of *A. naudinianus* tubers, large 30 x 10 m quadrats were marked out with ropes and metal stakes in each zone of each dune valley. The quadrats

Fig. 3. A typical dune valley adjacent to the Dune site. Note the trees *Acacia haematoxylon*, *A. erioloba*, and *A. mellifera* in the valley. Herds of ungulates, such as the gemsbok *Oryx gazella* shown, can cause extensive trampling and burrow collapse if burrows are situated at shallow depths (Chapter Three).

Fig. 4. The long carrot-shaped tubers of the Gemsbok cucumber *Acanthosicyos naudinianus* excavated from the Dune site. Ostrich egg for scale.

therefore represented a total sample area of 6300 m^2. Within each quadrat, the distance from the stalk on the top of every tuber to the stalk of its nearest neighbour was measured (1 cm). Measurements were made even if the nearest neighbour lay outside the quadrat. This procedure also gave the density of tubers in each quadrat.

Nearest-neighbour measurements were used to calculate a statistic of randomness, *R*, for each quadrat (Clark & Evans 1954). This statistic is a measure of the spatial relationship in populations, and can have a value $0 < R < 2.15$, where $R = 0$ indicates complete aggregation, $R = 1$ a comletely random distribution, and $R = 2.15$ a completely uniform distribution. The normal curve is then used to test whether the observed mean nearest-neighbour distance, r_A, departs significantly from the expected mean nearest-neighbour distance, r_E, for a random distribution. Simberloff (1979) has shown that when the diameters of the objects being measured is large, such that the ratio of object diameter to r_A approaches 0.5, or greater, the assumptions of the Clark & Evans (1954) procedure are violated, and *R* is overestimated. In such instances a correction procedure must be used (Simberloff 1979). In this study the ratio of tuber diameter to r_A was approximately 0.04, so I have assummed that tuber diameter had no influence on *R*.

The objective of the second sampling procedure was to identify the presence and abundances of non-sprouting *A. naudinianus* tubers, as well as any other geophyte species on which the molerats could potentially feed. Using the same sieving procedure as that decribed for the Nossob site, five 1 x 1 m quadrats were dug to a depth of 0.3 m at 6 m intervals within each 10 x 30 m quadrat described above.

In addition to the above two sampling procedures, a sample of tubers was excavated at random from all zones for mass and size measurements. Excavated tubers included tubers that showed indications of having been partially eaten by molerats within the previous six months. This was subjectively judged from the extent of healing of the bark. Eaten tubers could be located and excavated within close proximity to the characteristic feeding mounds thrown up by the molerats (Chapter Three). At the Nossob camp all tubers were weighed and measured (0.01 g and 1 mm). Measurements taken were tuber length, the top diameter, the maximum diameter (invariably measured near the middle of the tuber), and the base diameter (measured immediately dorsal to the start of the tap-root). Least-squares fit (Zar 1974) were performed on all diameter data of uneaten tubers as a function of their mass.

For the chemical analyses, samples were first weighed, and then oven dried at 60°C to constant mass. For *D. gracilimum* a sample size of 20 - 30 bulbs from each size class was used, whereas for *A. naudinianus*, sections 4 - 5 cm long were cut fron the middle of the tuber. Some of these sections were then further separated with a sharp knife into three components representing the outside bark, the parenchyma, and the pith. Three 0.5 g subsamples of each homogenised sample were then used to measure the protein content by the Kjeldahl method (Horwitz 1970), and the fibre content (neutral detergent fibre) using a Fibre-Tec 1020 apparatus according to the method of Von Soest (1964). The calorific content of 1 g samples of homogenised whole tuber sections was measured with a CP500 bomb calorimeter.

Results

An interesting aspect of the geophyte sampling at both sites was the remarkable dominance of one species of geophyte per site. All bulbs from the Nossob site were *D. gracillimum*. This species has small onion-like bulbs with a mass of 0.41 - 5.17 g (Table 1), and they only occur in the top 15 cm of sand. The mean ± SD density of these bulbs in the "low density" transect A was 39.9 ± 21.12.m^{-2}, in contrast to the "high density" transect B which had a density of 117.90 ± 22.04.m^{-2} (Table 1). There were significant differences ($p < 0.01$, Student's *t*-test) between the mean masses of each size class in each transect, but there were no significant

Table 1. The mean masses, densities, and biomasses, of four size classes of *Dipcadi gracillimum* bulbs sieved from 10 x 1 m^2 quadrats from each of two transects at the Nossob site.

Transect	Size class	Density ($No.m^{-2}$)		Mass (g)		Biomass ($g.m^{-2}$)	
		Mean	± SE	Mean	± SE	Mean	± SD
A	1	3.20	2.49	5.17	0.59	16.37	12.95
A	2	7.00	5.70	3.03	0.47	17.33	11.70
A	3	7.80	4.61	1.59	0.32	12.41	7.53
A	4	22.94	13.85	0.41	0.08	9.33	5.26
		39.90				55.44	
B	1	6.50	2.92	4.78	0.65	30.83	12.31
B	2	8.80	3.01	2.85	0.48	25.09	9.81
B	3	15.10	6.38	1.65	0.10	23.86	12.60
B	4	87.50	21.53	0.43	0.08	38.23	13.41
		117.90				118.01	

differences ($p > 0.01$, Student's t-test) between equivalent size classes between transects.

In transect A, the two largest size classes together made up the highest percentage by mass (60.79 %) of the total sample, although they only made up 25.56 % of the total number of bulbs in the total transect A sample (Table 1). In transect B, however, the two largest classes made up 47.38 % of the total mass of the sample, whereas the smallest sample alone made up 32.40 % of the total quadrat mass (Table 1). Therefore, despite the fact that the overall number of bulbs in transect B was nearly three times higher than that of transect A, the mass of bulbs in transect B was only twice that of transect A. The biomass of bulbs in both transects ranged from 55.4 - 118 $g.m^{-2}$ (Table 1).

The only geophytes collected or sampled during both procedures at the Dune site were tubers of *A. naudinianus*. No non-sprouting tubers were recorded. The mean density of tubers from all zones from the Dune site was $0.165.m^{-2}$, with a range of 0.017 - $0.407.m^{-2}$ (Fig. 5), considerably lower than the densities of *D. gracillimum* bulbs at the Nossob site. The frequency distribution of tuber densities was heavily skewed towards densities lower than the mean tuber density (Fig. 5). However, the tubers were much larger than the bulbs having a mean mass for uneaten tubers of 670 ± 500

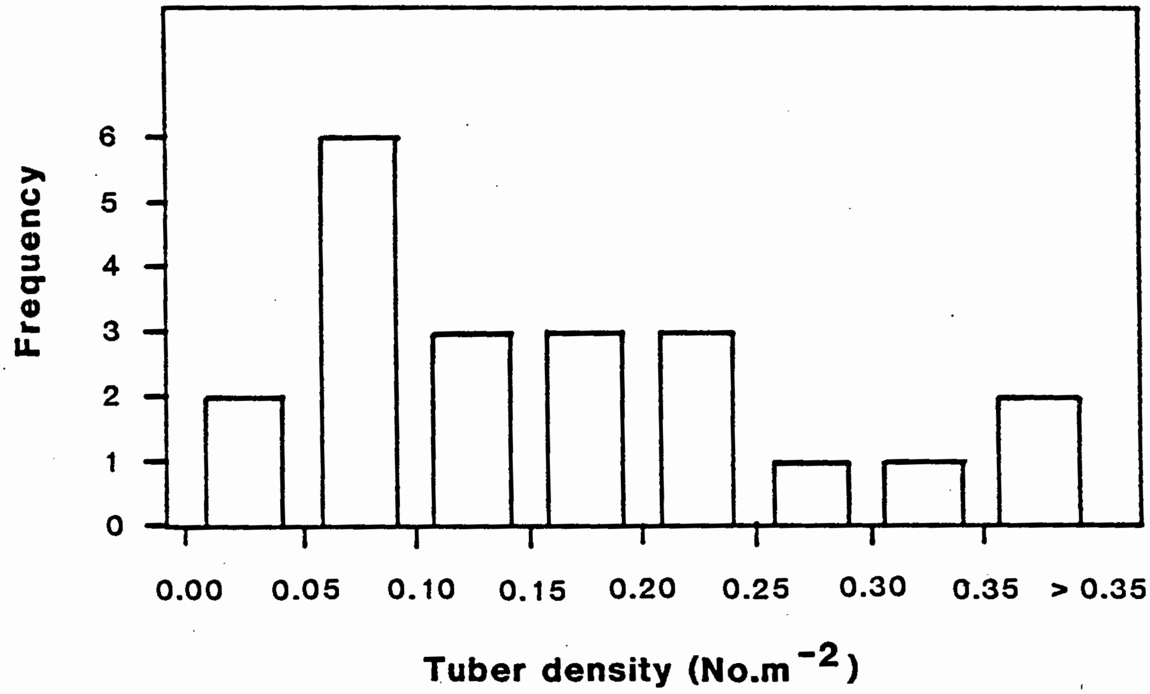


Fig. 5. Frequency distribution of densities of the tubers of *A. naudinianus* measured at the Dune site.

g. This gives an average biomass of 110.6 $g.m^{-2}$ for the site. A two-way ANOVA with replication (Zar 1974) showed that there was a significant interaction ($p < 0.01$, $F = 5.19$) between aspect (factor A) and slope (factor B) on the densities of tubers. There was no significant difference between the densities of tubers on the steep and gentle slopes ($p > 0.05$, $F = 0.76$), but the density of tubers on east-facing slopes was significantly higher ($p < 0.05$, $F = 9.85$) than the densities on west-facing slopes.

For the nearest-neighbour analyses, all quadrats with a density of tubers less than $0.100.m^{-2}$ i.e. 30 tubers per quadrat, were rejected from the analysis, because I considered the sample size to be too small for a meaningful calculation of the nearest-neighbour statistic. The remaining quadrats showed a random ($p < 0.05$) distribution for nine of the ten analyses, with values of R ranging from 0.916 - 1.045 (Table 2). The mean ± SE nearest-neighbour distance for all ten quadrats was 0.943 ± 0.145 m.

A total of 53 uneaten tubers and 30 eaten tubers were excavated and measured. The uneaten tubers had a mean mass of 670 ± 510 g, a mean top diameter of 3.79 ± 1.24 cm, a mean maximum diameter of 4.42 ± 1.52 cm, and a mean length of 60.02 ± 19.10 cm. The regression analyses of these data for uneaten tubers showed a positive correlation between tuber mass and the top diameter (D_{top}) of the tuber (Mass =

Table 2. Statistics of the dispersion patterns of the tubers of *Acanthisicyos naudinianus* in the dune valleys of the Kalahari Gemsbok National Park. Quadrat sizes were 30 x 10 m (300 m^3).

Abbreviations: C = dune crest, F = flat ground, GS = gentle dune slope, SS = steep dune slope, E = east-facing, and W = west-facing.

Site	Aspect	Slope	Sample size	Density $no.m^{-2}$	Nearest neighbour	SD	Expected NN*	SE*	R *	p *
2	E	SS	106	0.353	0.879	0.490	0.842	0.043	1.045	$p < 0.01$
3		C	56	0.187	1.205	0.567	1.156	0.081	1.042	$p < 0.01$
4		C	82	0.273	0.982	0.488	0.957	0.055	1.026	$p < 0.01$
4	E	GS	75	0.250	0.999	0.663	1.000	0.060	0.999	$p < 0.01$
4	E	SS	66	0.220	1.040	0.578	1.066	0.069	0.976	$p < 0.01$
3	E	SS	122	0.407	0.761	0.404	0.784	0.037	0.971	$p < 0.01$
2		F	99	0.330	0.800	0.460	0.870	0.051	0.927	$p < 0.01$
2	E	GS	60	0.200	1.024	0.640	1.118	0.075	0.916	$p < 0.01$
2	W	GS	74	0.247	0.799	0.516	1.006	0.061	0.794	$p > 0.05$
		Pop. mean		0.274	0.943				0.966	
		Pop. SE		0.074	0.145					

* Clark & Evans (1956)

0.038(D_{top}) - 0.506, $p < 0.05$, $r^2 = 0.86$, Fig. 6), and a weaker, but nevertheless significant correlation, between tuber mass and the maximum tuber diameter ($p < 0.05$, $r^2 = 0.79$). The former regression is therefore a convenient means of objectively estimating the mass of tuber material eaten by foraging molerats, because the D_{top} data for uneaten tubers, often the only reliable parameter measurable on these tubers, can be used to calculate the expected tuber mass of the tubers before they were eaten. Only five of the 30 eaten tubers excavated had masses which were greater than the mass predicted by the regression, but these tubers were all excavated from the dune crests, and were unusually short and barrel-like, a morphology which appears to be common to most tubers growing on the dune crests. If these five tubers are discarded from the analysis, the mean ± SD mass difference between the predicted and the observed masses of the uneaten tubers was 249 ± 129 g, whereas if these tubers are included in the analysis the mean mass difference was 183 ± 196 g. It appears that the molerats often ate the whole tuber, with the exception of a short 5 - 10 cm subsurface section, if the tuber was small, thin, and presumably younger. However, for the large tubers, the molerats often only ate parts of the outer bark and small sections of the parenchyma, but very seldom chewed through the whole tuber as far as the pith. This observation, together with the mass-difference analysis above, suggests that irrespective of the size or age of the tuber, molerats

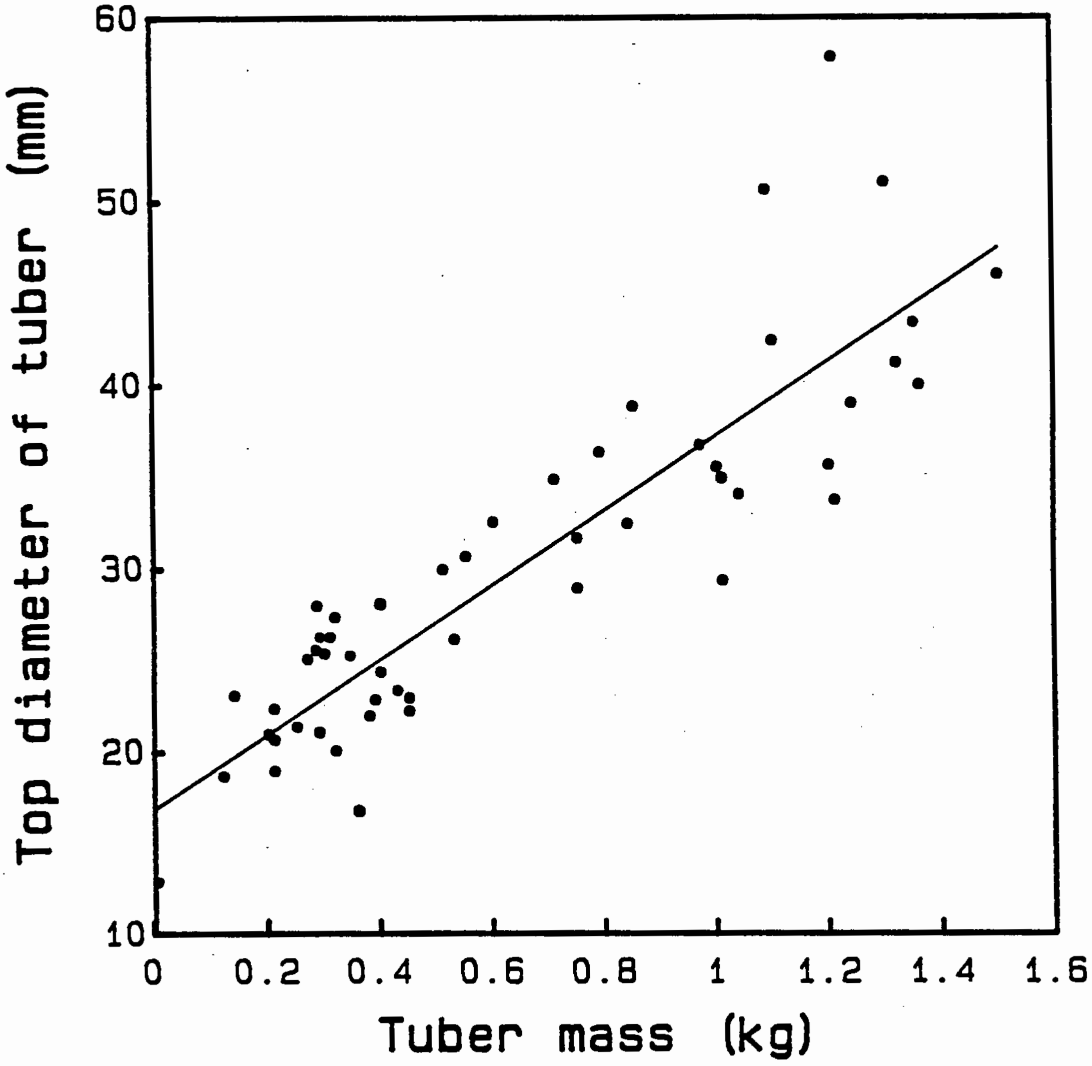


Fig. 6. Regression of the top diameter (D_{top}) of *A. naudinianus* tubers as a function of tuber mass.

are probably consuming approximately 200 - 250 g of every tuber encountered during foraging.

The percentage water content in *D. gracillimum* bulbs was very similar for all size classes, and ranged from 70.11 - 72.82 % (Table 3). Protein and fibre contents were also similar, ranging from 11.95 - 14.61 % and from 11.80 - 17.56 % respectively (Table 3). The water content of the section of whole tuber was 70.26 % (Table 3), which is consistent with the 66 % water content measured by Williamson (1987) for the same tuber in the central Kalahari Desert. An interesting aspect of *A. naudinianus* tubers, was their very high fibre contents, 45.16 - 66.46 %, and relatively low protein contents, 2.65 - 9.95 % (Table 3). The outside bark component had the highest protein content and the lowest fibre content (Table 3). The calorific content of the sections of whole tuber was 16.97 ± 0.07 $kJ.g^{-1}$.

Discussion

The distribution and quality of food resources available to *C. damarensis* in the southern Kalahari appears to be heavily dependent on habitat. At the Nossob site, bulbs are numerous and small, but represent a diet of relatively good quality. At the Dune site however, the tubers have a higher biomass, are more sparse, widely distributed, and larger, but represent a poor quality food resource. Although the

Table 3. The percentage composition of water, protein, and fibre, measured in the bulbs of *Dipcadi gracillimum*, and the tubers of *Acanthosicyos naudinianus*.

Geophyte species	Geophyte fraction	Mass (g)	Water (%)	Protein	Fibre
				% Dry mass	
D. gracillimum	whole bulb	5.17	70.11	13.13	13.92
	whole bulb	3.03	72.13	11.95	17.56
	whole bulb	1.59	72.82	13.05	11.80
A. naudinianus	whole bulb	670	70.26	8.49	58.81
	bark	-	-	9.95	45.16
	parenchyma	-	-	2.65	66.46
	pith	-	-	6.54	54.36

stratified sampling at the Dune site revealed a random distribution of tubers where density was influenced by slope and aspect, on a larger scale the distribution requires further discussion. My impression based on numerous observational surveys, is that the tubers tend to be distributed in 'macro-clumps' within the dune valleys. I would define a macro-clump as a minimum area of approximately 0.25 km^2 with a density of tubers within the range reported. As discussed, the spatial distribution of tubers within these clumps is random. However, the marco-clumps are separated by distances of approximately 0.5 - 2.0 km. The area between macro-clumps is either totally devoid of tubers, or, tubers occur in densities lower than those of the macro-clumps. Not surprisingly, molerat colonies are seldom found in these 'suboptimal' interclump zones. Ideally, stratified sampling should be conducted within these interclump zones in order to establish the overall distribution of tubers and macro-clumps more precisely.

It is probably safe to state that the resource distribution at the Dune site is more typical of the general pattern of resource distribution throughout most of the range of *C. damarensis* in the southern and central Kalahari Desert. Certainly in the southern Kalahari where this study was undertaken, the *D. gracillimum* communities appear to be restricted to the riverine habitats of the Nossob and Auob rivers and, as such, are the exception rather than the rule.

Consequently, I would expect that the adaptations displayed by *C. damarensis* would have been selected for primarily in response to the foraging and environmental constraints synonomous with the Dune site.

Consider the very high fibre content of *A. naudinianus* for instance. The fibre content of these tubers is comparable to those of most tropical grasses and stem material eaten by many specialised ruminants (Morris 1983). *C. damarensis* display at least two adapatations which probably ensure that sufficient cellulose digestion is accomplished to maintain a positive energy budget. Firstly, like most rodents, *C. damarensis* is coprophagous, thereby enhancing digestion. Secondly, it appears that *C. damarensis* has a highly specialised caecum facilitating microbial degradation of cellulose. In two animals with masses of 111 g and 186 g examined by the author at Nossob camp, the caecum was calculated to be 26 % of the total length of the hindgut. The caecum is therefore considerably larger than those measured for 18 southern African rodents (3.7 - 20.2 %), and is comparable to the large complex haustrated caecum of a closely related species *C. hottentotus* (29.1%), all measured by Perrin & Curtis (1980).

Despite these adaptations, the efficiency of digestion of *C. damarensis* is low. Jarvis & Bennet (pers. comm.) have shown that the digestive efficiency of *C. damarensis* fed on *A.*

naudinianus tubers was 52.5 %. This implies that of the 200 - 250 g of material eaten per tuber, only 105 - 131 g (or 2002 kJ) is digestible, and when the density of tubers at the dune site is considered, 11 - 48 $g.m^{-2}$ of digestible food material is potentially available to foraging molerats. This estimate of the availability of digestible food is lower than that for the Nossob site. Assumming a digestive efficiency of 97 % based on digestibility trials conducted by Du Toit *et al.* (1985) on *G. capensis* using sweet potato, approximately 54 - 114 $g.m^{-2}$ of digestible bulbous material is potentially available to molerats foraging within *D. gracillimum* communities. However, it is also likely that a proportion of this biomass can not be utilised by *C. damarensis*, either because the bulbs are too shallow to be excavated, or, because they are too small to be efficiently located and handled. The above estimate is therefore probably too high.

The higher fibre contents and lower protein contents of the parenchyma and pith components of *A. naudinianus* seem to be the factors which tend to restrict *C. damarensis* to the consumption of the outer bark component. Both geophyte species have a high water content, and considering that there is no alternative source of water available to *C. damarensis*, the molerats appear to be quite capable of maintaining a positive water balance feeding on geophytes alone. Potential water balance problems are further reduced by the high relative humidity and microclimatic constancy of closed burrow systems (Nevo 1979).

The feeding constraints outlined above are important considerations in the energy budget of *C. damarensis*, and will be discussed further in Chapters Six and Eight to Eleven concerning their role in influencing the physiological and social features of this species. The data concerning the spatial distribution of *A. naudinianus*, when compared with those of other bathyergids, will be used to develop the overall thesis on the energetic and other constraints of foraging, selecting for sociality in the bathyergid molerats.

Summary

The habitats of *C. damarensis* in the KGNP are characterised by a dominance of single geophytes, namely the small onion-like bulbs of *D. gracillimum*, and the large carrot-shaped tubers of *A. naudinianus*. At the Nossob site adjacent to the Nossob River, *D. gracillimum* occurs at shallow depths but in high densities, compared with the low densities of widely distributed *A. naudinianus* tubers at the Dune site. The tubers are randomly distributed within macro-clumps. Tuber density is influenced by the slope and aspect of the dune valleys. Molerats often only eat the outer bark of the tubers because of the lower fibre content, and higher protein content of this component.

CHAPTER THREE

Soil Temperatures, Burrow Temperatures, and the Burrow Structures of *Cryptomys damarensis*.

Introduction

As discussed in Chapter One, McNab (1979a) strongly advocates warm burrow temperatures as the primary factor selecting for the characteristically low mass-specific RMRs of subterranean rodents. However, one serious limitation of his study was that it failed to consider temporal and seasonal burrow temperature variations, as well as the pattern of soil temperature regimes as a function of soil depth. For instance, McNab's (*op. cit.*) study dealt primarily with summer burrow temperatures, and did not consider winter burrow temperatures. This point is, however, not critical to the "overheating hypothesis". The important limitation of the study is that it overlooks other potential physical and/or ecological factors which may have selected for certain physiological parameters of subterranean rodents, such as a low RMR. Consequently, this chapter investigates the summer and winter burrow and soil temperatures to which *C. damarensis* is exposed on a circadian basis. It also investigates aspects of the burrow structures of *C. damarensis* in terms of the resource characteristics of both sites (Chapter Two) in the KGNP.

Methods

Attempts were made to trap all molerats from four systems at the Nossob site, and three systems at the Dune site, before any excavations were made of the burrow systems. Although nine animals were trapped from one system, it is unlikely that all of the animals in the colonies were trapped. Initially trap success was good (2 - 3 animals.day^{-1}), but this dropped dramatically as the colony was depleted. No reproductively active females were caught (see Bennett & Jarvis 1987). All trapped animals were subsequently used to measure metabolic rates in the laboratory at the University of Cape Town. The depths and diameters of molerat burrows at both sites were measured. The depths of the primary burrows (see later) were measured by digging down to the burrow at random along the relatively straight sections of the primary burrow. The depths of the secondary burrows were measured by excavating 10 complete secondary burrows. During the August fieldwork, all open primary burrows of two entire systems were excavated at the Nossob site.

Measurements of the temperature of the primary burrow and of soil temperatures at various depths were recorded at the Nossob site with an MCS 101 computing data logger fitted with thermistor probes, during the hottest and coolest months in the KGNP, January and July, respectively. The data logger was programmed to record instantaneous temperatures at 30 min intervals for three consecutive days. The thermistors were placed in a narrow trench at various depths, and were allowed to equilibrate for 48 hrs after the trench was filled with compacted sand. During summer, temperatures were recorded 1 - 2 mm under the suface of the sand, at 10 cm, and in the primary burrow at a depth of 25 cm. During winter, soil temperatures were recorded at depths of 5 cm, 10 cm, 20 cm, and 30 cm. All data from thermistors set at 60 cm were lost through thermistor malfunction (winter), and when the thermistor cable was chewed and destroyed by a Brown hyena (summer). Soil temperatures were also recorded during behavioural studies in summer at the Dune site, and are discussed in the next chapter. Data are presented as the mean half-hourly temperatures for three consecutive days. For purposes of graphic clarity standard deviations are not presented, but they were very low, and seldom exceeded 2.0°C, particularly at the deeper soil depths. Also , data points are joined by solid lines.

Results

Nossob site

Two distinct burrow types, termed here the primary and secondary burrows, were identified at the Nossob site. The primary burrow, which is associated with the characteristic molehills, forms the main artery of the burrow system, and is generally the straightest and largest section of the system (Figs 7 & 8). For example, the total length of an unblocked primary burrow excavated from one system was 82 m. The mean depth of the primary burrow from the surface was

Fig. 7. A row of molehills thrown up during construction of the primary burrows at the Nossob site. Note *D. gracillimum* stems and seed-pods.

Fig. 9. The effect of trampling by ungulates on the secondary burrows at the Nossob site. Note the holes in the foreground exposing the shallow secondary burrows. The molehills are from the primary burrows.

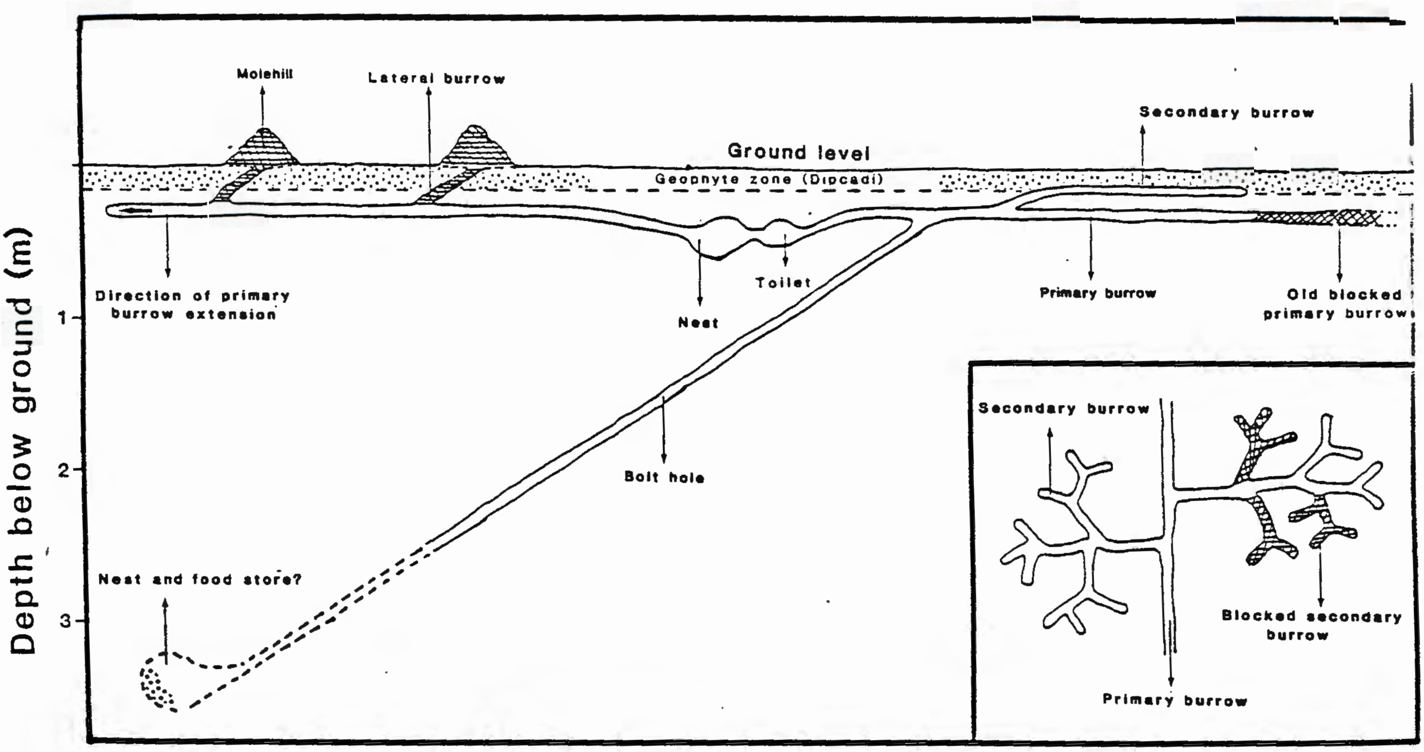


Fig. 8. A schematic lateral representation of the burrow types and structures of *C. damarensis* at the Nossob site. Inset shows a dorsal aspect of the secondary burrows and is not to scale.

25.1 cm to the top of the burrow, and 31.7 cm to the bottom, giving a mean diameter of 6.6 cm (Table 4). The mean distance between molehills was 122.5 cm (Table 4). It is assumed that this mean distance closely approximates the mean distance between the lateral burrows leading off from the primary burrows to the molehills (Fig. 8).

Generally, the secondary burrows lead off at right angles to the primary burrows, invariably branching after 0.5 - 2 m into a number of hand-like burrows (Fig. 8). The mean depth of the secondary burrows was 10.3 cm to the top of the burrow, and 16.1 cm to the bottom, with a mean burrow diameter of 6.0 cm (Table 4). When the system was excavated in winter, all of the secondary burrows were solidly blocked with sand. During summer, however, many of the secondary burrows were found to be open, or only partially blocked. These burrows are not associated with molehills, and their presence can only be detected where trampling by ungulates has collapsed these shallow burrows (Fig. 9). When the secondary burrow system is exposed, the molerats either repair the burrow at the collapse site, or more typically, they block the entire secondary burrow leading to the collapse site as far as the primary burrow.

A chamber measuring 20 cm in diameter, possibly a nest site, was located leading off from the primary burrow at its deepest point (45 cm). There was no nesting material, food,

Table 4. Depths, diameters, and segment lengths, of the burrows of *C. damarensis* in the Kalahari Gemsbok National Park.

Site	Burrow type		Depth to top (cm)	Depth to bottom (cm)	Burrow diameter (cm)		Segment length (cm)
		n	Mean ± SD	Mean ± SD	Mean ± SD	n	Mean ± SD
Nossob	Primary	38	25.1(2.8)	31.7(2.9)	6.6(0.8)	54	122.5(52.1)
Nossob	Secondary	50	10.3(2.1)	16.1(2.3)	6.0(1.1)	-	- -
Dune	Primary	30	29.8(6.4)	36.5(6.6)	6.7(0.9)	75	151.1(62.0)

or faeces associated with this chamber. A toilet chamber was located at the same depth along the primary burrow approximately 25 cm from the entrance to the nest chamber. This chamber was loosely filled with sand mixed with faeces. The entrance to a bolthole was located leading from the primary burrow at a depth of 27 cm. This burrow descended for 5 m at an angle of 23° to a depth of 2.2 m. At this point, further excavation of the bolthole had to be terminated to avoid the risk of the excavation collapsing on top of the author. However, by pushing a long stick down the hole, it was concluded that the burrow continued for at least another 3 m at the same angle, which would put the final depth of the bolthole at more than 3 m.

Dune site

The primary burrows at the Dune site were also characterised by typical molehills. By examining the rough extent of individual burrow systems from the arrangement of molehills, it was noted that the burrow systems were restricted to the dune valleys and the slopes of the sand dunes. No molehills were found on the loosely compacted dune crests.

The mean depth of the primary burrow was 29.8 cm to the top of the burrow, and 36.5 cm to the bottom, with a mean burrow diameter of 6.7 cm (Table 4). The mean distance between molehills (segment length) was 151.1 cm (Table 4). Although no extensive excavations were made of burrow systems at the

Dune site, no evidence of the shallow secondary burrows typical of the Nossob site were found. All burrows that were opened up for depth measurements, and for the setting of traps, were at the depths described for the primary burrows.

Close inspection of the molehills at the Dune site revealed two distinct types. The first type represents the molehills characteristically associated with the extension of the primary burrows i.e. soil from the digging face discarded via the lateral burrows. The second type of molehill is typically either a single mound, larger than the primary burrow molehills, or two or three mounds pushed up in very close proximity to each other. The latter molehills are associated with feeding, as they are always located next to a *A. naudinianus* tuber which has been eaten by the molerats (Fig. 10). When these tubers are excavated an arrangement of burrows can be found surrounding the tuber (Figs 11 & 12). Usually the burrows take the form of a spiral leading up and down the length of the tuber from the primary burrow. These spiral burrows can go down as far as 1.2 m, which is roughly the maximum depth to which the tubers grow. The upper limit of the spiral burrow is usually about 10 cm from the surface. The sand from these spiral excavations is pushed up close to the tuber to form the feeding molehills. During excavations it was noted that the uneaten subsurface part of the tubers, or, partially eaten tubers, whether

Fig. 10. A typical single, large feeding molehill surrounding a *A. naudinianus* tuber at the Dune site. Note the surface runners leading out of the mound from the tuber.

Fig. 11. Excavation showing a section of a spiral burrow surrounding a A. naudinianus tuber at the Dune site (see also Fig. 12).

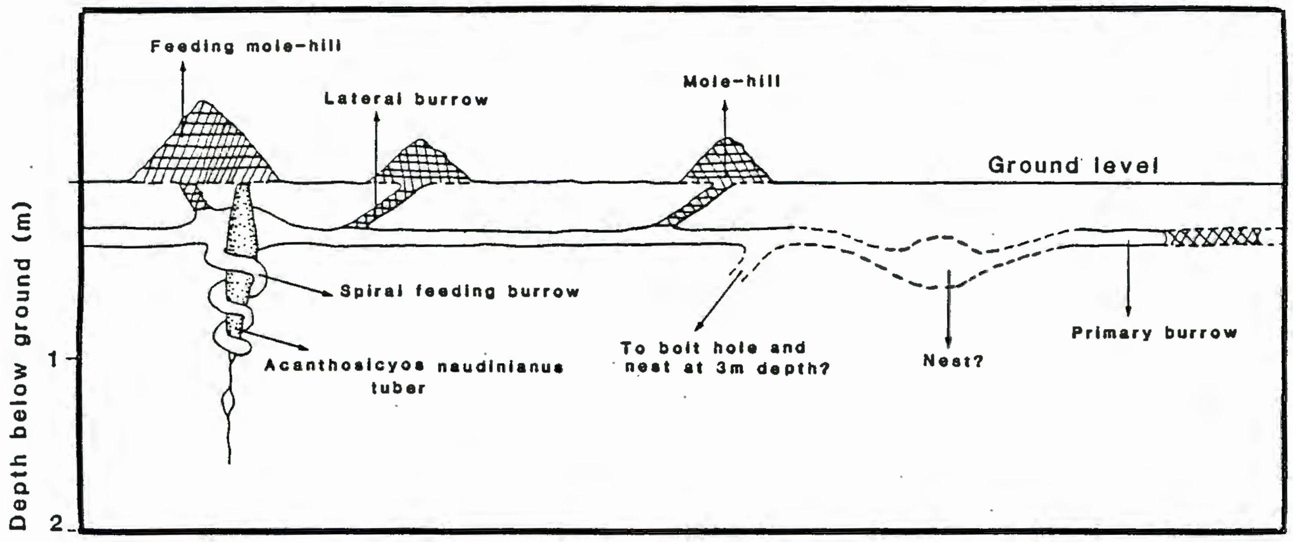


Fig. 12. A schematic lateral representation of the burrow types and structures of *C. damarensis* at the Dune site.

large or small, are capable of recovering from this herbivory, and will sprout and grow during the next growing season (Fig. 13). During the six months separating the January and August field work, no additional molehills had been pushed up at two colonies where a note was made of the original arrangement of molehills.

Soil and burrow temperatures

The daily temperature of the primary burrow at 25 cm during summer was fairly constant at $33.45 \pm 1.31^{\circ}C$ (Fig. 14a). There was, however, a large daily fluctuation at the soil surface with temperatures ranging from a maximum of $65.9^{\circ}C$ at 14h00, to a minimum of $17.8^{\circ}C$ recorded at 06h30 (Fig. 14a). Daily temperature fluctuations were less pronounced at 10 cm ranging from $41.8^{\circ}C$ at 19h00, to $26.3^{\circ}C$ at 09h00 (Fig. 14a).

The mean soil temperature during winter at 30 cm was also very constant at $18.84 \pm 0.06^{\circ}C$ (Fig. 14b). Daily temperature variations at shallower depths were greater, but were lower than those measured during summer. For instance, at 10 cm the maximum daily range was $10.5^{\circ}C$ between a minimum of $12.5^{\circ}C$ at 09h30, and a maximum of $23.0^{\circ}C$ at 18h30 (Fig. 14b), whereas the daily range for the same depth in summer was $15.5^{\circ}C$.

Fig. 13. Two *A. naudinianus* tubers showing the effect of, and recovery from, herbivory by *C. damarensis* at the Dune site. The tuber on the left had recently (few weeks) been eaten by molerats and the tuber on the right had recovered from this type of herbivory by growing new roots and surface runners.

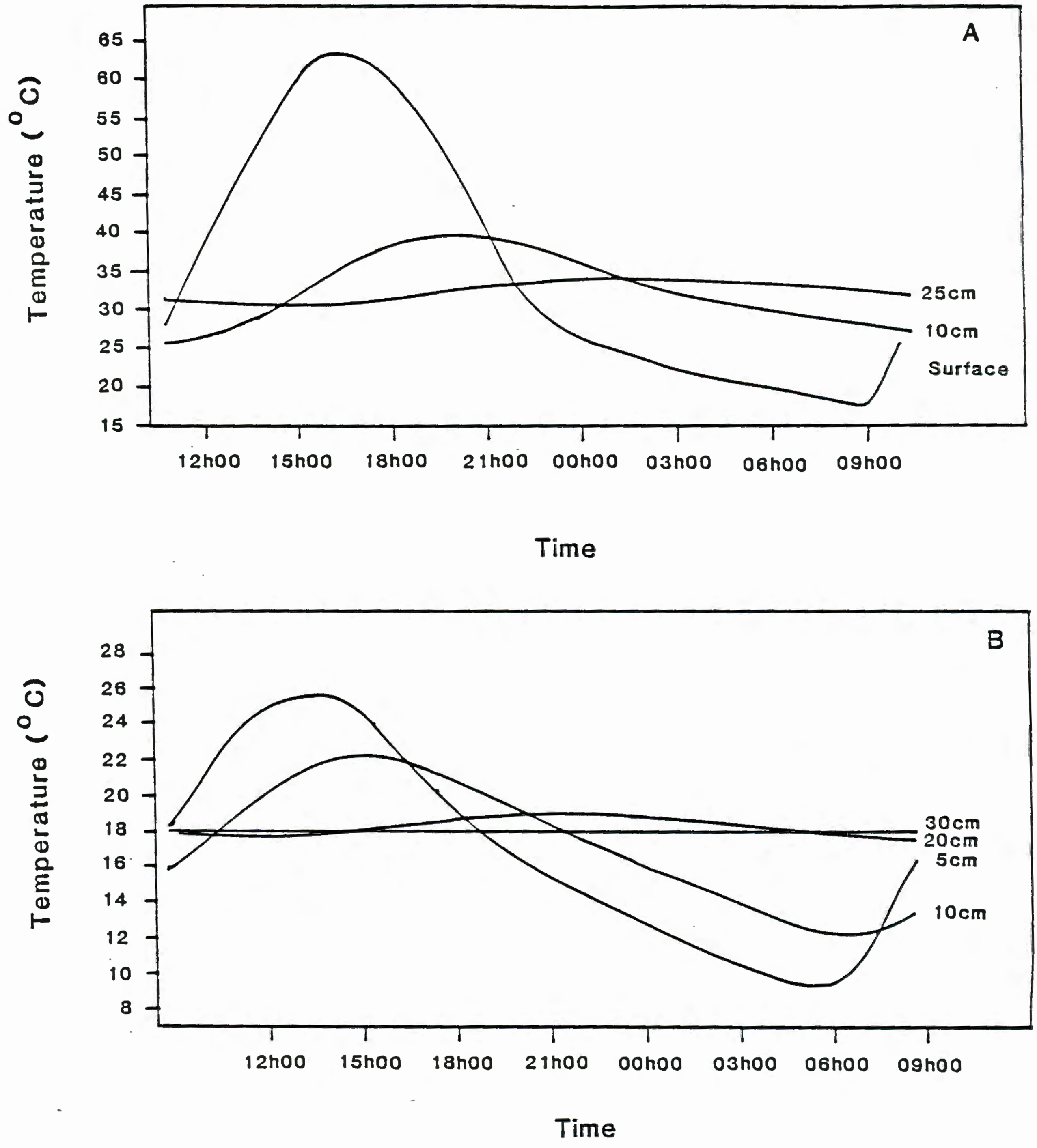


Fig. 14. The daily soil and burrow temperatures as a function of soil depth at the the Nossob site during mid-summer (A) and mid-winter (B).

Discussion

Two foraging patterns can be identified by the burrow structures of *C. damarensis* in the KGNP. These patterns appear to represent a compromise between predatory pressures, microclimatic factors, and most importantly, species-specific resource dispersion patterns. Although geophytes appear to be the exclusive food items at both sites, the dispersion patterns of the two main geophytes concerned varies quite considerably (Chapter Two).

The secondary burrows at the Nossob site quite obviously represent foraging burrows excavated at a depth optimally suited to harvest the shallow *D. gracillium* bulbs. The non-association of molehills with these burrows suggests that soil excavated from the digging face of the secondary burrows is pushed around the burrow system and essentially 'dumped' in old foraging burrows. This burrowing behaviour has been observed in *H. glaber* (Jarvis & Sale 1971, Brett 1986), *H. argenteocinereus, Tactyoryctes splendens* (Jarvis & Sale 1971), *C. hottentotus* (Genelly 1965, Davies & Jarvis 1986), and *B. suillus* (Davies & Jarvis 1986). Although this behaviour may be energetically expensive (Vleck 1979, 1981) if sand has to be moved over large distances, it is very likely that it is necessitated by the low moisture content of the sand in the shallower subsurface layers prevalent during most of the year in the KGNP. As discussed below, this factor may be one of the most important physical constraints faced by *C. damarensis* in the Kalahari.

Observations on the production of molehills by other bathyergids such as *G. capensis*, *B. suillus* and *C. hottentotus*, have shown that molehills are mostly produced in aggregated soils, or soils that are moist (Davies & Jarvis 1986, pers.obs). Although the sands of the Kalahari can be quite compacted and aggregated at deeper depths even when very dry, the top 8 cm (approximately) is always very loose when dry. Attempts by *C. damarensis* to excavate lateral burrows to the surface during dry periods undoubtedly results in sand cascading down the burrow even if these burrows approach the surface at moderate inclines. This situation would totally defeat the purpose of the laterals, namely to discard excess sand excavated from the digging face. This problem partially explains why no molehill production has been observed during dry periods in the KGNP, whereas good rainfalls are immediately followed by intense mound production (M. Knight pers. comm., pers. obs).

The post-rain burrowing activity appears to be associated with the extension of the primary burrow system into new unharvested areas adjacent to the main colony. The excavation of a long straight primary burrow would be the optimal burrowing behaviour for ensuring future access to a large unforaged area on each side of the primary burrow. This would be achieved provided that sufficient resources are available to maintain the molerats during this important digging period. These resourses would probably be stored food in the case of *D. gracillimum* bulbs, or reliable *in situ* food in the case of previously located *A. naudinianus* tubers. As previously suggested, sand from secondary foraging burrows (Nossob site), or excavations associated with the spiral feeding burrows around *A. naudinianus* tubers (Dune site), can then be dumped in old foraging burrows when surface soils dry out. Based on this hypothesis, it is likely that the feeding molehills are probably only produced after rains. Besides the cooperative foraging effort required to locate widely dispersed food resources (see Chapter Nine & Eleven), the cooperative effort, required to extend the primary burrow as far as possible during the relatively short period when the surface sands are moist, is presumably one of the various factors selecting for group size and sociality in this species. The energetic costs and benefits of cooperative foraging and digging are investigated in Chapters Eight to Eleven.

The similarity in depths between the primary burrows of the Nossob and Dune site colonies suggests that molerats have selected this depth in response to factors other than those associated with the optimal procurement of resources, as appears to be the case with the secondary burrows. Factors such as the risk of predators gaining access to the burrow system when burrows are collapsed following trampling, and soil compactness, are likely to be the important determinants of primary burrow depth. At a depth of 25 - 29 cm the primary burrows can withstand intense trampling above ground and will even withstand the weight of an off-road vehicle. At depths above 25 cm the sand may not be compacted enough to ensure a permanently open burrow system. The higher costs of establishing the primary burrows at deeper depths (Vleck 1981), probably sets the lower depth limit.

One interesting feature of the burrow systems of *C. damarensis* is the great depth to which the bolthole descends. Although the boltholes of the burrow systems of other bathyergids are primarily regarded as escape routes or points of safe refuge from predators (Jarvis & Sale 1971, Brett 1986, Davies & Jarvis 1986), a strong argument can be developed suggesting that the boltholes in *C. damarensis* burrow systems play an important thermoregulatory role as well. The mean winter and summer temperatures of the primary burrows, or the soil at the depth of the primary burrows, are physiologically stressful because they are above and below the upper and lower limits of thermoneutrality for *C. damarensis* (Chapter Six) during summer and winter respectively.

To supplement the temperature data recorded in this study, I obtained daily soil temperature data for six years (1980 - 1985) from the South African Weather Bureau for Upington (400 km south of Nossob). These data showed a mean daily soil temperature of 33.6°C for a soil depth of 30 cm during January, which is consistent with the 33.5°C recorded at 25 cm in this study. The soil temperatures from Upington are therefore probably fairly reliable estimates of soil temperatures in the KGNP at soil depths below 30 cm. The Upington mean daily, January soil temperatures were 33.3°C and 32.1°C for depths of 60 cm and 120 cm respectively. Mean July daily temperatures were 16.0°C and 17.8°C for depths of 60 cm and 120 cm respectively. What these data show, is that soil temperatures at depths deeper than 120 cm are cooler and warmer than the shallow depths in summer and winter respectively. Presumably therefore, molerats should avoid energetically costly temperatures if possible, simply by moving up and down the soil column to depths where temperatures are closer to the lower and upper thermoneutral limits during the respective seasons. Although I predict that this is probably what happens, this supposition has yet to be substantiated.

Brett (1986) has used radiotelemetry in Kenya to show that *H. glaber* thermoregulates behaviourally by moving up and down the soil column in various parts of the burrow system. This is a particularly important behavioural response, because this species is virtually incapable of maintaining endothermy over even a small range of environmental temperatures (McNab 1966, Withers & Jarvis 1980). *C. damarensis* on the other hand, is exposed to a considerably wider seasonal range of environmental temperatures than occurs in Kenya, and consequently it has a relatively low thermal conductance and good thermoregulatory control down to ambient temperatures of 10°C (Chapter Six). The nest chamber found leading off from the primary burrow may therefore represent one of a number of semi-permanent nest sites at various depths. The fact that a faecal chamber was located near to the nest would suggest that the nest is at least occupied during periods when temperatures are suitable.

At this stage, it is not yet clear if *C. damarensis* regularly stores food, a practice typical of *C. hottentotus* (Davies & Jarvis 1986, Lovegrove & Jarvis 1986), *G. capensis* (Lovegrove & Jarvis 1986), and *H. argenteocinereus* (Jarvis & Sale 1971). It seems likely that at the Nossob site, where bulbs are small but numerous, food hoarding would take place. Moreover, Jarvis (pers. comm.) has recently excavated a large food cache of *Dipcadi sp.* bulbs from the bolthole of a colony of *C. damarensis* in south-eastern Namibia.

In closing, it may be valuable to speculate on the different behaviours of *C. damarensis* at the two sites. It is, for example, interesting that the foraging behaviour and burrow structure of molerats at the Nossob site is quite similar to that of *C. hottentotus* in the Cape (Davies & Jarvis 1986, Lovegrove & Jarvis 1986). This similarity in foraging behaviour probably stems from the fact that both species exploit abundant, but small-sized geophytes, at relatively shallow depths. On the other hand, the foraging behaviour of *C. damarensis* at the Dune site is more similar to that of *H. glaber* in Kenya (Jarvis & Sale 1971) which also forage for widely dispersed, large tubers (Jarvis & Sale 1971, Brett 1986).

One hypothesis, based partially on the intuitions of Jarvis (1978) and Brett (1986) that I develop and test in Chapters Nine and Eleven, is that the group size of molerat societies is a positive function of the mean distance between individual geophytes. In short, a cooperative effort is required to locate widely and randomly dispersed geophytes by random foraging, thereby effectively excluding a solitary existence from such habitats. Provided that reliable trapping is undertaken, it may be possible to test this hypothesis intraspecifically with *C. damarensis* in the KGNP. Therefore, we might expect larger group sizes in molerats feeding exclusively on *A. naudinianus* tubers (i.e. at Dune site), and smaller group sizes in molerats feeding exclusively on *D. gracillium* bulbs (i.e. at Nossob site). One of the complications involved in the testing of this hypothesis may be that group size is determined by the time-dependent cooperative effort required to extend the primary burrow after rains; a factor which only indirectly concerns the dispersion patterns of specific geophytes. Also, as mentioned in Chapter Nine, the role of predation may also be an important complicating factor.

Summary

Three factors appear to determine the burrow structures of *C. damarensis* in the KGNP. Firstly, the primary burrows are at a depth which avoid the chance of burrow collapse from trampling, thereby reducing the probability of predators gaining access to the burrow system. Secondly, the secondary burrows at the Nossob site are situated at shallow depths to facilitate the harvesting of small bulbs. Thirdly, the bolthole can be more than 3 m deep, and apart from its function as a place of safe refuge, probably plays an important role in facilitating behavioural thermoregulation. Observational evidence suggests that the production of molehills, and probably therefore the extension of the primary burrow, appears to be heavily dependent on rainfall, with maximum activity following rains.

There is a 15°C difference between the mean temperature of the primary burrow during winter and summer. Furthermore, the winter and summer temperatures are below, and above, the lower and upper limits of thermoneutrality of *C. damarensis*, respectively. Molerats can theoretically reduce thermoregulatory costs and stresses by nest-huddling and nesting at shallower depths in winter, and nesting at greater depths during summer.

CHAPTER FOUR

Colony Size and Structure, Activity Patterns, and Foraging Behaviour of *Cryptomys damarensis*

Introduction

A comprehensive understanding of the ecophysiology of the bathyergids is hampered at present by the marked lack of field data on the daily activity patterns of most species. This is not surprising considering that observations of free-ranging bathyergids can only be obtained using telemetric techniques. Brett (1986) has recently completed an important study on *H. glaber*, and has shown that valuable data can be obtaining using radio-telemetry. Other than than this study and that of Jarvis and Sale (1971) on *H. argenteocinereus*, little is known about the daily activity patterns of the bathyergids.

This chapter investigates the activity patterns of a colony of *C. damarensis* in the KGNP. Specifically it addresses the following questions: What is the group size and colony structure of *C. damarensis*? Is the activity of this species influenced by factors such as photoperiod and soil temperature? Is there any evidence of differentiation of labour among individuals in the colony? How do *C. damarensis* partition their daily activities? Can these questions be answered using current radio-telemetry techniques?

At the outset of this project, nothing was known about the colony structure of *C. damarensis*. However, on completion of the project, Bennett & Jarvis (1987) reported new data on the colony structure and reproduction of this species, based on field and laboratory observations. Wherever possible I have altered the text to refer to this work, but for the sake of originality, I have retained my original interpretation of the data I obtained.

Methods

Field work was carried out at the Dune site between December 1986 and February 1987. Three 9 g type SR-1 collar-mounted radio transmitters fitted with mercury, tilt-switch, pulse interval modulators for activity sensing were used (Biotrack, Dorset). A Mariner 57 radio reciever, two yagi antennae, and three loop antennae, were used to recieve radio signals. Initially four males were trapped with Hickman traps. Transmitters were fitted to the two largest animals (197 g and 179 g; Fig. 15). They were then released into the original burrow system the following day. These two animals were tracked on foot for three days in order to roughly ascertain the whereabouts and extent of the burrow system. In this way a commonly used nest site and five foraging areas were identified. Foraging areas were characterised by feeding mounds (Chapter Three). The antennae were then mounted on 3 m high wooden poles in various combinations and orientations enabling radio signal reception from virtually all sections of the burrow system (Fig. 16). The antennae were connected via co-axial cables to the reciever stationed at a common monitoring base. When particular signals could not be picked up at the base, a hand-held yagi antennae was used to locate the signal on foot.

During data gathering the procedure was to locate each animal every 10 mins, at the same time quantifying its activity state. Activity was quantified by counting the number of times the pulse modulation of the signal changed within a 60 s period. These changes were quantified from 0 - 10, with 0 representing no change (completely inactive), and 10 representing 10, or more, changes in pulse modulation (maximum activity). It was intended to monitor each animal for a total of three days and nights, but towards the end of the study equipment failure meant the loss of one day and two nights from the study of three particular animals. In the end, non-consecutive data were obtained for three days (08h00 - 20h00) and nights (20h00 - 08h00) for two molerats, and for two days and one night for three animals, giving a total monitoring time of 252 animal hours. During all sessions soil temperatures were recorded every 20 mins at depths of 5 cm, 20 cm and 40 cm by the method described in Chapter Three.

In order to retrieve the radio transmitters from the first two animals collared, the colony, numbering 20 animals, was trapped over a period of eight days. Four burrows were then left open for three days to establish whether there were any more molerats in the burrow system. Bathyergids are known to block opened burrows within a maximum period of 12 hours after burrows have been opened (Jarvis pers. comm., Pers. obs). No further blocking took place, suggesting that the entire colony had been trapped. Radio collars were then fitted to three molerats, one male (182 g), and the two largest females (126 g and 143 g). The whole colony was then released into the original burrow system. Three days were then allowed for the molerats to normalise behaviour before data gathering commenced.

Results

Colony size

The colony consisted of five females and 15 males, and appeared to represent three size classes (Fig. 17). Size class 1 (SC1) consisted of eight males (150 - 200 g), size class 2 (SC2) consisted of two females and a male, whereas size class three (SC3), consisted of three females and six males all between 80 - 100 g. SC1 molerats were invariably the first molerats to be trapped in each trapping session, but SC3 molerats were invariably the last to be trapped (Fig. 18). During the period when the colony was held in

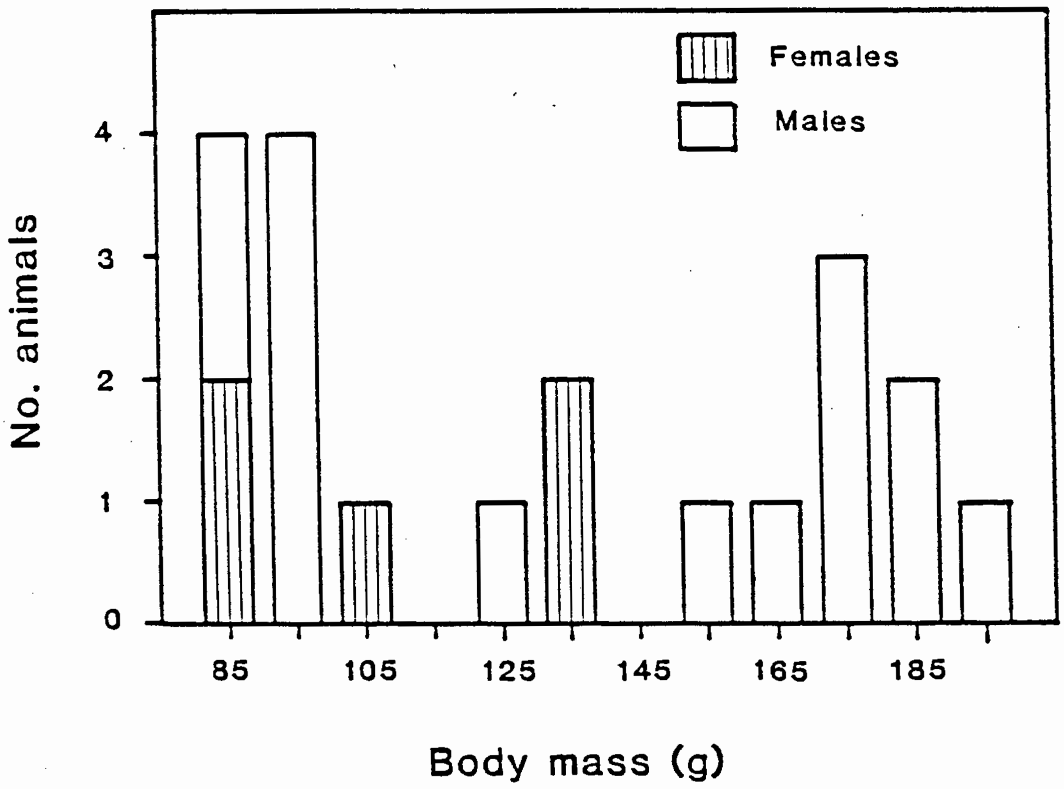


Fig. 17. Frequency distribution of the body masses of the colony of *C. damarensis* trapped at the Dune site.

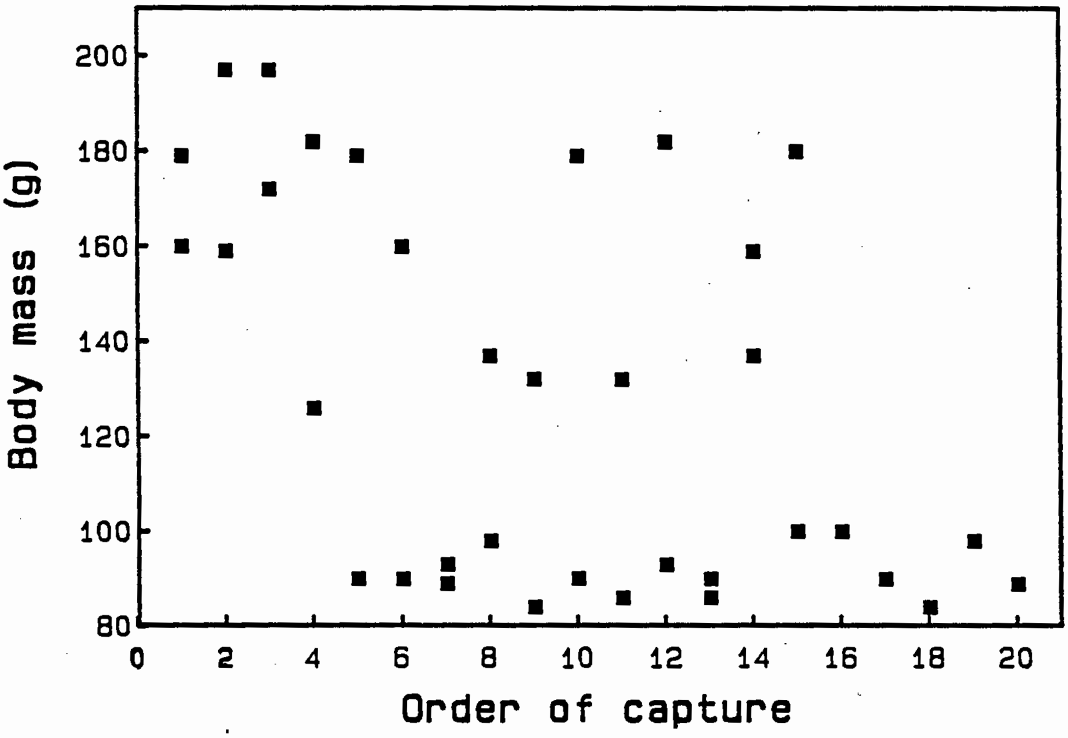


Fig. 18. The order of capture of the trapped colony of *C. damarensis* as a function of body mass.

captivity, all molerats in the colony displayed submissive behaviour towards the 197 g male, so it is likely that this molerat was the dominant breeding male (see Bennett & Jarvis 1987). From external features it could not be established whether any of the females in the colony were in a breeding condition (*op. cit.*). There was no evidence of enlarged teats, and all vaginas were non-perforate.

Burrow system

The burrow system covered an area of approximately 13000 m^2, 218 m long x 60 m wide (Fig. 19). The system was divided into five large foraging zones labelled SF, SW, SE, MF and NF. Three nest sites were identified. The main nest, SN, was situated in the southern part of the burrow system, the second, MN, was roughly in the middle, and the third, NN, was situated in the northern-most region of the burrow system. *A. naudinianus* tubers were distributed throughout the area of the burrow system, but were particularly dense in the lowest part of the system between MF and NF (Fig. 19). To avoid disturbance, the density of tubers was not measured at this site, but it is likely that, with the exception of the dense patch, their density fell within the range of 0.017 - 0.407 tubers.m^{-2}, measured in an adjacent dune valley (Chapter Two). The foraging zones which contained the most evidence of feeding mounds were, in decreasing order, SF, MF and NF.

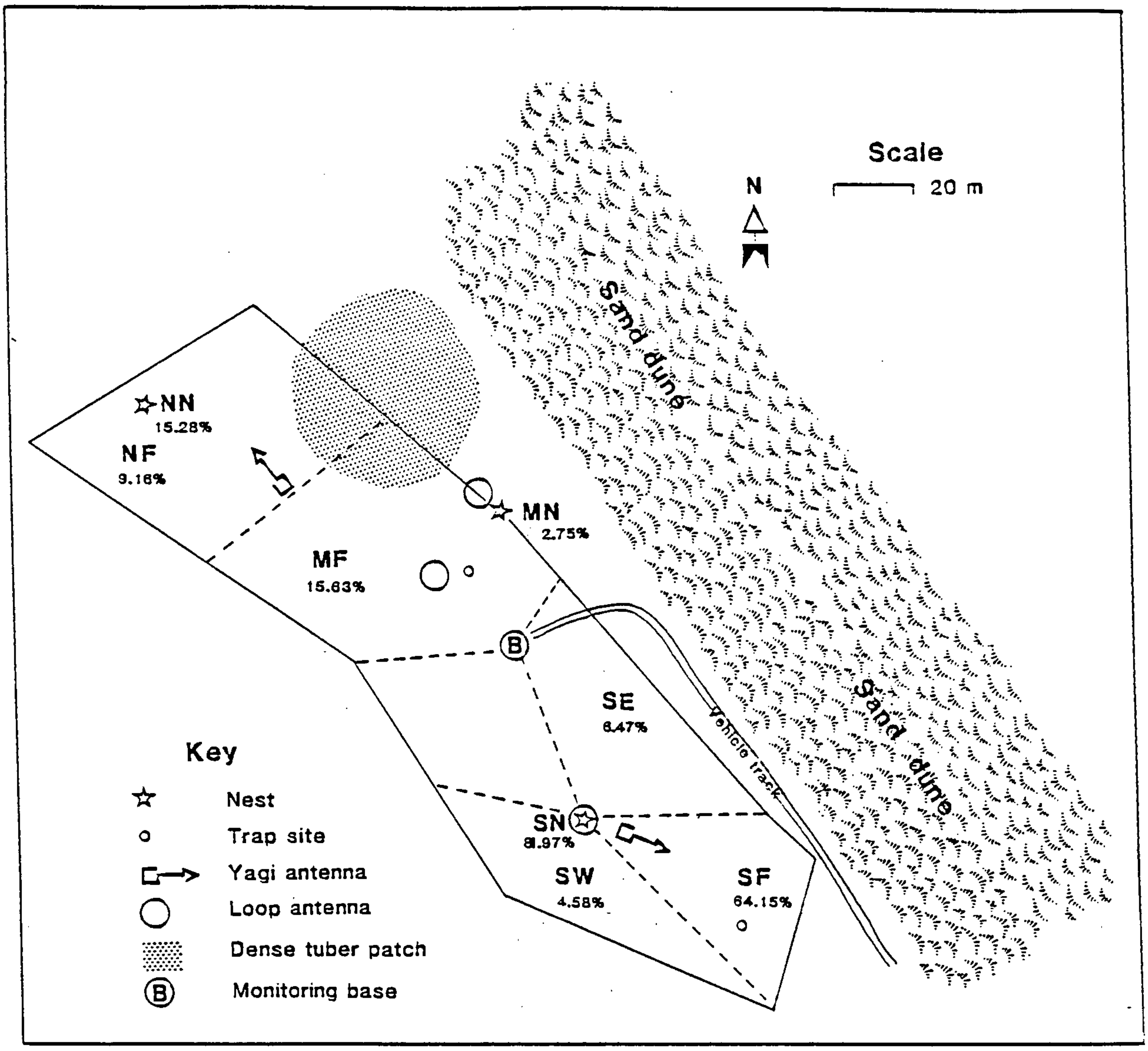


Fig. 19. The layout of the burrow system of the colony of *C. damarensis* that was radio-tracked at the Dune site. The percentages show the percentage of the total time spent in different foraging zones and nest sites.

Activity patterns

The strength of the radio signal was always strong and clearly audible when the molerats were active in the foraging zones, but when in the nest areas, particularly NN, the signal was weak, and was frequently barely audible. This suggests that the nests were situated at much deeper depths than the primary foraging burrows. The five molerats monitored did not respond to photoperiod and appeared to be equally active during the day and night (Fig. 20). There was no correlation ($p > 0.05$) between activity and soil temperature at 5 cm ($r^2 = -0.11$), 20 cm ($r^2 = -0.10$), and 40 cm ($r^2 = 0.17$). The mean ± SD soil temperatures were 36.8 ± 4.8°C at 5 cm, 35.5 ± 1.4°C at 20 cm, and 33.8 ± 0.2°C at 40 cm (Fig. 20). The shallowest soil depth (5 cm) showed the greatest daily temperature fluctuation (29.7 - 43.7°C), whereas the temperature at 40 cm remained fairly constant (33.4 - 34.4°C).

On average, the five molerats spent 76.39 % of the total time in the nest, and 23.61 % of the time out of the nest (Table 5). The two smallest molerats, both females, spent the highest, and the 180 g male the lowest percentage of time out of the nest. Data on time spent in, and out, of the nest were pooled for all five molerats (Fig. 21). The mean time spent out of the nest was 60.4 ± 31.1 mins (n = 50, median: 60.0), and the mean time spent in the nest was 167.1 ± 103.2 mins (n = 38, median: 150). There was a large

Table 5. The percentage time that *C. damarensis* spent in the nest, and out of the nest, at the Dune site.

Animal number	Body mass (g)	Transmitter mass (% of body)	Sex	Time in nest (%)	Time out nest (%)
11	132	6.82	F	72.22	27.78
9	137	6.57	F	75.46	24.54
22	179	5.03	M	75.69	24.31
18	180	5.00	M	81.02	18.98
26	197	4.57	M	77.55	22.45
				76.39	23.61

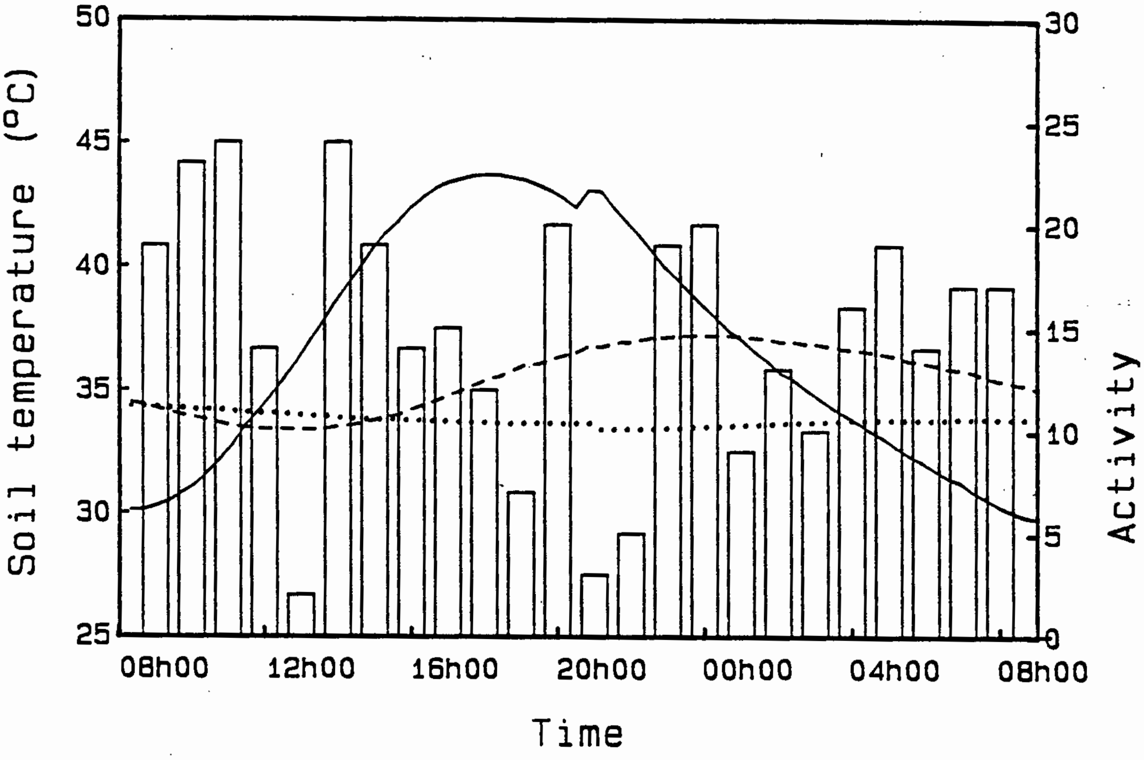


Fig. 20. The daily soil temperatures at various depths at the Dune site. The soilid line represents a depth of 5 cm, broken line 20 cm, and the dotted line 40 cm. Pooled data on the distribution of the activity time spent out of the nest are superimposed.

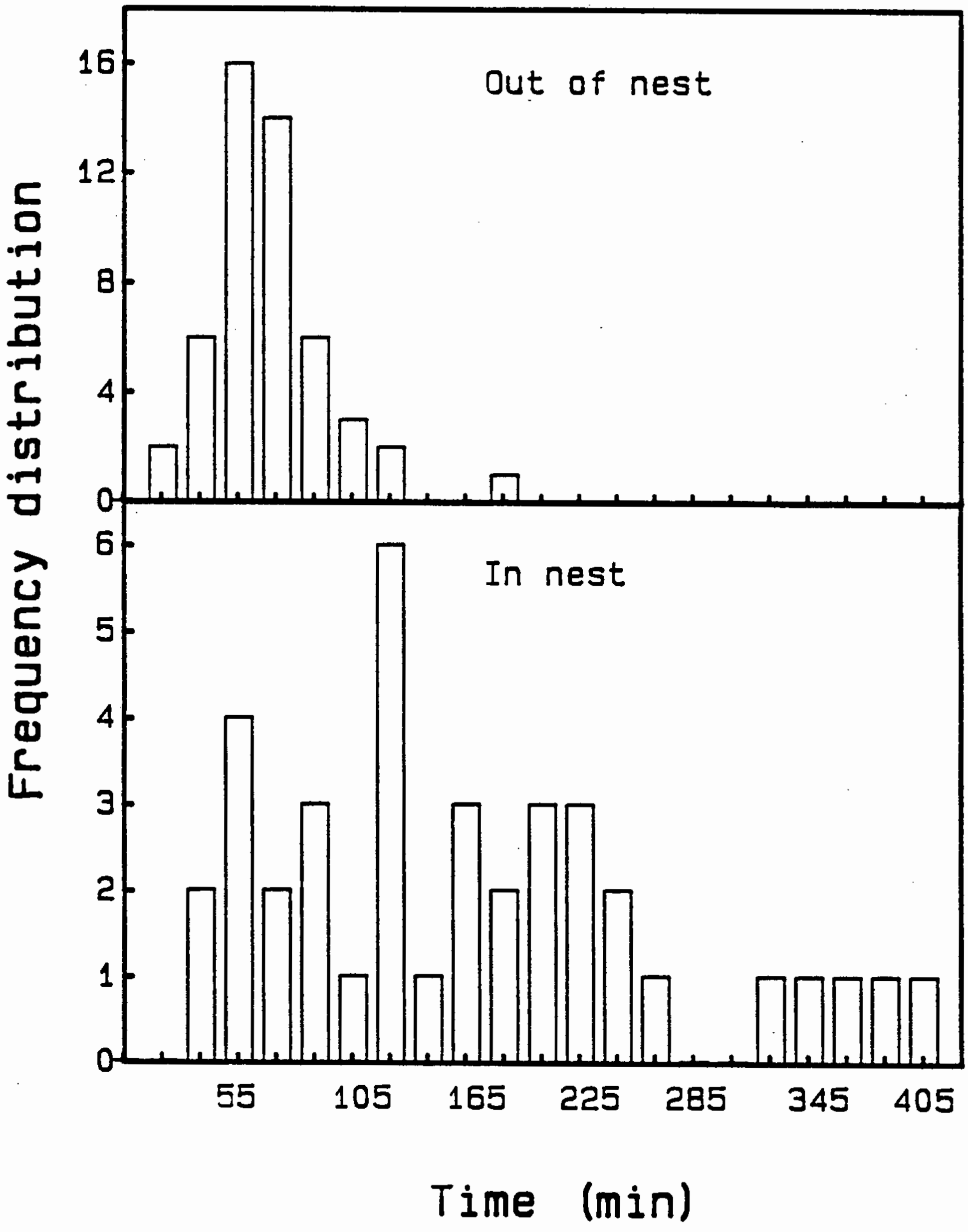


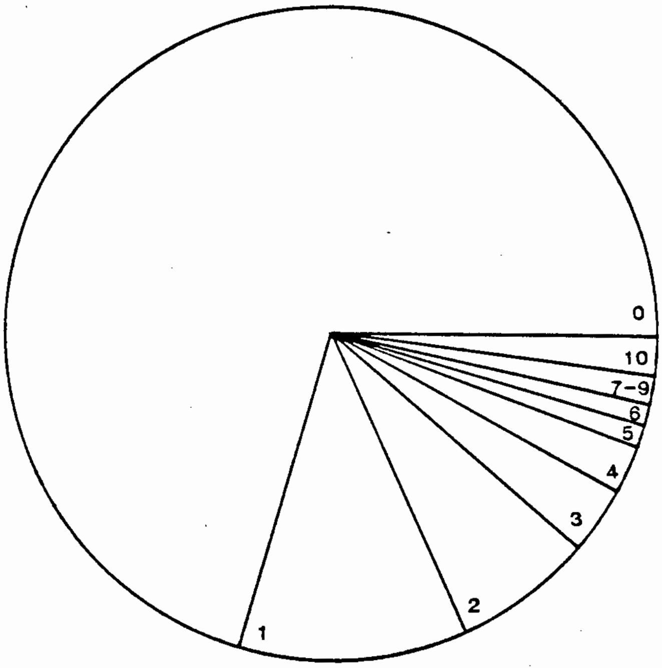
Fig. 21. Frequency distribution of the time spent in the nest and out of the nest. Data pooled for five animals.

variation in the time spent in the nest ranging from 30 - 400 mins (Fig. 21). Pooled data on the state of activity in, and out, of the nest, are shown in Fig. 22. On average, while in the nest the molerats spent 70.79 % of the time in activity state 0 and 1.77 % of the time in activity state 10. However, when out of the nest, 53.97 % of the time was spent in activity state 10, 6.61 % in activity state 0, and the balance fairly evenly distributed among the other activity states.

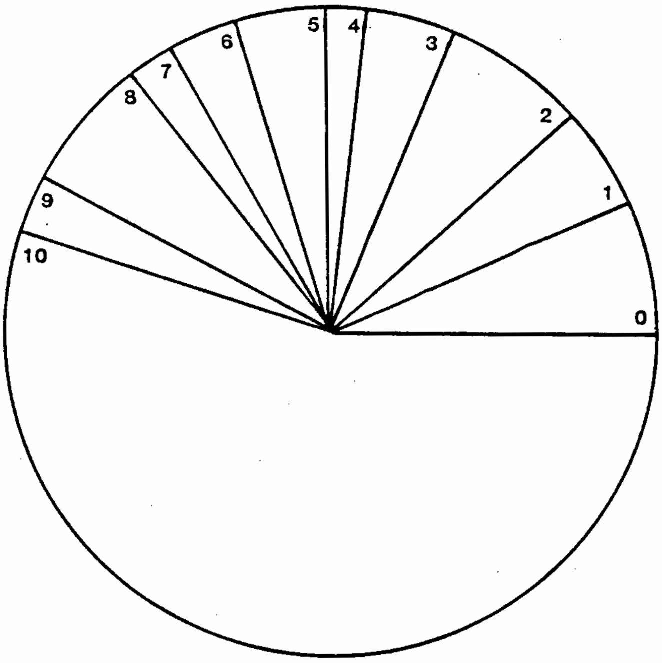
Nest SN was the most commonly used nest, being used 81.97 % of the total time spent in the nests. Nests NN and MN were used only infrequently, 15.28 % and 2.75 % of the nest time, respectively. Of the total time spent out of the nest, 64.15 % was spent in foraging zone SF, 15.63 % in MF, 9.16 % in NF, 6.47 % in SE, and 4.58 % in zone SW.

Discussion

At the outset, two limitations of this study should be considered. Firstly, all interpretations of activity data obtained by radio-telemetry will always be partially subjective, involving assumptions based on the best intuition of the worker. Nevertheless, provided that the data are not evaluated too rigourously, and all assumptions are considered, tentative conclusions can be reached concerning the ecology and behaviour of subterranean

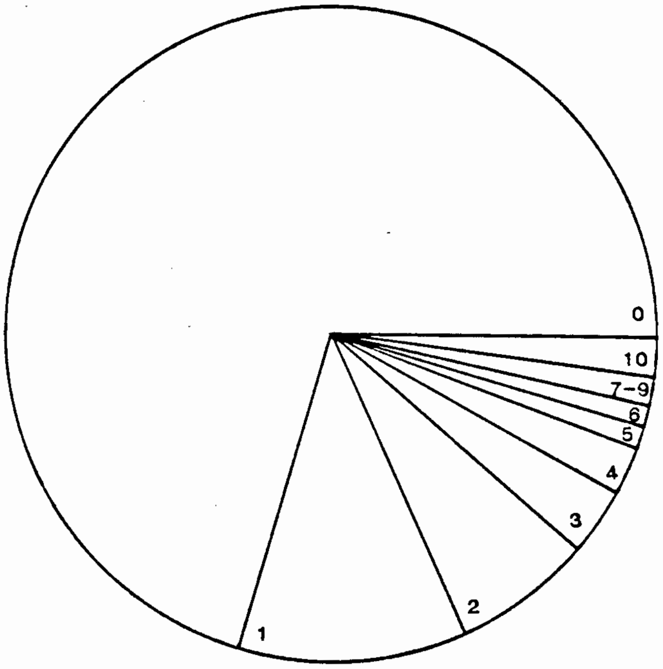


A. In the nest

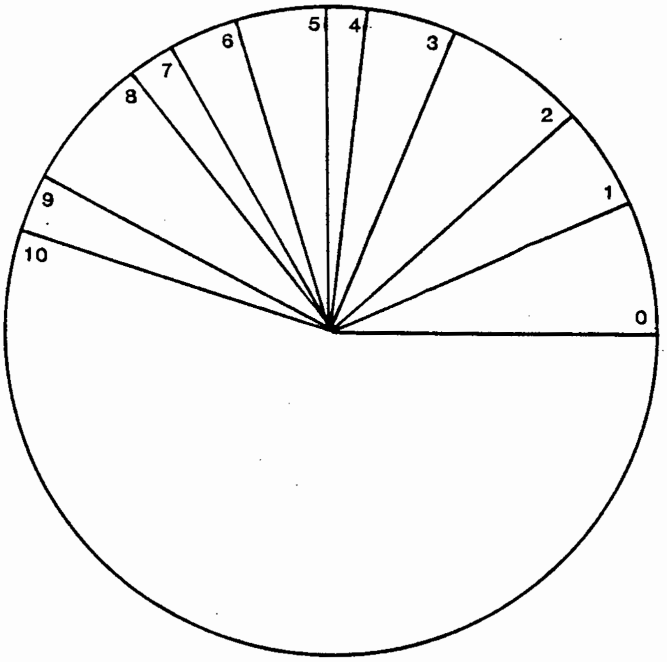


B. Out of the nest

Fig. 22. Pie diagrams showing the average (for five animals) percentage time that *C. damarensis* spent in each activity state (0 - 10) while in the nest (A) and out of the nest (B).



A. In the nest



B. Out of the nest

Fig. 22. Pie diagrams showing the average (for five animals) percentage time that *C. damarensis* spent in each activity state (0 - 10) while in the nest (A) and out of the nest (B).

rodents. Moreover, this study deals with one colony of molerats, from one habitat, at one time of the year, so the patterns reported do not necessarily reflect the yearly patterns for the species throughout its geographical range. Radio-telemetry studies on social subterranean rodents such as this one, and that of Brett (1986), are difficult and time consumming. They have been conducted in remote habitats where the risk of predator attack on field workers at night is a constant concern and, in the Kalahari, daytime temperatures frequently reach 43°C in the shade. Conditions were therefore far from ideal for collecting consecutive data.

Colony size and structure

The fact that the colony had a male/female sex ratio of 3.75 strongly in favour of males might not be completely typical of the overall pattern for the species. For instance, Bennett & Jarvis (1987) report sex ratios of 0.71 - 0.78 for *C. damarensis* in Namibia. Nevertheless, the fact that *H. glaber* colonies also show sex ratios in favour of males suggests that the ratio may have some adaptive significance for social molerats in more arid habitats. *H. glaber* colonies had sex ratios of 0.87 - 1.67, mean of 1.12 for 14 colonies (Brett 1986), and 1.08 - 1.67, mean of 1.29 for seven colonies (Jarvis 1985). Additional complete colonies of *C. damarensis* need to be trapped in different areas to establish a more definite sex ratio trend. In any event, these sex ratios are considerably higher than the range of 0.25 - 0.5 reported for solitary subterranean rodents (Nevo 1979).

The three size classes evident in the colony raises the question of the possible existence of size-related worker castes in the colony. For instance, is it possible that the nine small SC3 molerats represent a worker caste? Considering that *C. damarensis* tends to be K-selected with an average litter size of 2.8 precocial pups (Bennett & Jarvis 1987), it is unlikely that the nine similar sized molerats in SC3 represent the most recent single litter. In *H. glaber* colonies, Jarvis (1981) reports the existence of a worker caste comprised almost entirely of the smallest molerats in the colony (mean mass: 28 g), and an infrequent worker caste with a significantly greater mean mass of 35 g. Furthermore, Jarvis (1981) mentions that those molerats apparently destined to remain in the worker caste permanantly show very slow growth rates, whereas other workers display polyethism in that they undergo a progressive change of roles accompanied by an increase in growth rate. Behavioural observations of captive colonies of *C. damarensis* also show indications of the existence of a worker caste and polyethism, synonomous with that of *H. glaber* (Bennett & Jarvis 1987). I would tentatively conclude therefore that SC3 represents a worker caste and that these molerats are subjected to very slow growth rates to maintain an 'optimal' worker caste size (see Chapters Eight and Eleven). It is, however, important that this suggestion be substantiated with additional comparative radio-telemetry using smaller transmitters than were used in this study so that molerats weighing less than 130 g may be monitored. Although at the outset of the study I had no idea of the existence of the worker caste, I was nevertheless unable to obtain powerful transmitters smaller than the 9 g ones I used. The transmitters I did use would have added 10 % to the body mass of molerats 80 - 100 g, which would undoubtedly have affected natural foraging behaviour.

The fact that SC1 molerats were invariably the first four or five molerats caught in each trapping session, suggests that this male-dominated size class may perform a soldier function in that they are the first molerats to be exposed to potential danger. When the two large molerats were monitored simultaneously, they often occupied separate nests (SN and NN) during the same periods. Although it is very speculative at this stage, this observation might suggest a patrolling function whereby large males maintain a presence at the two opposite extremes of the burrow system. Considering that SN and NN are separated by a distance of 152 m (Fig. 19), having soldiers at both ends of this distance would reduce the probability of predators gaining access to the burrow system undetected. Brett (1986) has also suggested a patrolling function for individual *H. glaber.*

Unfortunately I am unable to offer a sound explanation for the absence of a female showing any obvious breeding indications. It is possible that the breeding female was not trapped, but considering the total trapping intensity (1536 trap hours), it was unlikely, unless she was tending newly born young and would not, or could not, attend to the opened burrows. She could also have died recently. In both *C. damarensis* colonies examined by Bennett & Jarvis (1987), the breeding females were the largest *(ca.* 200 g) females in the colony.

An interesting aspect of the soil temperatures at the depth of the primary burrow between 20 - 40 cm, also discussed in Chapter Three, was that these temperatures were 3 - 4°C higher than the upper limit of thermoneutrality of *C. damarensis* (Chapter Six). Admittedly the animals used in the metabolic study were temperature acclimated to 23°C, suggesting that the upper limit of thermoneutrality of free-ranging animals in summer could be higher than the observed laboratory temperature of 30°C. Even so, it is unlikely that the limit can shift by more than 1 - 2°C meaning that *C. damarensis* should still experience elevated body temperatures and oxygen consumption at primary burrow temperatures in summer. Considering the added input of metabolic heat produced during foraging and burrowing (Chapter Eight), and the reduced evaporative and convective cooling ability caused by a closed burrow system with a high relative humidity (McNab 1979a), heat storage problems should constrain foraging and activity patterns. This is true, particularly considering that the temperature of the primary burrow remains constantly high, and has very little daily fluctuation. The comparatively small variance about the mean time spent out of the nest, and the sharply defined normal distribution of these activity periods (Fig. 21), support this suggestion. This observation infers that molerats can spend about an hour foraging before heat storage and elevated body temperatures necessitate that the animals return to the deeper, cooler parts of the burrow system, such as the nest or bolthole, to offload excess body heat through conductance.

There is no objective means of establishing whether the activity states recorded from pulse modulations of the transmitter tilt-switches do in fact correspond with the assumed activity state of the animal. Nevertheless, the data do show logical trends. When molerats were out of the nest I could very easily distinguish between a count of 10 (and greater) and a count of nine. Often the count of 10 was reached well within the 60 s counting period, and there was no doubt that the molerat was exceptionally active and probably engaged in maximum burrowing activity. The large difference between the percentage times spent in activity state 9 and activity state 10 illustrates this dichotomy (Fig. 22). On the other, hand when molerats were in the nest the gradual decrease from activity state 10 to activity state 1, followed by the large decrease to activity state 0, represents a logical trend suggesting sleeping and resting behaviour mostly (Fig. 22). In Chapter Eight I have assigned rates of energy expenditure to these component activity states and have attempted to calculate a daily energy expenditure for *C. damarensis*.

Conclusions

This study has answered some of the questions posed at the outset. It provides one good example of the colony size and colony structure of *C. damarensis*. It has shown that size classes exist which cannot be interpreted as representing single litters of a single breeding pair. It provides some indication of the possible existence of a size-related caste system of workers and soldiers. It has shown that the activity of *C. damarensis* is not influenced by photoperiod or soil temperature. It suggests that *C. damarensis* may employ a certain degree of behavioural thermoregulation to maintain homeothermy, and that the burrow system is constructed in such a manner e.g. the bolthole, so as to allow behavioural thermoregulation.

CHAPTER FIVE

Thermoregulation of the Subterranean Rodent Genus *Bathyergus* (Bathyergidae).

Thermoregulation of the subterranean rodent genus *Bathyergus* (Bathyergidae)

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The thermoregulation of the largest subterranean rodent, genus *Bathyergus*, comprising two species, *B. suillus* and *B. janetta*, occurring in mesic and semi-arid habitats respectively, was investigated and compared with that of other subterranean rodents. Both species display low resting metabolic rates and low body temperatures characteristic of subterranean rodents. The lower metabolism and smaller body size of *B. janetta*, may be an 'energy-saving' adaptation to its semi-arid habitat.

S. Afr. J. Zool. 1986, 21: 283 – 288

Termoregulering in die grootste ondergrondse knaagdier, genus *Bathyergus*, wat uit twee spesies, *B. suillus* en *B. janetta*, bestaan, is ondersoek en met die van ander ondergrondse knaagdiere vergelyk. *B. suillus* en *B. janetta* kom onderskeidelik in gematigde en droë streke voor. Beide spesies vertoon lae rustende metaboliese tempo's en lae liggaamstemperature, wat kenmerkend is van ondergrondse knaagdiere. Die laer metabolisme en kleiner liggaamsgrootte van *B. janetta* mag 'n energiebesparingsaanpassing by sy droë habitat wees.

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Subterranean rodents spend their lives underground in closed burrows, rarely, if ever, coming on to the surface (Nevo 1979). The commitment of these animals to a subterranean existence is reflected in several convergent structural and functional adaptations within the subterranean taxa (Ellerman 1956; McNab 1966; Dubost 1968; Nevo 1979). For instance, they show distinctive physiological traits, such as low body temperature (T_b), low resting metabolic rate (*RMR*), and high conductance (C_m) (McNab 1979, for general review). Various hypotheses have been proposed to explain these unusual physiological states.

It has been suggested that the combination of low *RMR*, low T_b, and high C_m, reduces the possibility of overheating in burrows where evaporative cooling and convection play minor thermoregulatory roles (McNab 1966; MacMillen & Lee 1970; McNab 1979). A low *RMR* could represent an adaptation to hypoxia and hypercapnia (Arielli 1979; Arielli, Arielli, Heth & Nevo 1984). Finally, it has been suggested that a low resting metabolic rate may represent an energy-saving adaptation in response to the enormous energetic cost of burrowing (Vleck 1979, 1981), and limited food availability and resource patchiness (Jarvis 1978).

The task of establishing the relative roles and influences of each of the above possible physiological determinants, as well as the possible interplay between them, is very difficult. One approach is to investigate interspecific comparisons of the ecophysiological characteristics of subterranean mammals differing in body size, social status, and habitat.

This paper examines the thermoregulation of the genus *Bathyergus*, which is represented by two solitary species *B. suillus*, and *B. janetta*, occurring allopatrically in mesic and semi-arid habitats respectively, in the western Cape Province of South Africa. *B. suillus* is probably the largest extant subterranean rodent. The data obtained from this study should therefore assist the future determination and interpretation of the allometry of the metabolism of subterranean rodents.

Methods

The Namaqua dune molerat *B. janetta* is rare, and is listed in the 'South African Red Data Book' of rare and endangered species. Its distribution is limited to the loose, calcretic sand dunes along the north-western Cape coast, from Port Nolloth to the Orange River (De Graaff 1981). This region is arid to semi-arid, with cool, moist oceanic winds and fog providing frequent relief from high temperatures and low relative humidity (Louw & Seely 1982).

Ten *B. janetta* were trapped near Oranjemund, Namibia, in December 1983. Each animal occupied its own burrow system (Jarvis & Lovegrove, unpubl.) contrary to the notion that this species is social (De Graaff 1981). Solitary animals were housed in 32 × 60 cm glass terraria under a continuous light at 23°C for at least two months prior to experimentation, and were fed on fresh grasses, herbaceous plants, chopped vegetables, and 'Pronutro' (Cerebos Food Corporation Ltd., Wadeville), a nutritionally-balanced cereal food. A 5 – 6 cm layer of dry sandy soil was placed in the bottom of the terraria every two days. The molerats regularly shifted the sand around the cages, but were unable to actually construct burrows. Of the 10 molerats, only three, one male and two females, survived. After losing weight for the first two weeks, they regained capture weights (354 g, 380 g, and 485 g) and thereafter remained in good condition prior to, and including the entire experimental period.

The Cape dune molerat, *B. suillus*, occurs in the mediterranean winter rainfall region of the western Cape, South Africa, wherever loose coastal calcereous sand dunes and sand flats are present (De Graaff 1981). De Graaff (1981) describes *B. suillus* as living in small colonies of two to five individuals, but again, Davies & Jarvis (1986) found this species to be strictly solitary. De Graaff (1981) also gives mean body masses of 750 g for males, and 500 g for females, whereas Davies & Jarvis (1986) give mean masses obtained from larger sample sizes of 933 g for males (maximum recorded: 1700 g), and 635 g for females.

In April 1984 eight *B. suillus* were trapped at various localities in the western Cape. Solitary animals were housed in 44 × 90 cm fibreglass tanks, and were kept under the same conditions and fed the same diet as *B. janetta*. Four animals, two males and two females, maintained weights (520 g, 633 g, 703 g and 800 g) throughout the experimental period, and were used to measure metabolic rate. In addition, eight metabolic measurements were obtained from a large 1004-g male before it began to lose weight and condition.

In general, molerats of the genus *Bathyergus*, particularly the rare *B. janetta*, do not adapt well to captivity and seem to require a long period of adjustment before body weights stabilize. This is a serious problem with respect to obtaining large sample sizes, which can only really be achieved at the expense of high mortality in captivity.

Oxygen consumption ($\dot{V}O_2$) was measured at ambient temperatures (T_a) of 13 – 34°C using a negative pressure flow-through system. The respirometer was a transparent 4,54 ℓ cylindrical perspex chamber fitted with a plastic base-plate and 6 mm inlet and outlet ports, and was placed inside a 110 ℓ temperature-controlled cabinet. Air was drawn through the respirometer at a constant rate of 900 and 1200 cm^3min^{-1} for *B. janetta* and *B. suillus* respectively. Airflow was monitored with a calibrated 'Rotameter 1100' flow-meter placed downstream from the respirometer, but upstream from a set of CO_2 and H_2O scrubbers. A subsample of the expired air was drawn off downstream from the gas scrubbers and analysed with an 'Applied Electrochemistry S-3A' oxygen analyser. An 'Esterline Angus P.D.2064' data logger recorded the electrical output of the analyser (equivalent to percentage oxygen), at 2-min intervals for 2 – 3 h. Control 'blank' readings of the percentage of atmospheric O_2 were obtained from a parallel circuit consisting of a replicate respirometer and gas scrubbers.

Animals were deprived of food for 3 h prior to measurement of metabolic rate in order to reduce the influence of specific dynamic action. Rectal temperatures were recorded with a rectal thermocouple inserted approximately 3 cm into the rectum, within 1 min of the termination of each run. The existence of a possible endogenous diel metabolic rhythm was determined by continuous 24-h monitoring of metabolic rate of a single animal of each species, at 27°C and 28°C for *B. suillus* and *B. janetta* respectively. Readings were taken at 5-min intervals, with the mean of the five lowest readings per hour being used to plot the pattern of metabolism.

Results were analysed for individual animals, and for various groups, depending on the individual results. The mean body size of *B. janetta* was 406 g. The *B. suillus* were divided into three groups; all five animals (mean body size of 732 g), the four 520 – 800-g animals (mean body size of 664 g), and the three 633 – 800-g animals (mean body size of 712 g). The first hour of exposure was regarded as a period of adjustment. The mean of the ten lowest $\dot{V}O_2$ values after the first hour was used to calculate *RMR* in $cm^3g^{-1}h^{-1}$ (STP) using the equation of Durnin & Passmore (1967). Resting metabolic rates within the thermoneutral zone (TNZ) are expressed as the means (±*SD*) for individual animals, and as the population mean (±*SE*) for the groups. Conductance below the lower limit of thermoneutrality (T_l) was calculated using the formula: $C_m = \dot{V}O_2/(T_b - T_a)$ McNab (1980), and expressed as individual means (±*SD*), and population means (±*SE*) for the groups, in $cm^3g^{-1}h^{-1}°C^{-1}$ (STP). Conductance was compared with the value predicted by the equation of McNab & Morrison (1963); $C_m = 1,00\ M^{-0,50}$. All statistical tests are from Zar (1974).

Results

For the individuals of both species there was no marked difference in metabolic rate between the normal light and dark hours. Typically, the 24-h period was characterized by 1 – 2-h periods of relatively constant metabolic rate when the molerats were involved in grooming, feeding, resting and coprophagous behaviour, interspersed by shorter 20 – 30-min periods of elevated metabolic rates associated with scratch-digging behaviour and the gnawing of the inside of the respirometer. The lack of a marked endogenous diel metabolic pattern in *Bathyergus* is consistent with observations in other subterranean rodents (Vaughan & Hansen 1961; Gettinger 1975; Andersen & MacMahon 1981). I assumed that I could ignore diel endogenous fluctuations in metabolic rate.

The body temperature of *B. suillus* remained stable at T_a between 13 – 27°C (Figure 1b). The mean T_b of the 664-g group in this temperature range was 35,3 ± 0,1°C (Table 1). The 1004-g molerat had a lower T_b of 34,8 ± 0,4°C (Table 1). Above 27°C, T_b increased to approximately 38°C at a T_a of 34°C, the highest temperature to which *B. suillus* was exposed. The mean body temperature of *B. janetta* between 24 – 27°C was 34,7 ± 0,3°C, and was stable (Figure 2b). However, below 24°C the mean body temperature, 34,8 ± 0,8°C, was significantly more variable ($p < 0,05$; one-tailed *F* test) (Figure 2b). The mean T_b at T_a between 16 – 27°C was 34,7 ± 0,3°C (Table 1), which was significantly lower than that of the 664-g *B. suillus* group ($p < 0,05$; Student's *t* test). Above 27°C, T_b increased to approximately 39°C at a T_a of 35°C.

The 664-g group of *B. suillus* had a resting metabolic rate of 0,48 ± 0,02 $cm^3g^{-1}h^{-1}$ (Table 1) within a thermoneutral zone of 25 – 31°C (Figure 1a). The 1004-g molerat had a *RMR* of 0,32 ± 0,02 $cm^3g^{-1}h^{-1}$ (Table 1), which was significantly lower than the population mean for the 664-g group ($p < 0,05$; Student's *t* test). Below T_l to a T_a of 13°C, there was a significant linear increase in metabolism with decreasing T_a in all *B. suillus* ($p < 0,05$; least-squares fit) (Table 2). The smallest molerat showed the greatest metabolic increase below T_l; $\dot{V}O_2 = -0,050\ T_a + 1,698$

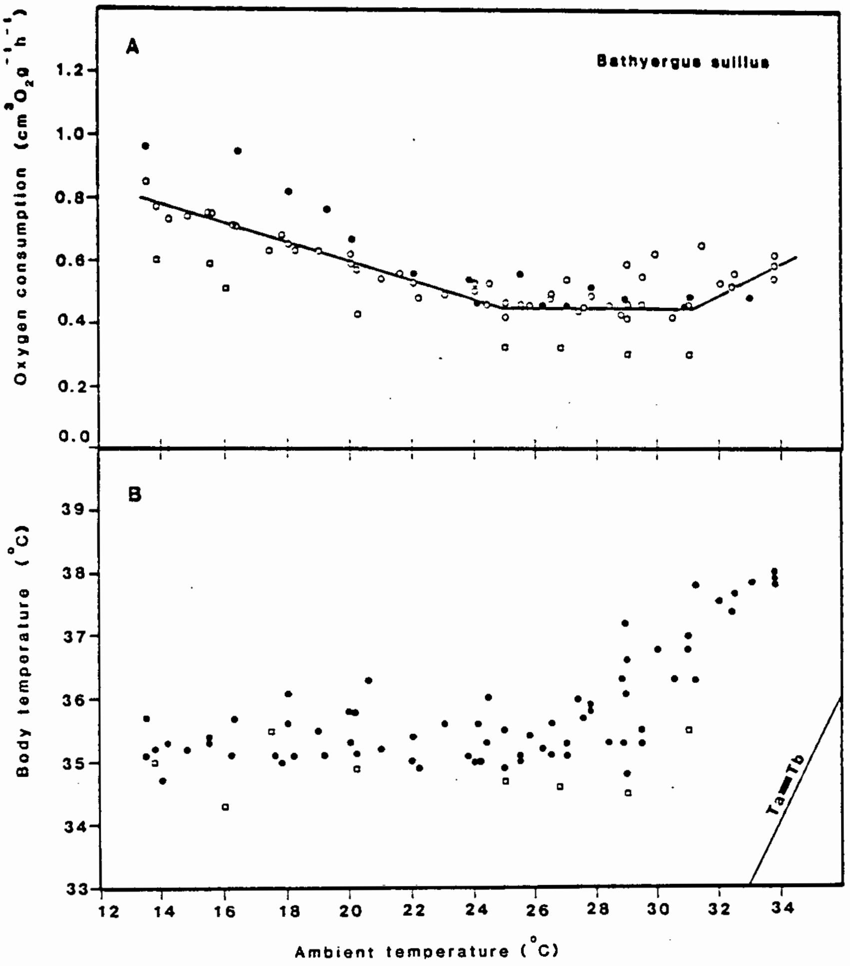

Figure 1 The Cape dune molerat *Bathyergus suillus*. (A) Oxygen consumption as a function of ambient temperature. Symbols represent three size groups; three molerats with a mean body mass of 712 g (circles), a single 520-g animal (dots), and a single 1004-g animal (squares). The horizontal line represents the mean resting metabolic rate of the 712-g and 520-g groups. The line below the lower limit of thermoneutrality represents the regression of the 712-g data. (B) Body temperature as a function of ambient temperature. The 712-g and 520-g groups are pooled (dots), and the squares represent the 1004-g animal.

Table 1 Mean body sizes, resting metabolic rates (at thermoneutrality), body temperatures, and conductances (below the lower limit of thermoneutrality), of five *B. suillus*, and three *B. janetta*; population means and standard errors of various size groups are also given

Species	Animal number	Body mass (g)	*RMR* cm^{3}g^{-1}h^{-1} (*n*)	*SD*	T_b °C (*n*)	*SD*	C_m cm^{3}g^{-1}h^{-1}°C^{-1} (*n*)	*SD*
B. suillus	2	520	0,51 (7)	0,05	35,4 (10)	0,3	0,045 (7)	0,003
B. suillus	1	633	0,45 (6)	0,01	35,2 (9)	0,3	0,039 (7)	0,003
B. suillus	3	703	0,52 (7)	0,07	35,3 (10)	0,3	0,037 (6)	0,002
B. suillus	5	800	0,46 (7)	0,03	35,5 (6)	0,3	0,038 (9)	0,001
B. suillus	6	1004	0,32 (3)	0,02	34,8 (6)	0,4	0,029 (4)	0,001
B. suillus	1,3,5	712	0,48	0,02	35,3	0,2	0,038	0,001
B. suillus	1–3,5	664	0,48	0,04	35,3	0,1	0,040	0,003
B. janetta	1	485	0,50 (7)	0,05	34,9 (9)	0,6	0,066 (9)	0,001
B. janetta	2	354	0,57 (6)	0,08	34,9 (12)	0,6	0,070 (12)	0,001
B. janetta	4	380	0,54 (6)	0,08	34,4 (8)	0,5	0,069 (8)	0,001
B. janetta	1,2,4	406	0,54	0,03	34,7	0,3	0,069	0,003

(r^2 = 0,942), whereas the largest *B. suillus* had the lowest; $\dot{V}O_2 = -0{,}025T_a + 0{,}936$ ($r^2 = 0{,}952$) (Table 2). There was no significant difference between the regression coefficients of the three intermediately sized molerats comprising the 712-g group ($p < 0{,}05$; comparison of slopes). The pooled data for this group showed the best fit of the groups, given by the equation $\dot{V}O_2 = -0{,}029 + 1{,}182T_a$ ($p < 0{,}05$; $r^2 = 0{,}931$, least-squares fit) (Table 2, Figure 1a). The regression coef-

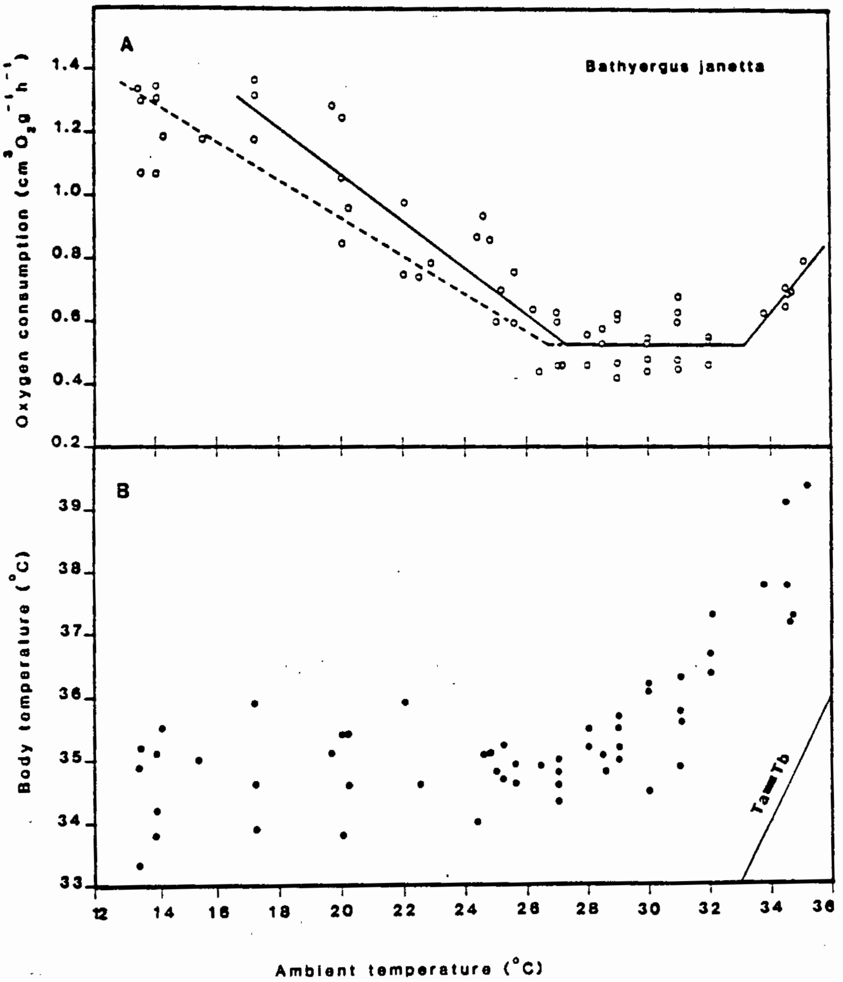

Figure 2 The Namaqua dune molerat. (A) Oxygen consumption as a function of ambient temperature. The horizontal line represents the mean resting metabolic rate. The lines below the lower limit of thermoneutrality represent the regression of all $\dot{V}O_2$ and ambient temperature (broken line), as well as $\dot{V}O_2$ as a function of ambient temperatures down to 16°C (solid line). (B) Body temperature as a function of ambient temperature.

Table 2 Statistics of the linear regressions of metabolic rate as a function of ambient temperature below 25°C and 27°C, for *B. suillus* and *B. janetta* respectively; regressions were calculated on data from individual animals, as well as from data pooled for various groups

Species	Animal number	Sample size	Regression coeff.	*SE*	*Y* intercept	*SE*	Correlation coeff. (r^2)	*p* slope = 0
B. suillus	2	8	−0,050	0,005	1,698	0,017	0,942	< 0,05
B. suillus	1	8	−0,029	0,004	1,188	0,014	0,903	< 0,05
B. suillus	3	8	−0,031	0,002	1,194	0,008	0,969	< 0,05
B. suillus	5	11	−0,027	0,002	1,152	0,006	0,972	< 0,05
B. suillus	6	5	−0,025	0,003	0,936	0,013	0,952	< 0,05
B. suillus	1−3,5,6	40	−0,030	0,004	1,195	0,014	0,617	< 0,05
B. suillus	1−3,5	35	−0,033	0,003	1,287	0,011	0,787	< 0,05
B. suillus	1,3,5	27	−0,029	0,002	1,182	0,006	0,931	< 0,05
B. janetta	1	10	−0,056	0,013	2,060	0,059	0,710	< 0,05
B. janetta	2	14	−0,052	0,006	2,066	0,031	0,846	< 0,05
B. janetta	4	9	−0,051	0,010	1,988	0,052	0,772	< 0,05
B. janetta	1,2,4	33	−0,053	0,005	2,050	0,025	0,773	< 0,05

ficients of the 520-g and 1004-g animals were significantly greater and lower respectively, than that of the 712-g group ($p < 0,05$, comparison of slopes).

B. janetta had a TNZ from 27,5 − 33,2°C, and a *RMR* of 0,54 ± 0,03 cm^{3}g^{-1}h^{-1} within this range (Figure 2a, Table 1). All three *B. janetta* showed a significant linear increase in metabolic rate below T_l ($p < 0,05$; least-squares fit). There was no significant difference between individual regression coefficients ($p < 0,05$; comparison of slopes). The regression of the pooled data for the group is given by the equation $\dot{V}O_2 = -0,053 + 2,050T_a$ ($p < 0,05$; $r^2 = 0,773$; least-squares fit) (broken line in Figure 2a, Table 2). The regression coefficient for this group was significantly greater than that of the 712-g group of *B. suillus* ($p < 0,05$; comparison of slopes).

An interesting observation of the metabolic increase below T_l for the *B. janetta* group, is that it decreases at T_a below 16°C (Figure 2a). A sign-test, significant at the 1% level, showed that all eight data points below 16°C, fall below the values predicted by the equation of the regression of $\dot{V}O_2$ and T_a between 16–27,5°C ($\dot{V}O_2 = -0,075T_a + 2,566$; $p < 0,05$; $r^2 = 0,800$; least-squares fit, solid line in Figure 2a). The regression coefficient of this curve was significantly greater than that for the curve relating $\dot{V}O_2$ to all T_a below T_l ($p < 0,05$; comparison of slopes).

Conductance in *B. suillus* ranged from 0,045 ± 0,003 $cm^3g^{-1}h^{-1}{}^{\circ}C^{-1}$ for the 520-g molerat, to 0,029 ± 0,001 $cm^3g^{-1}h^{-1}{}^{\circ}C^{-1}$ for the 1004-g animal (Table 1). The mean conductance for the 712-g group was 0,038 ± 0,001 $cm^3g^{-1}h^{-1}{}^{\circ}C^{-1}$ (Table 1). The conductances of the 520-g and 1004-g molerats were significantly greater and lower respectively, than the mean conductance of the 712-g group ($p < 0,05$; Student's *t* test). The mean conductance over all T_a below T_l of the *B. janetta* group, was 0,069 ± 0,003 $cm^3g^{-1}h^{-1}{}^{\circ}C^{-1}$ (Table 1), which was significantly greater than the mean conductance of the 712-g group of *B. suillus* ($p < 0,05$; Student's *t* test). The highest mean group estimate of C_m was 0,072 ± 0,003 $cm^3g^{-1}h^{-1}{}^{\circ}C^{-1}$ between 16 –27,5°C. The mean group conductance below 16°C, 0,060 ± 0,007 $cm^3g^{-1}h^{-1}{}^{\circ}C^{-1}$, was significantly lower than the mean group conductance between 16–27,5°C ($p < 0,05$; Student's *t* test).

Discussion

Overall, the various statistics for the 712-g group of *B. suillus*, are probably the most representative of the species. This group showed the least mass-specific variation in *RMR*, conductance and body temperature, over all ambient temperatures.

The fact that the body temperature of *B. janetta* was variable below 24°C, and that the metabolic increment decreased at ambient temperatures below 16°C, suggests that *B. janetta* does not thermoregulate as effectively as *B. suillus* over the same temperature range. Although the results for *B. janetta* suggest that this molerat was able to reduce conductance below 16°C, the fact that in a few instances body temperatures fell below 34°C at ambient temperatures below 14°C, might suggest that this species is incapable of producing sufficient metabolic heat to compensate for heat loss below 14°C. It is not known whether *B. janetta* enters torpor at ambient temperatures lower than 14°C.

The resting metabolic rates of both species are lower than expected for rodents (Hayssen & Lacey 1985), being 83% (664-g group) of expected for *B. suillus*, and 79% of expected for *B. janetta*. The resting metabolic rate of *B. janetta* is not as low as that measured in smaller arid-adapted subterranean rodents, such as *Heterocephalus glaber* (39 g) (McNab 1979), *Thomomys umbrinus* (85 g) (Bradley, Miller & Yousef 1974), *Heliophobius argentocinereus* (88 g) (McNab 1966) and *Spalax ehrenbergi* (2n = 60 chromosome species) (121 g) (Nevo & Shkolnik 1974). These smaller subterranean rodents appear to be more flexible in adapting to thermal stresses (McNab 1979), and the energetic demands of a subterranean existence (Vleck 1979, 1981; Jarvis 1978; Lovegrove 1986), by manipulating metabolic rate, body temperature and conductance.

The eusocial naked molerat *Heterocephalus glaber* (Jarvis 1981), which inhabits semi-arid regions of Kenya, is completely hairless and virtually incapable of thermoregulation, having the highest conductance (242% of expected), and the lowest resting metabolic rate (43% of that predicted by Hayssen & Lacey 1985) and body temperature (32,1°C) of any eutherian (McNab 1979; Withers & Jarvis 1980). *B. suillus* on the other hand, may represent the largest size that a completely subterranean rodent can attain while maintaining a 'precise' thermoregulatory ability over a wide range of ambient temperatures.

Exactly which physical or ecological factors select for low metabolic rates, low body temperatures and body size in subterranean rodents, is not clearly understood. The fact that *B. janetta* is smaller than *B. suillus*, does not necessarily suggest that an adaptation to warm burrows or thermal stress (McNab 1979) is the only factor selecting for body size. The conductance of *B. janetta* (125% of expected) is higher than that of *B. suillus* (103% of expected; 712-g group), lending some support for the 'overheating' hypothesis. However, the low *RMR* and smaller body size of *B. janetta* may also represent 'energy-saving' adaptations. From the *RMR*s and body sizes of these two species, it can be calculated that the daily energetic expenditure of *B. janetta* is approximately 30% lower than that of *B. suillus*, despite its higher mass-specific *RMR*. Assuming that the semi-arid habitat of *B. janetta* has a lower productivity than that of *B. suillus*, it is possible that constraints involved in foraging for low abundance, poor quality food resources, have optimally selected for a low *RMR* and small body size in this molerat.

The interspecific differences in metabolic rate, conductance, and body size of the bathyergids, may represent a compromise between the energetic constraints of foraging in soils differing in hardness and resource parameters, and the energetic constraints imposed by different thermal regimes. It is important to establish the relative habitat-specific roles that these two factors play in the inclusive fitness of the various bathyergids. This will enable a better understanding of not only the eco-physiology of the bathyergids, but also of the adaptive significance of their various social systems.

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CHAPTER SIX

The metabolism of Social Subterranean Rodents: Adaptation to Aridity.

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Oecologia

The metabolism of social subterranean rodents: adaptation to aridity

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Summary. The social Damara mole-rat *Cryptomys damarensis* (124 g), has a mean (±SD) resting metabolic rate of 0.57 ± 0.09 cm^3 O$_2$ g^{-1} h^{-1}, within a thermoneutral zone of 27–31° C. This rate of metabolism is 43% lower than that predicted by the curve for rodents, and 29% lower than that predicted by the subterranean rodent curve. These data support the hypothesis that the resting metabolic rates of social and solitary subterranean rodents are lower than those of solitary species inhabiting mesic habitats. These low resting metabolic rates may represent an energy-saving adaptation to aridity. The energetic cost of burrowing, in relation to the dispersion patterns of food in arid habitats, may explain these low metabolic rates.

Subterranean rodents are those rodents that display morphological, behavioural, and physiological commitments to a totally subterranean existence (Ellerman 1956; Nevo 1970). These animals feed on corms, bulbs, rootstocks, and roots. They rarely, if ever, come to the surface. Energetically, subterranean rodents are quite different from aboveground rodents (McNab 1979). For instance, at thermoneutrality most subterranean rodents have resting metabolic rates (RMR) substantially lower than those of aboveground rodents (McNab 1979). Furthermore, body temperatures (T_b) are low (32–36° C; McNab 1979), and are in fact more characteristic of the body temperatures of marsupials (34–36° C; Dawson and Hulbert 1970), than of aboveground rodents (36–40° C; Morrison and Ryser 1952).

There are various explanations for these atypical mammalian physiological states. Firstly, McNab (1966, 1979) and MacMillen and Lee (1970), maintain that the combination of a low RMR, high conductance (C_m) and low T_b, minimises the chance of overheating in closed burow systems where evaporative water loss and convective cooling play minor roles in the animal's heat balance. Secondly, it has been suggested that a low RMR, along with a low heart rate, may normalise the partial pressures of oxygen and carbon dioxide in the blood and tissues, under the hypoxic and hypercapnic conditions which are characteristic of burrow systems (Darden 1972; Chapman and Bennett 1975; Ar et al. 1977; Arieli et al. 1977; Arieli and Ar 1981). Thirdly, Vleck (1979, 1981) has suggested that a low RMR could represent an adaptation to compensate for the enormous energetic demands of a burrowing existence. Lastly, Jarvis (1978) has suggested that the low RMR of the eusocial Naked mole-rat, *Heterocephalus glaber*, could be an energy-saving adaptation in the face of widely dispersed and scarce food resources.

An analysis of the relative importance of these explanations is difficult. In this study I have tested the hypothesis that social subterranean rodents display resting metabolic rates which are markedly lower than those of other subterranean rodents. I present new data on the energetics of the Damara mole-rat *Cryptomys damarensis*, and review all available literature on the energetics of other social subterranean rodents. In order to compare these findings with solitary subterranean rodents, I have calculated an allometric equation which best describes the RMR of all subterranean rodents studied to-date.

Methods

Study animals

C. damarensis (Ogilby) occurs widely in northern Namibia and Botswana, especially in the western arid areas of the Kalahari desert (De Graaff 1972). Seven mole-rats, four males and three females, were used in this study. Two mole-rats were trapped in northern Namibia in 1980, three at Tweerivieren in the Kalahari Gemsbok National Park, South Africa, in 1984 and two were bred in captivity. Their mean body mass was 124.5 ± 21.0 g (SD). Animals were housed in pairs in glass terraria under a continuous light cycle at 23° C, and were fed on chopped sweet potatoes, apples, and gem squash. The animals were not fasted prior to the experiments. If started, the animals became extremely restless and aggressive, and would in any event practice coprophagy. Therefore, values of RMR, are, if anything, slightly overestimated.

Apparatus and protocol

Oxygen consumption ($\dot{V}O_2$) was measured at nine ambient temperatures (T_a) ranging from 7–36° C, between March and September 1985, using a positive pressure flow-through system. I assumed that the mole-rats do not have an endogenous rhythm in metabolic rate; nevertheless, measurements were made only between 08h00 and 18h00. Using copper-constantan thermocouples, rectal temperatures were measured within 1 min of termination of each experiment. Airflow was measured with a calibrated flow meter placed downstream from the respirometer and the CO_2 and H_2O scrubbers.

The respirometer was a cylindrical perspex chamber (1.17 l) fitted with 6 mm inlet and outlet ports, and a perforated plastic base plate on which the mole-rats rested. Temperatures were kept constant within the respirometer by placing it inside a small (0.11 m^3) temperature controlled cabinet. Outside air was pumped through the respirometer, scrubbers, and oxygen analyser at 280–500 $cm^3\ min^{-1}$. 'Blank' readings were provided by a parallel flow-through system incorporating a replicate, but empty, respirometer.

The techniques of Bartholomew et al. (1985) and Lighton (1985) were used to measure $\dot{V}O_2$ on one channel of an Applied Electrochemistry S-3A two channel oxygen analyser. Each run was programmed to last for 213 min, but if the animal was calm and resting, and oxygen consumption was stable for 10–15 min, the run was terminated after 160 min. Data from successful runs were then stored on disc for later analysis. When the data for an animal were analysed, the first hour of each run was regarded as a minimum period of adjustment to a different T_a. The 5–6 min portion of the trace corresponding to the lowest stable oxygen consumption was integrated, calculated in $cm^3\ O_2\ g^{-1}\ h^{-1}$ (STP), and presented as the mean ± SD for each T_a. The relationship of $\dot{V}O_2$ and T_a, when T_a was below the lower limit of thermoneutrality (T_l), was analysed using the method of least squares (Zar 1974). Conductance below T_l was calculated from individual measurements of $\dot{V}O_2$ using the formula: $C_m = \dot{V}O_2/(T_b - T_a)$ (McNab 1980), and presented as the mean ± SD in $cm^3\ O_2\ g^{-1}\ h^{-1}\ {}^\circ C^{-1}$.

The allometric equation

Log transformed RMRs and body masses of 17 species of subterranean rodents were used to obtain a regression of RMR as a function of body mass by the method of least squares (Zar 1974). In cases where repeated studies have been conducted on one species, I have taken the mean RMR and body mass of the independent studies. Data from studies which used less than three animals to measure RMR were not used. Because insectivores tend to display higher resting metabolic rates than rodents (Hayssen and Lacey 1985), subterranean insectivores were not included in the regression.

Results

The body temperature of *C. damarensis* remains stable at T_a's from 7–30° C, with a mean of $35.2 \pm 0.8°$ C (Fig. 1). Above 30° C, T_b increases to a mean of $39.2 \pm 0.6°$ C at a T_a of 36° C. The mean resting metabolic rate was $0.57 \pm 0.09\ cm^3\ O_2\ g^{-1}\ h^{-1}$ within a thermoneutral zone of 27–31° C (Fig. 2). Below T_l the increase in metabolic rate is given by the equation: $\dot{V}O_2 = 3.28 - 0.10\ T_a$ ($n = 35$, $r = 0.96$, $P < 0.001$). The mean metabolic rate at 7° C was $2.52 \pm 0.22\ cm^3\ O_2\ g^{-1}\ h^{-1}$, which is 4.4 times greater than the RMR. The mean conductance for all T_a's below 27° C was $0.085 \pm 0.012\ cm^3\ O_2\ g^{-1}\ h^{-1}\ {}^\circ C^{-1}$.

Discussion

The resting metabolic rates and body masses (M) of 16 species of subterranean rodents, taken from the literature, together with the data from this study on *C. damarensis* (Table 1), gives the power curve:

$$RMR = 3.79\ M^{-0.322}\ (r = -0.67,\ P < 0.05,\ \text{Fig. 3}) \qquad (1)$$

For comparative purposes, these data are also expressed as the percentages of the resting metabolic rate predicted by the curve for rodents (Hayssen and Lacey 1985), and Eq. 1. The resting metabolic rate of *C. damarensis* is about half (57%) of that predicted by the rodent curve, and 71% of that predicted by Eq. 1. With the exception of *H. glaber*, *C. damarensis* has the lowest mass-specific resting metabolic rate of all subterranean rodents.

The body temperature of *C. damarensis* is low compared with those listed by Morrison and Ryser (1952) for above-ground mammals, but is similar to the T_b's of other subterranean rodents (Bradley and Yousef 1975; McNab 1979). The fact that body temperatures remained stable at 7° C, suggests that despite its low T_b, *C. damarensis* thermoregulates well. The conductance of *C. damarensis* is 95% of that predicted by the equation for rodent conductance: $C_m = 1.00\ M^{-0.50}$ (McNab and Morrison 1963). This equation has been used to compare the conductances of subterranean

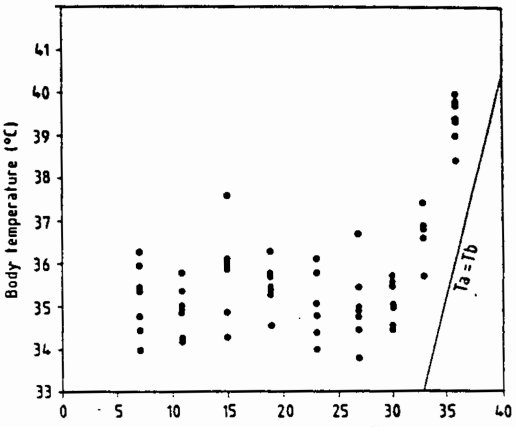

Fig. 1. Body temperature (°C) of seven Damara mole-rats *Cryptomys damarensis*, as a function of ambient temperature (°C)

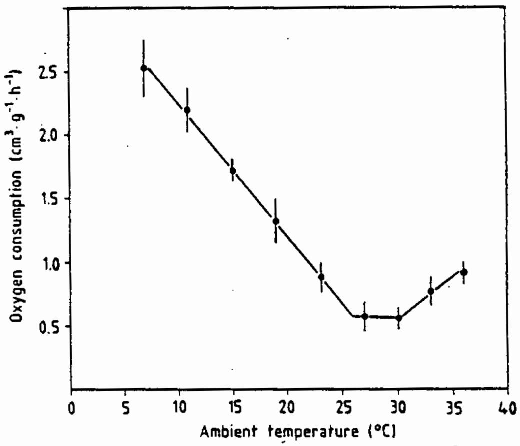

Fig. 2. Mean (±SD) oxygen comsumption ($cm^3\ O_2\ g^{-1}\ h^{-1}$) of seven Damara mole-rats *Cryptomys damarensis*, as a function of ambient temperature (°C)

Table 1. The resting metabolic rate of 17 species of subterranean rodents

Species	Body mass (g)	RMR $cm^3\ g^{-1}\ h^{-1}$	%[a]	%[b]	Social status	Habitat	Reference
Pitymys pinetorum	25.5	2.29	134	171	Solitary	Mesic	1, 9
Thomomys talpoides	105.5	1.22	115	144	Solitary	Mesic	4, 7, 12
Spalax ehrenbergi ($2n=52$)	116.0	0.95	92	115	Solitary	Mesic	5
Tachyoryctes splendens	191.0	0.79	90	113	Solitary	Mesic	9
Spalax leucodon	151.9	0.84	89	112	Solitary	Mesic	2, 3, 4, 8
Spalacopus cyanus	185.0	0.79	89	112	Solitary?	Mesic?	9
Geomys pinetis	152.2	0.83	88	111	Solitary	Mesic	9, 10
Spalax ehrenbergi ($2n=58$)	120.5	0.86	84	106	Solitary	Mesic/Semi-Arid	5
Bathyergus suillus	620	0.49	83	102	Solitary	Mesic	14
Geomys bursarius	197	0.70	81	101	Solitary	Mesic	6
Bathyergus janetta	406.0	0.53	78	97	Solitary	Semi-arid	14
Thomomys umbrinus	95.3	0.85	77	97	Solitary	Semi-arid	4
Heliophobius argentocinereus	88.0	0.85	75	95	Solitary	Semi-arid	9
Cryptomys hottentotus	95.0	0.68	62	78	Solitary	Semi-arid	13
Spalax ehrenbergi ($2n=60$)	121.0	0.62	61	77	Solitary	Semi-arid	5
Cryptomys damarensis	125.0	0.57	57	71	Social	Arid	15
Heterocephalus glaber	39.5	0.64	43	55	Social	Arid	9, 11

References: (1) Pearson (1947); (2) Gorecki and Christov (1969); (3) McNab (1973); (4) Bradley et al. (1974); (5) Nevo and Shkolnik (1974); (6) Bradley and Yousef (1975); (7) Gettinger (1975); (8) Arieli et al. (1977); (9) McNab (1979); (10) Ross (1980); (11) Withers and Jarvis (1980); (12) Kenagy and Vleck (1982); (13) Haim and Fairall (1986); (14) Lovegrove (1986); (15) This study

[a] RMR as percentage of that predicted by rodent curve: $RMR = 4.98\ M^{-0.331}$ (Hayssen and Lacey 1985)

[b] RMR as percentage of that predicted by subterranean rodent curve: $RMR = 3.79\ M^{-0.322}$ (This study) (M = body mass in grams)

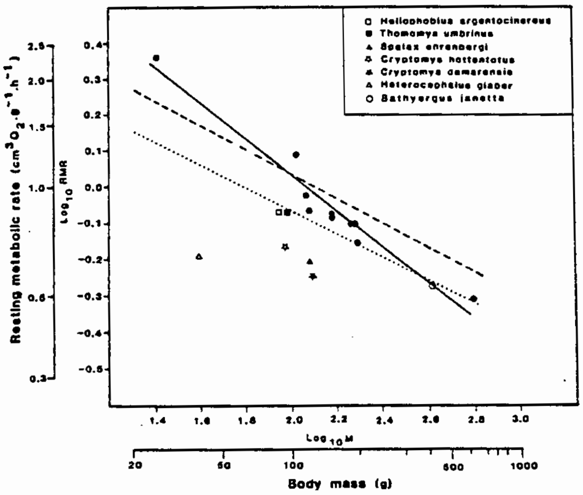

Fig. 3. Log-log plots of resting metabolic rate (RMR) at thermoneutrality as a function of body size (M, in grams). The broken line represents the regression of 122 rodent species, equivalent to the power curve: $RMR = 4.98\ M^{-0.331}$ (Hayssen and Lacey 1985). The dotted line represents the regression of 17 species of subterranean rodents (all symbols, data from Table 1), equivalent to the power curve: $RMR = 3.79\ M^{-0.322}$. The solid line was obtained by excluding all arid and semi-arid adapted species (listed in Fig.) from the previous curve. This line is equivalent to the power curve: $RMR = 10.62\ M^{-0.497}$

rodents in the past (McNab 1979). In short, the low resting metabolic rate of the Damara mole-rat greatly exaggerates the trend found in most subterranean rodents. However, the body temperature fits the normal subterranean pattern, whereas conductance is unexpectedly low when compared with other subterranean rodents with low resting metabolic rates (McNab 1979).

It is noteworthy that all species with resting metabolic rates lower than that predicted by Eq. 1 are animals which inhabit semi-arid or arid areas (Table 1). When these seven species are omitted from the allometry for all subterranean rodents, the correlation coefficient of the new curve; $RMR = 10.62\ M^{-0.497}$, is considerably improved from $r = -0.67$ to $r = -0.97$ (Fig. 3). This latter curve is therefore distinctly more representative of the resting metabolic rates of subterranean rodents in general; the outlying species constituting a secondary source of variation in the general allometric pattern for subterranean rodents.

These data not only support the hypothesis that social subterranean rodents display resting metabolic rates lower than most solitary subterranean rodents, but also suggest that solitary species inhabiting semi-arid habitats are similarly adapted. It would seem that aridity-related factors are instrumental in selecting for low metabolic rates and sociality in these mole-rats. We need to decide which physical or ecological feature of arid habitats is the important selective pressure. It would be worthwhile to briefly evaluate the existing hypotheses in order to choose the most feasible alternative(s) with which we can proceed to investigate the influence of aridity.

Concerning the question of blood-gas compositions, we would predict, based on a study in Israel by Arieli (1979) and Arieli et al. (1984), that physiological adaptations to hypoxic and hypercapnic conditions are not important in arid and semi-arid habitats. The thermoregulatory data for *C. damarensis* are also inconsistent with the predictions of the "overheating" hypothesis (McNab 1979); namely that this species, given its low T_b and RMR, should have a high thermal conductance. Irrespective of this discrepency, the hypothesis does not adequately address the ecophysiological adaptive significance of low metabolic rates in subterranean rodents. Instead, the data suggest that energetic constraints related to burrowing and food resources are likely to be more fundamental in selecting for low 'energy-saving' metabolic rates, than the "necessity" to prevent overheating.

Vleck (1979) has shown that the energetic cost of burrowing from one point to another can be 360–3,400 times as expensive as moving the same distance across the surface. His burrowing model (Vleck 1981) suggests that these enormous energetic demands can only be achieved given a certain level of habitat productivity. This threshold imposes certain limitations on subterranean rodent distributions and body size. Jarvis (1978) has suggested that the unusual physiological and behavioural features of *H. glaber* can be attributed to the need to maintain a low energy budget for the colony in response to scarce and widely dispersed food resources. I believe we would be well advised to consider these two hypotheses as being mutually supportive in the investigation of the metabolism of arid-adapted subterranean rodents.

Considering these two lines of thought, we might therefore expect all subterranean rodents to show metabolic adaptations, such as a low RMR, which would conserve as much energy as possible. This is particularly relevant to subterranean rodents which may be prevented from burrowing, and hence finding food, at times of the year when soil hardness or soil temperatures may be energetically expensive and unsuitable. Low resting metabolic rates should be selected for in these animals as a means of conserving energy during inactive periods. Adaptations which conserve energy and increase the probability of finding food under the foraging constraints of arid habitats, might include the following: namely, cooperative searching and food sharing such as is found in social mole-rats, and, a reduction in RMR to compensate for the increased energy demands of a number of animals in the colony, as well as the probable poor quality of the food, and the long distances required to burrow in order to find widely dispersed food resources.

A comparative study of the predictions of a model which considers the energetic cost of burrowing in relation to ecological aspects, such as geophyte dispersion patterns and abundances, should prove to be a rewarding ecophysiological approach to isolating the causes of the secondary RMR variation displayed by subterranean rodents inhabiting arid areas. A similar approach by Du Toit et al. (1985) has recently highlighted an interesting energy balance problem in the solitary Cape mole-rat, *Georychus capensis*.

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CHAPTER SEVEN

Thermoregulation in the Subterranean Rodent *Georychus capensis* (Rodentia: Bathyergidae).

THERMOREGULATION IN THE SUBTERRANEAN RODENT GEORYCHUS CAPENSIS (RODENTIA: BATHYERGIDAE)[1]

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Thermoregulation of the mesic-habitat Cape mole rat, *Georychus capensis* (mean mass 193 g), was investigated, and the data was used to test the hypothesis that exceptionally low mass-specific rates of metabolism are common to the arid-habitat subterranean rodents only. The mean body temperature was 36.4 C, resting metabolic rate was 68% of that expected for rodents, and conductance was 62% of the predicted value. This mole rat maintained a constant body temperature independent of ambient temperatures between −0.5 and 28 C. The data refuted the above hypothesis. A possible explanation for the low rate of metabolism of *G. capensis* is given.

INTRODUCTION

Subterranean rodents spend their entire lives underground (Ellerman 1956; Nevo 1979) and display physiological traits that are markedly different from those of aboveground rodents (McNab 1979; Lovegrove 1986*a*). Body temperature (T_b) is low (32–36.5 C; McNab 1979), and, with two exceptions, mass-specific resting metabolic rates (RMR) are 43%–100% of those predicted by mass when using Hayssen and Lacey's (1985) allometric equation for all rodents (Lovegrove 1986*a*). The seven species with the lowest mass-specific RMRs (five bathyergids, one geomyid, and one spalacid) are all arid- or semiarid-habitat animals, especially the three social bathyergid mole rats (Lovegrove 1986*a*).

It is not yet known which ecological or physical features associated with arid regions are instrumental in selecting for low metabolic rates, and, until such time as the results of more ecophysiological studies become available, the causes will remain speculative. Of the six species of bathyergid mole rats whose thermoregulation has been studied to date (four of the five genera), only the large (600–1,500 g) solitary dune mole rat, *Bathyergus suillus*, occurs in mesic habitats (Lovegrove 1986*b*). Because this species is considerably larger than the five arid-habitat species, its outlying status makes it difficult to evaluate its metabolism in terms of its mesic habitat.

To test the hypothesis that mesic-habitat subterranean rodents have higher mass-specific rates of metabolism than do those occurring in arid habitats (Lovegrove 1986*a*), I present data on the metabolism and thermoregulation of the solitary Cape mole rat *G. capensis*, the remaining unstudied mesic-habitat bathyergid genus. The body size of this mole rat is similar to those of nonbathyergid, mesic subterranean rodents, and it is therefore a convenient species with which to evaluate the metabolism of mesic-habitat bathyergid mole rats. On the basis of the mass and habitat of *G. capensis*, the hypothesis predicts a mass-specific RMR that should be 80%–92% of that predicted by Hayssen and Lacey's (1985) equation for all rodents. Most of the nonbathyergid, mesic-habitat subterranean rodents of similar body size to *G. capensis* have rates of metabolism that fall within this range (Lovegrove 1986*a*).

The Cape mole rat *G. capensis* is mainly confined to the mediterranean winter-rainfall region of the Western Cape Province of South Africa (De Graaff 1981). Small isolated "relict" populations also occur in summer-rainfall regions in parts of Pondoland, Natal, and the Transvaal highveld (De Graaff 1981). Its distribution does not extend into the drier regions of the northern Cape. The species can be found sympatrically with *B. suillus* and *Cryptomys hottentotus* in sandy, granite-derived soils, or,

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more commonly, with just *C. hottentotus* on more consolidated, acid-leached sandstone-derived soils and on soils derived from shales (B. G. Lovegrove, personal observation). It is also found in many of the Cape mountain ranges wherever soils are deep enough for burrowing (B. G. Lovegrove, personal observation). Although *C. hottentotus* occurs predominantly in arid and semiarid habitats, it has an extensive distribution in southern Africa and often occurs in areas of high rainfall and high humidity (De Graaff 1981).

MATERIAL AND METHODS

Eight animals, one male and seven females, with a mean ± SD body mass of 192.6 ± 16.69 g and a range of 176–218 g were used in this study. These body sizes are comparable with the species' mean body mass of 181.8 g (Taylor et al. 1985). Seven animals were trapped on the slopes of Table Mountain, Cape Town, during September 1985, and one was trapped near Bredasdorp in August 1985. Animals were housed in glass terraria under continuous light at 23 C and were fed on chopped sweet potatoes, apples, and gem squash. The animals were not fasted prior to the experiments. If starved, the animals became extremely restless (and would, in any event, practice coprophagy). Therefore, values of RMR are, if anything, slightly overestimated.

Rate of oxygen consumption ($\dot{V}O_2$) was measured at nine ambient temperatures (T_a), ranging from −0.5 to 34 C, between November and December 1985, using a positive-pressure flow-through system. All measurements were made between 0800 hours and 1800 hours. It was assumed that *Georychus capensis* did not have a circadian rhythm in metabolism. Rectal temperatures were measured within 1 min of termination of each experiment by inserting a rectal thermocouple 2–3 cm into the rectum. The respirometer was a cylindrical perspex chamber (1,170 cm^3) fitted with 6-mm inlet and outlet ports and a perforated plastic base plate on which the mole rats rested. Temperatures were kept constant within the respirometer by placing it inside a small (0.11 m^3) temperature-controlled cabinet. Outside air was pumped through the respirometer and oxygen analyzer at 350–500 $cm^3\ min^{-1}$. Control readings were provided by a parallel flow-through system incorporating an identical, but empty, respirometer. Airflow was measured with a calibrated flowmeter placed downstream from the respirometer. A silica gel/soda lime scrubber placed downstream from the respirometer removed the H_2O and CO_2 from the stream.

The procedures of Bartholomew, Lighton, and Louw (1985) and Lighton (1985) were used to measure $\dot{V}O_2$ with an Applied Electrochemistry S-3A oxygen analyzer and a BBC microcomputer. This procedure records the voltage output of the analyzer as the difference between the fractional concentrations of oxygen in the respiratory and calibration streams. The progress of each run can be visualized in real time on a monitor, and markers can be set on the trace to correspond with behavioral observations. A sampling period of 19–20 s was selected, and each run lasted three h. Each data point stored on disk represented the mean of a number of voltages recorded by the computer during each sampling period. Voltage files for each run were converted to steady-state $\dot{V}O_2$ values using the formula $\dot{V}O_2 = V(FIO_2 - FEO_2)/(1 - FIO_2)$, where FIO_2 and FEO_2 are incurrent and excurrent fractional concentrations of oxygen and V is flow rate in $cm^3\ min^{-1}$.

When the data were analyzed, the first hour of each run was regarded as a minimum period of adjustment, and these data were discarded from the analyses. The RMR of each run was taken to be the mean $\dot{V}O_2$ (STP) during the 5–6-min period with the lowest mean $\dot{V}O_2$. The behavioral observation data showed that this period corresponded with the period when the mole rats were calm and resting. Data are presented as the mean ± SD mass-specific RMR ($\dot{V}O_2/m$) of all eight mole rats at each temperature. The relationship of $\dot{V}O_2/m$ and T_a below the lower limit of thermoneutrality (T_l), was analyzed using the method of least-squares fit (Zar 1974). Conductance below T_l was calculated from individual measurements of $\dot{V}O_2/m$ using the formula: $C = (\dot{V}O_2/m)/(T_b - T_a)$ (McNab 1980) and presented as the mean ± SD for all eight mole rats at each temperature.

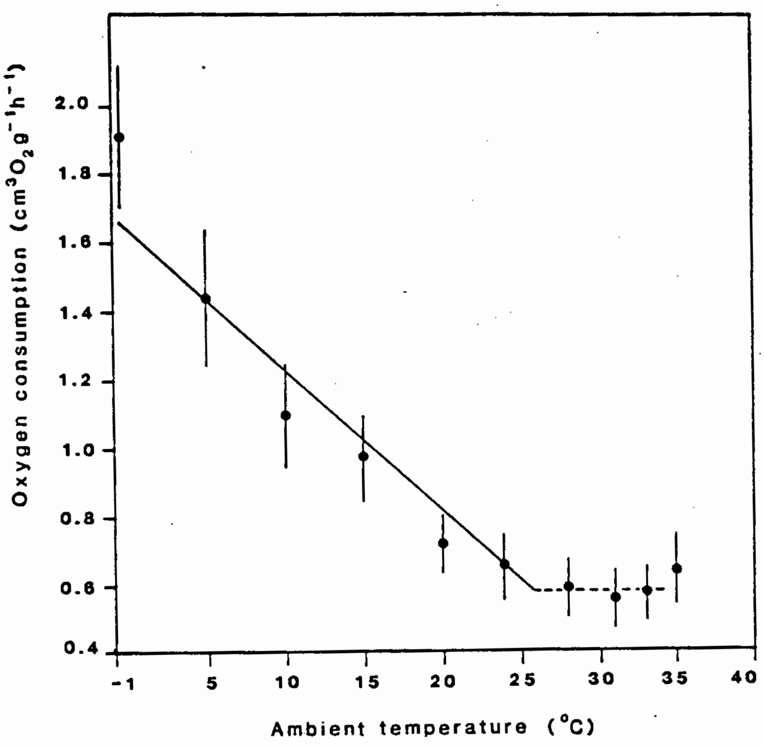

FIG. 1.—Body temperature of eight Cape mole rats, *Georychus capensis*, as a function of ambient temperature.

RESULTS

Georychus capensis has a mass-specific RMR of 0.59 ± 0.09 $\mathrm{cm}^3\ \mathrm{g}^{-1}\ \mathrm{h}^{-1}$ within a thermoneutral zone of 26.3 C to ~34 C (fig. 1). The lower limit of thermoneutrality represents the intercept of the regression of $\dot{V}O_2/m$ and $T_a < 25$ C, and the mean $\dot{V}O_2/m$ at 28–33 C. The regression is given by the equation $\dot{V}O_2/m = 1.64 - 0.04T_a$ ($r = -0.86$, $P < .01$). At 35 C the mean metabolic rate was 0.64 ± 0.09 $\mathrm{cm}^3\ \mathrm{g}^{-1}\ \mathrm{h}^{-1}$. Generally T_b's were stable (36.4 ± 0.6 C; fig. 2) at T_a's between −0.5 and 28 C. One animal became hypothermic after 90 min exposure to −0.5 C. Its T_b dropped to 34.2 C, and its $\dot{V}O_2/m$ dropped from a stable level of 2.23 $\mathrm{cm}^3\ \mathrm{g}^{-1}\ \mathrm{h}^{-1}$ to 0.76 $\mathrm{cm}^3\ \mathrm{g}^{-1}\ \mathrm{h}^{-1}$ in a period of 15 min. When rewarmed, this animal recovered completely. Intense shivering was observed in all animals at −0.5 C after 45 min in the respirometer. At $T_a > 28$ C T_b's increased approximately linearly, to a maximum of 38.3 ± 0.4 C at 35 C. Conductance below T_l was 0.046 ± 0.008 $\mathrm{cm}^3\ \mathrm{g}^{-1}\ \mathrm{h}^{-1}\ \mathrm{C}^{-1}$. These data are compared with those of other bathyergids in table 1.

DISCUSSION

The T_b of *Georychus capensis* is similar to those of other mesic-habitat subterranean rodents, such as *Geomys pinetis* (36.3 C; McNab 1966) and *Spalacopus cyanus* (36.4 C; McNab 1979). It does, however, exhibit the highest T_b of all the bathyergids (table 1). Conductance was 62% of that predicted by McNab and Morrison (1963) (table 1), and, when compared with those of other subterranean rodents (McNab 1979), it had the lowest percentage expected conductance of any subterranean rodent.

The mass-specific RMR of *G. capensis* was 68% of that predicted for all rodents (Hayssen and Lacey 1985) and 85% and 75% of that predicted for all subterranean rodents and mesic-habitat subterranean rodents, respectively (Lovegrove 1986*a*) (table 1). This is an interesting and surprising result, because a low RMR is more closely allied to the arid-habitat subterranean rodents than to those in mesic habitats. For instance, its RMR is lower than that measured for *Bathyergus janetta* and *Heliophobius argentocinereus* (table 1). The hypothermia observed in one mole rat at

TABLE 1

THE RESTING METABOLIC RATES, CONDUCTANCE AND BODY TEMPERATURES OF SEVEN AFRICAN MOLE RATS REPRESENTING ALL FIVE GENERA OF THE FAMILY BATHYERGIDAE

SPECIES	BODY MASS (g)	BODY TEMPERATURE (°C)	RMR (cm^3 O_2 g^{-1} h^{-1})	RMR AS % OF THAT PREDICTED BY		CONDUCTANCE (cm^3 O_2 g^{-1} h^{-1} $°C^{-1}$)	CONDUCTANCE AS % OF THAT PREDICTED BY $cm = 1.00\ m^{-.50\,c}$	HABITAT	SOCIAL STATUS	REFERENCE
				$RMR = 4.98^{-.331}$	$RMR = 3.79\ m^{-.322}$					
Bathyergus suillus	620	35.3	.49	83	102	.038	103	Mesic	Solitary	Lovegrove 1986*b*
B. janetta	406	34.8	.53	78	97	.061	125	Semiarid	Solitary	Lovegrove 1986*b*
Heliophobius argentocinereus	88	35.1	.85	75	95	.139	130	Semiarid	Solitary	McNab 1979
Georychus capensis	193	36.4	.59	68	85	.046	62	Mesic	Solitary	Present study
Cryptomys hottentotus	95	35.8	.68	62	78	.085	96	Semiarid	Social	Haim and Fairall 1986
C. damarensis	125	35.2	.57	57	71	.085	95	Arid	Social	Lovegrove 1986*a*
Heterocephalus glaber ..	39	32.1	.64	43	55	.387	242	Arid	Social	McNab 1966; Withers and Jarvis 1980

Rodent curve; Hayssen and Lacey 1985.
Subterranean rodent curve; Lovegrove 1986*a*.
[c] McNab and Morrison 1963.

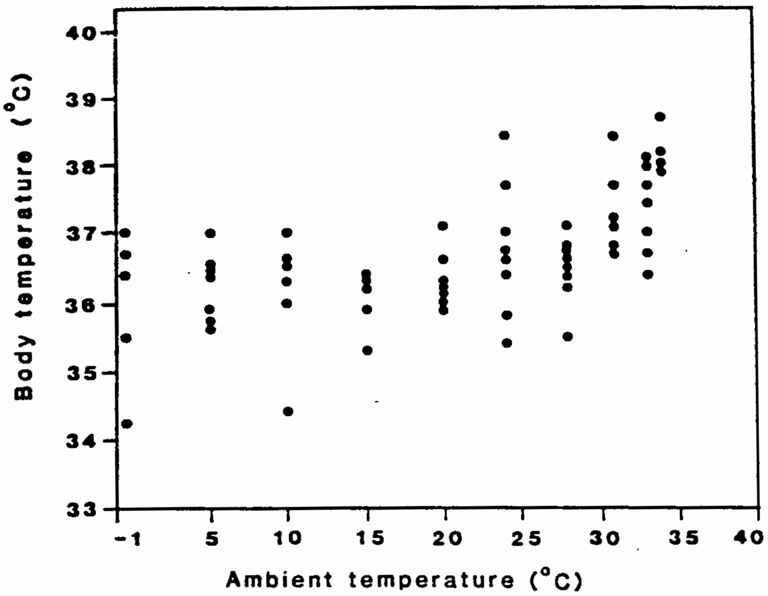

FIG. 2.—Oxygen consumption of eight *Georychus capensis* as a function of ambient temperature. Each dot represents the mean (±SD represented by vertical lines) of eight measurements of oxygen consumption. The broken line represents the mean resting metabolic rate in the thermoneutral zone. The solid line represents the regression of oxygen consumption as a function of ambient temperature below the lower limit of thermoneutrality.

−0.5 C was probably pathological, rather than adaptive obligatory torpor. According to McNab (1983), an animal of the size of *G. capensis* should only employ obligatory torpor if its mass-specific RMR is <0.46 $cm^3\ g^{-1}\ h^{-1}$. This is an interesting point, because J. U. M. Jarvis (personal communication) on three occasions has found this species in an apparently completely torpid state. These animals were capable of spontaneous arousal within 5 min of being handled. The possibility of the existence of seasonal facultative torpor in this species requires investigation. These results would seem to refute the hypothesis that exceptionally low mass-specific rates of metabolism are common to arid-habitat subterranean rodents only (Lovegrove 1986*a*). Although it is difficult at this stage to fully explain this anomaly, I suggest one possible explanation.

My principal argument is that possible ecological and/or physical pressures that select for low mass-specific RMRs in subterranean rodents in certain arid habitats may be operative in mesic habitats as well. According to the "overheating hypothesis" (McNab 1979), the principal factor selecting for low RMRs is warm burrow temperature, often a prevalent feature in arid habitats. However, the exceptionally low conductance of *G. capensis* suggests that this mole rat is more likely to be adapted to cool burrow temperatures. Given the low mass-specific metabolism of *G. capensis,* this study has shown that a low conductance ensures endothermy at T_a's between −0.5 and 28 C.

It could be argued that the metabolism of *G. capensis* has been modified because of the low conductance, as a means of reducing the temperature differential between T_b and the T_a at the lower limit of thermoneutrality (McNab 1979). However, in this case, it is not a good argument because the observed temperature differential (10.0 C) is more consistent with the temperature differentials of mesic-habitat subterranean rodents than with those of rodents in arid habitats (McNab 1979). The overheating hypothesis cannot adequately account for the similarity of the metabolism of *G. capensis* to those of arid-habitat subterranean rodents.

According to Vleck (1979, 1981), factors such as primary production (above and below ground), soil hardness and cohesiveness, etc.—and the consequent problems of balancing an energy budget in the face of a high energy cost of foraging by burrowing—may be important pressures selecting for low rates of metabolism in subterranean rodents. Furthermore, Jarvis (1978), Brett (1986), and Lovegrove (1986*a*) have suggested that the low probabilities that *H. glaber* and *C. damarensis* can locate widely dispersed food resources in arid habitats may select for low mass-specific RMRs as well as sociality in these mole rats.

If we assume that the primary production of arid habitats is lower than that of mesic habitats, we would expect that more food should be available to *G. capensis* than to subterranean rodents in arid habitats—and that therefore this mole rat might be expected to have a relatively higher mass-specific RMR. However, in the case of the bathyergids in particular, this assumption may well be flawed because it does not consider the difference between above-ground and below-ground productivity; for instance, it is known that *G. capensis,* as well as smaller bathyergids such as *H. glaber, C. hottentotus,* and *C. damarensis,* feed almost exclusively on geophytes (underground storage organs in the form of tubers, bulbs, and corms) (Beviss-Challinor 1980; Broll 1981; Du Toit, Jarvis, and Louw 1985; Brett 1986; Lovegrove and Jarvis 1986). In other words, these mole rats do not feed on above-ground plant material as is commonly reported for pocket gophers (see Nevo 1979 for general reference).

An interesting observation concerning the abundance of geophytes is that whereas their average size and nearest-neighbor distances vary considerably between arid and mesic habitats, the overall below-ground biomass of this plant form does not vary markedly between these habitats (B. G. Lovegrove, unpublished data). It is possible, therefore, that the productivity threshold (Vleck 1981) of below-ground food resources may impose an upper limit on the mass-specific metabolism of subterranean rodents that feed exclusively on geophytes, irrespective of habitat. For the moment, this is the best explanation for the low metabolism of *G. capensis.*

It would be interesting to establish whether the arid-habitat *Spalax ehrenbergi,* which also has a very low mass-specific RMR (Nevo and Shkolnik 1974), is also dependent on geophytes as its major food item. Whatever the case, it seems clear that a comprehensive evaluation of the metabolism of subterranean rodents cannot be achieved unless the feeding ecology of these animals is considered together with the possible influence of physical selective pressures such as temperature and humidity. It can be concluded that, whereas the low conductance of *G. capensis* has been selected for as a means of ensuring endothermy during winter, factors related to foraging and burrowing costs are the most likely determinants of the low metabolism of *G. capensis.*

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CHAPTER EIGHT

The Cost of Burrowing by *Cryptomys damarensis* and *Heterocephalus glaber*: The Role of Soil Moisture

Introduction

Potentially the greatest constraint faced by animals that have to burrow exclusively to find food is the cost of burrowing. The definitive cost-of-burrowing studies by Vleck (1979, 1981) and Vleck & Kenagy (1987) have, amongst many important findings, shown that the cost of burrowing by the pocket gopher *Thomomys bottae*, can be 360 - 3,400 times more expensive than covering the same distance on the surface. Furthermore, as pointed out by Vleck (1981), optimal foraging theory has tended to underplay the quantitative costs of foraging, concentrating more on optimal diet breadth. Considering the comparatively simple and homogeneous nature of the habitat of *C. damarensis* in the Kalahari Desert, both in terms of food resources and edaphic features, the habitat provides an excellent system for modelling various aspects of foraging theory, including the cost of burrowing.

Vleck's (1979) study was primarily concerned with the influence of soil type on the cost of burrowing, and did not investigate the role of soil moisture content *per se*. For many months of the year the sands of the Kalahari remain dry, recieving at most only two or three rainfalls greater than 50 mm every summer. Therefore, apart from obtaining general data on the energetics of burrowing in the bathyergids, this study attempts to simulate the two extremes of soil conditions, by measuring the cost of burrowing in *C. damarensis* and *H.glaber* in dry, and damp, compacted soils.

Materials and Methods

Both species were housed in simulated burrow systems consisting of rectangular tubes of clear perspex, inside climatically controlled chambers maintained at 30°C for *H. glaber*, 26°C for *C. damarensis*, and a relative humidity of 50 % for both species. A continuous dark cycle was used, except for the periods when the animals were being fed and maintained. Each burrow system was provided with a series of circular perspex containers which served as nests, toilet areas, feeding and food storage chambers, as well as waste disposal chambers. For *C. damarensis* a large hopper (60 l) with an outlet tube attached to a 'burrowing tube' forming part of the burrow system, was used as a 'burrowing exerciser'. The hopper was filled, three times daily, with dry sand collected from the Dune site (Chapter Two) in the KGNP. All food was mixed with the sand, so that the molerats were forced to burrow for their food. This they did by pushing the sand back along the burrowing tube for a distance of 0.7 m, where the sand then fell through a wire grid, mounted in the floor of the tube, and into a recycling bin. For *H. glaber* a similar system was used, but instead of the hopper, a perspex tube (4 cm inside diameter, 1.5 m long) was continuously filled with sand. For *C. damarensis*, this training was maintained for a month prior to, and during, the experimental period, whereas *H. glaber* was trained for three weeks. During the training of *H. glaber* a note was made of those molerats which burrowed frequently in the tube, and these animals were selected for the burrowing experiments. I felt it necessary to perform these training sessions because in the case of *C. damarensis*, most of the animals used were trapped six months previously and had not had the opportunity of burrowing in sand since then, whereas in the case of *H. glaber*, all animals used were born in captivity, and had never had the opportunity of burrowing in sand. Nevertheless, *H. glaber* responded instinctively, and those that had successfully competed for a position in the burrowing tube burrowed excitedly every time the tube was replaced.

The molerats were fed a diet of chopped vegetables, mostly sweet potato in the case of *C. damarensis*, and fruit. The diet of *H. glaber* was supplemented with 'Pronutro' (Cerebos Food Corp. Ltd., Wadeville), a nutritionally balanced cereal food, moistened with water. For *C. damarensis*, eleven molerats with a mean mass of 152.1 ± 25.4 g, ten males (102 g - 203 g) and one female (149 g), were used to measure the cost of burrowing. Five of these animals were trapped in January 1987, and two in July 1987, at both sites (Chapter

Two) in the KGNP. An additional four males were trapped in Namibia in November 1986. For *H. glaber*, nine molerats (six males and three females) with a mean mass of 31.5 ± 3.0 g, were used.

Sand was collected from the Dune site (KGNP) for *C. damarensis*, and from various *H. glaber* habitats in Kenya by Jennifer Jarvis for *H. glaber*. For the damp sand trials the sand was moistened with water, thouroughly mixed to a standard consistency (damp enough to be moulded by hand), and compacted as hard as possible into the burrowing tubes with a heavy wooden pole (1.5 m long, diameter 3.5 cm). Before compaction, a steel plastic-coated rod (diameter 4 mm) was placed along the inside upper surface of the burrowing tube. This was removed after the tubes were filled thereby leaving a cylindrical airspace running from the inlet port of the burrowing tube to the burrowing face. The purpose of this procedure was to avoid changes in air pressure within the system during burrowing, and to provide an unimpeded flow of air over the borrowing face during experiments. When using dry sand the burrowing tubes were prepared as described above for damp sand, but then dry compressed air was passed through the tube for 24 hrs to thouroughly dry out the sand. The result was that the sand particles bonded together when dried, forming a continuous core of hard, compacted, dry sand.

Before being placed in the respirometer, the body temperatures (T_b) and body masses (M_b) of all molerats were measured. Body temperature was measured with a copper-constantan rectal thermocouple inserted 1 - 2 cm into the rectum, and attached to a thermocouple meter. The thermocouple meter was calibrated against a standard mercury thermometer. The respirometer was a rectangular perspex box measuring 8.8 x 29.0 x 19.7 cm with a volume of 5.03 l (Fig. 23). Molerats were restricted to the top 8 cm of the respirometer by a wire grid (Fig. 23). Sand excavated from the burrowing tube, bolted to one end of the respirometer, fell through the grid and into the sandbox below. During the *H. glaber* runs, most of the volume within the respirometer and sand box was taken up with sealed blocks of polythene to reduce the volume to 1.8 l, thereby decreasing the response time and increasing the sensitivity of the system. The burrowing tubes consisted of clear perspex tubing, 1.0 m long, with an inside diameter of 41 mm for *H. glaber*, and 0.92 m long with an inside diameter of 63 mm for *C. damarensis*. The diameter of the burrowing tubes was selected to approximate burrow diameters in the field (Brett 1986, Chapter Three). Sand was glued to the lateral and ventral inside surfaces of both tubes to provide a rough surface. The tubes were marked every 10 cm for measuring burrowing speed. All burrowing experiments were conducted in a climatically controlled chamber at 27°C and a relative humidity of 50%.

Fig. 23. The respirometer and burrowing apparatus used to measure the cost of burrowing by *C. damarensis* and *H. glaber* in dry and damp sand, showing the burrowing tube, the sandbox, and the respirometer chamber (above white grid).

Fig. 24. *C. damarensis* using its incisors to shear sand loose from the digging face during a dry sand trial.

The procedure consisted first of recording the control or blank baseline readings for approximately 5 mins, during which time the molerats within the respirometer were bypassed. Air was then passed through the experimetal line and the experiments were allowed to proceed until either the burrowing tube had been emptied, as was often the case during the damp sand runs, or if the molerats ceased burrowing. During the course of burrowing, event markers were stored in the computer for every 10 cm burrowed, or, every time the molerats stopped or started intensive burrowing periods. After subtracting the inactive periods, the time between event markers was used to calculate the speed of burrowing in $m.hr^{-1}$. If molerats spent too much time inactive or gnawing at some part of the respirometer, the run was terminated and the data discarded. At the end of each run, the molerats were removed as quickly as possible (< 1 min), and body temeperatures were recorded. The sand pushed into the sand box was removed and weighed, and a subsample was dried at 60°C to constant mass to calculate the percentage water content of the sand.

Oxygen consumption was measured with a positive pressure open flow-through system using an Applied Electrochemistry S-3A/1 single channel oxygen analyser, and a R-1 flow control pump as described in Chapters Six and Seven. Sampling intervals were 3.5 sec for the dry sand trials, and 5.5 sec for the damp sand trials. Flow rates of 600

$cm^3.min^{-1}$ and 450 $cm^3.min^{-1}$ were used for *C. damarensis* and *H. glaber* respectively. Air was pumped from a large bell-jar, ventilated with outside compressed air, through a calibrated flow meter into the burrowing tube. The outlet of the respirometer was vented into an empty 60 ml syringe casing, from which a subsample of air at a flow rate of 200 $cm^3.min^{-1}$ was drawn for analysis. Two sets of carbon dioxide and water vapour scrubbers removed these gases from the airstream proximal to the flow meter, and immediately proximal to the oxygen analyser. The 5 min section of trace, that showed the most constant consecutive maximum oxygen consumption during uninterupted burrowing periods, was selected for analysis. Data are presented as the mean ± SD oxygen consumption ($cm^3.g^{-1}.h^{-1}$, STP) of 86 data points for each damp soil run, and 54 data points for each dry sand run. For significance testing between means, a Student's *t*-test was used, and least-squares fit analyses were used to calculate all regressions (Zar 1974).

Where possible, data were evaluated in terms of Vleck's (1979) cost-of-burrowing model:

$$E_{seg}/M_{soil} = K_s(S) + 0.5K_p(S)^2 \qquad .... (1)$$

where E_{seg} = energy cost of constructing a burrow segment of length S (cm), K_s = energy cost of shearing 1 g of soil loose ($J.g^{-1}$); K_p = energy cost of pushing 1 g soil 100 cm ($J.(g.cm)^{-1}$); and M_{soil} = mass of soil excavated per distance burrowed (g.cm^{-1}). Also, M_{soil} = (b^2r), where b = burrow radius (cm), and p = soil density (g.cm^{-3}).

Results

Burrowing behaviour

C. damarensis burrowed well during both the damp, and dry sand experiments. They often burrowed continuously until they reached the end of the burrowing tube and seldom stopped to investigate the interior of the respirometer. Good data were obtained for all eleven molerats used. However, *H. glaber* were more reluctant to burrow, particularly during the dry sand experiments, and would spend long periods gnawing at the wire grid. I discarded 75 % of the data, but did manage to obtain data for nine animals during the damp sand experiments and for six animals during the dry sand experiments.

Both species used their incisors to shear soil loose from the digging face (Fig 24.). This they did by bracing themselves against the sides of the burrowing tube with fore- and hindfeet. This behaviour served to anchor the molerats firmly, so that maximum shearing force could be applied to the burrowing face. *C. damarensis* used both forefeet simultaneously to push loosened soil underneath its body to the hind feet. Once it had sheared sufficient soil for one pushing load, it moved steadily backwards pushing the sand backwards with rapid, sharp kicks of the hindfeet, at the same time continously sweeping the burrow in front of it with scooping, scratching, actions of the forefeet. Once the sand had been pushed into the sand box, the molerats would immediately run back to the digging face and start shearing soil again. *H. glaber* burrowed in much the same manner, but when pushing the soil they did not sweep the burrow with the forefeet as they progressed backwards. Also, instead of moving backwards steadily, they tended to stop and vigorously kick the sand backwards a few times before moving further back and repeating the procedure. Generally, they would shear a lot of sand loose before pushing it back, which they did often, but only when the burrow behind them was congested with loosened sand.

Burrowing metabolic rate

The mean burrowing metabolic rate of *C. damarensis* in damp sand, 2.86 ± 0.31 $cm^3.g^{-1}.h^{-1}$, was not significantly different ($p > 0.05$) from that in dry sand, 2.58 ± 0.32 $cm^3.g^{-1}.h^{-1}$ (Table 6). Burrowing metabolic rates were therefore 5.02 and 4.53 times greater than resting metabolic rates (Chapter Six) in damp, and dry sand, respectively. During the dry sand experiments there was a significant ($p < 0.05$) 1.3°C increase in mean T_b from 34.8 ± 0.92°C at the start of the run, to 36.1 ± 0.57°C at the end of the run (Table 6).

Table 6. The mean body masses, burrowing metabolic rates, and body temperatures of *C. damarensis* and *H. glaber* during damp sand, and dry sand, burrowing trials.

Species	N	Body mass (g)	Burrowing met. rate ($cm^3g^{-1}h^{-1}$)	n	Body temperature (°C) Before	After
		Mean ± SD	Mean ± SD		Mean ± SD	Mean ± SD
Damp sand						
C. damarensis	11	152.1(25.4)	2.86(0.31)	-	- -	- -
H. glaber	9	31.5(3.0)	3.36(0.25)	8	32.2(0.86)	29.9(1.12)
Dry sand						
C. damarensis	11	152.1(25.4)	2.58(0.32)	8	34.8(0.92)	36.1(0.43)
H. glaber	6	32.3(2.8)	2.78(0.25)	6	32.5(1.44)	32.8(0.43)

For *H. glaber*, the mean burrowing metabolic rate in damp soil, 3.36 ± 0.25 $cm^3.g^{-1}.h^{-1}$, was significantly ($p < 0.05$) greater than that in dry soil, 2.78 ± 0.25 $cm^3.g^{-1}.h^{-1}$ (Table 6). Burrowing metabolic rates were therefore 5.25 and 4.34 times higher than resting metabolic rates (Chapter Six) in damp and dry sand, respectively. Although there was no significant ($p > 0.05$) increase in T_b between the start, and end of the dry sand trials (32.5 - 32.8°C), during the wet sand trials there was a significant ($p < 0.05$) drop of 2.3°C between the mean T_b at the start, 32.2 ± 0.86°C, and the mean T_b at the end of the runs, 29.9 ± 1.12°C (Table 6).

Burrowing speed

The mean percentage water content of the damp sand was 3.17 % and 7.88 % for *C. damarensis* and *H. glaber* respectively. The difference between these percentages can probably be attributed to the fact that the sand used for *H. glaber* was finer and required less moisture to reach the same consistency as that for *C. damarensis*. In damp sand, *C. damarensis* burrowed at a rate, 3.53 ± 0.75 $m.h^{-1}$, which was 3.8 times faster ($p < 0.05$) than the rate in dry sand, 0.92 ± 0.33 $m.h^{-1}$. Similarly, *H. glaber* burrowed at a rate in damp sand, 0.75 ± 0.23 $m.h^{-1}$, which was 2.5 times faster ($p < 0.05$) than the rate of 0.30 ± 0.02 $m.h^{-1}$ in dry sand.

Cost of burrowing

The results of the regression analyses of E_{seg}/M_{soil} as a function of distance burrowed are given in Table 7 and Figs 25 & 26. This representation of the cost of burrowing is useful because it is not influenced by burrow diameter (Vleck 1979). The only data which fitted the predictions of the Vleck (1979) cost-of-burrowing model was that of *C., damarensis* in damp soil, where a positive polynomial equation (r^2 = 0.858) fitted the data better than a positive linear equation (r^2 = 0.845). Using the method of least-squares fit, Vleck's (1979) model, equation (1), also showed a good significant fit to the data (r^2 = 0.95, Fig. 24). This regression gave estimates of the proportionality constants for shearing and pushing of K_s = 0.277 and K_p = 0.0036 respectively. All other regressions showed that a negative polynomial equation fitted the data better than either a positive polynomial, or a positive linear equation (Table 7). However, for *C. damarensis* in dry sand, there was very little difference between the fit of the polynomial (r^2 = 0.685) and the linear equation (r^2 = 0.684). The most significant regression for each burrowing trial type was used to calculate the cost of burrowing various distances represented by the equations (Table 8).

Table 7. Statistics of linear and polynomial regressions performed on E_{seg}/M_{soil} data as a function of distance burrowed (see Figs 25 & 26) for *C. damarensis* and *H. glaber*.

		Polynomial equation				Linear equation		
Species	N*	1 deg coef.	2 deg coef.	Const	r^2	Reg. coef.	Y-int.	r^2
Damp sand								
C. damarensis	11(55)	0.237	0.0037	3.35	0.858	0.642	-5.608	0.845
H. glaber	9(29)	3.149	-0.016	-5.70	0.843	2.036	8.647	0.823
Dry sand								
C. damarensis	11(55)	1.753	-0.0017	4.23	0.685	1.608	6.605	0.684
H. glaber	6(11)	6.705	-0.0089	-22.37	0.915	3.939	-3.975	0.910

* N = number of individual molerats used in the study. Figure in brackets is the total number of data points for all for all molerats.

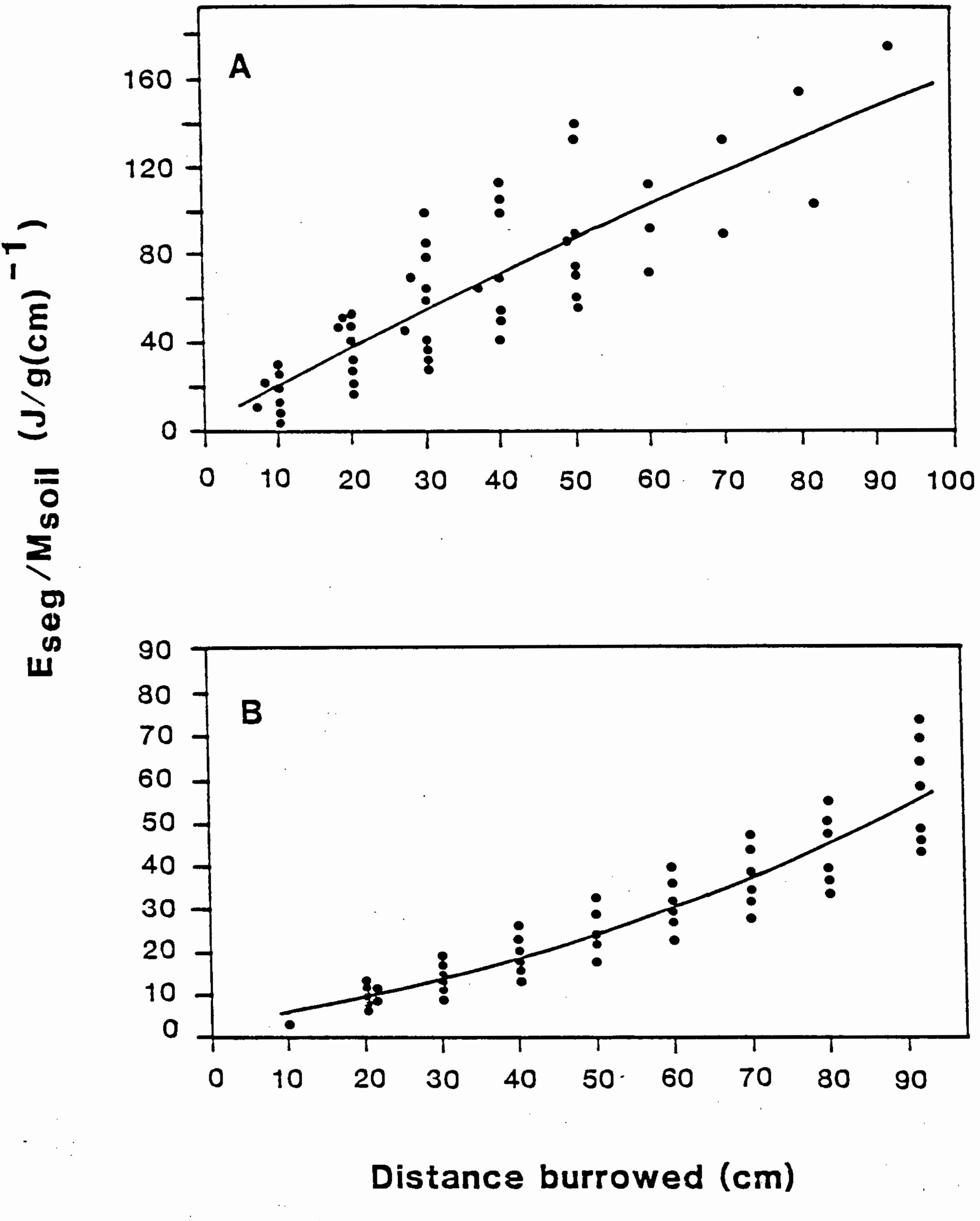

Fig. 25. The cost of burrowing (E_{seg}/M_{soil}) as a function of distance burrowed by *C. damarensis* in dry sand (A) and damp sand (B).

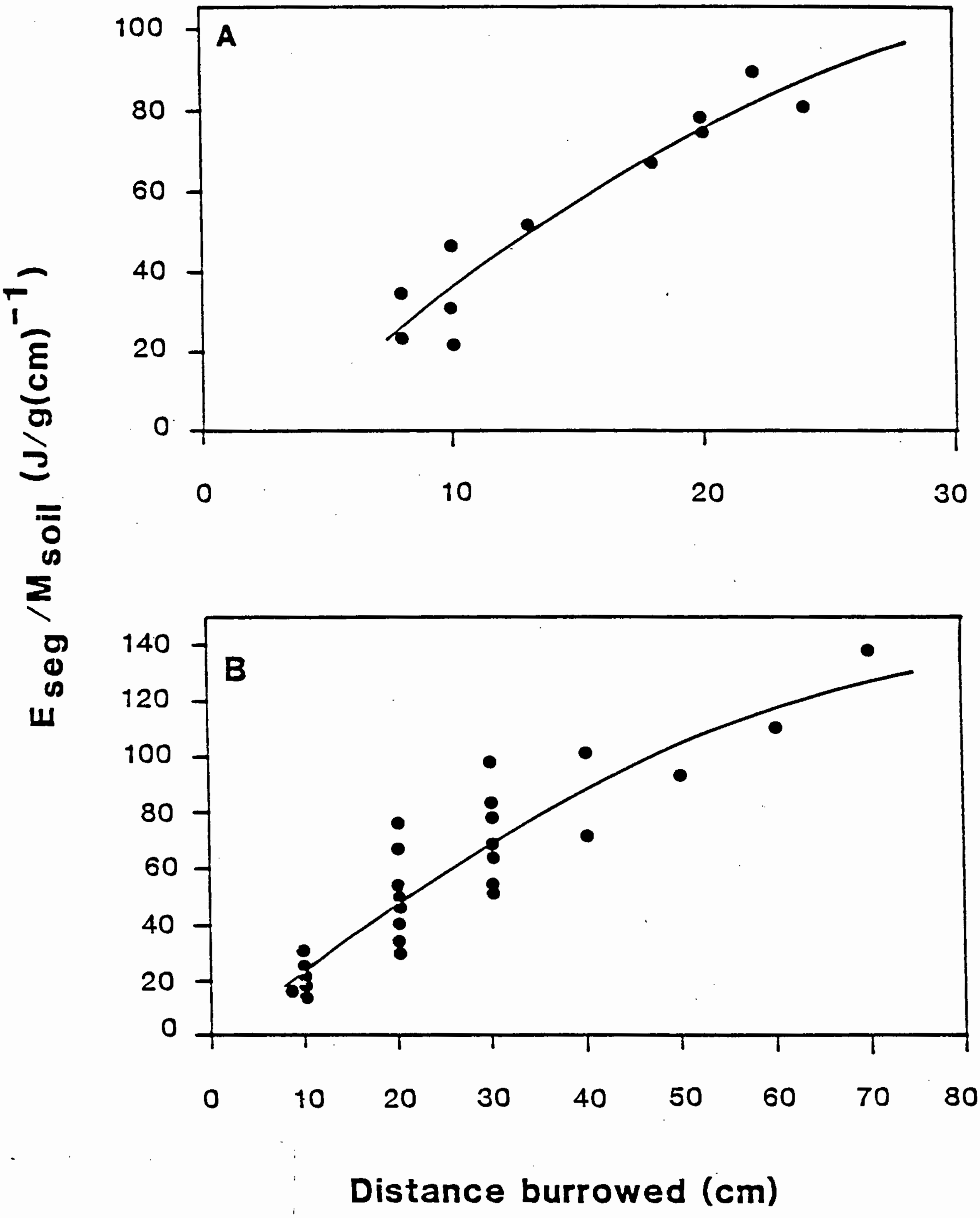

Fig. 26. The cost of burrowing (E_{seg}/M_{soil}) as a function of distance burrowed by *H. glaber* in dry sand (A) and damp sand (B).

Table 8. The cost of burrowing various distances (S) in damp and dry sand for subterranean rodents and insectivorous moles as calculated from the best-fitting equations (Table 7) and Vleck's (1979) model. Data for non-bathyergids from Vleck (1979) and Vleck & Kenagy (1987).

Species	Soil type and density ($g.cm^{-3}$)		M_{soil} ($g.cm^{-1}$)	Equation used	E_{seg} (kJ)	S (cm)
Heterocephalus glaber	damp sand	1.59	11.98	Table 7	0.77	20
	dry sand	1.47	15.22	Table 7	1.15	20
Cryptomys damarensis	dry sand	1.63	44.07	Table 7	3.86	50
	dry sand	1.63	44.07	Table 7	1.70	20
	damp sand	1.70	42.82	Table 7	1.04	50
	damp sand	1.70	42.82	Table 7	0.41	20
	damp sand	1.70	42.82	Vleck (1979)	1.19	50
	damp sand	1.70	42.82	Vleck (1979)	0.29	20
Thomomys bottae	damp sand	1.37	52.70	Vleck (1979)	1.24	50
Thomomys talpoides	damp clay	1.50	38.00	Vleck (1979)	1.58	50
Scapanus townsendii	damp clay	1.50	48.00	Vleck (1979)	1.95	50
Scapanus orarius	damp clay	1.50	31.00	Vleck (1979)	1.69	50

* Assuming 19.94 $J.(cm^3O_2)^{-1}$

Discussion

The decrease in body temperature by *H. glaber* during the damp sand trials shows that the metabolic heat produced during burrowing was insufficient to compensate for heat lost during the burrowing period. Presumably, burrowing in both wet and dry sand would increase vasodilation of peripheral circulations to parts of the body heavily involved in burrowing, namely jaw, stomach, and leg muscles. It would, therefore, appear that convective and conductive heat loss in damp sand at 27°C is greater than that in dry sand. The difference in burrowing metabolic rate between the damp sand, and dry sand trials, may therefore be complicated by differences in thermoregulatory costs. The stable body temperatures of *H. glaber* during the dry sand trials, suggests that metabolic burrowing heat produced, more than compensated for heat lost. On the other hand, the increase in body temperature by *C. damarensis* during the dry sand trials can be attributed to increased metabolic heat produced during burrowing and the lower conductance of this species (Chapter Six). Presumably, at burrow temperatures greater than 27°C (Chapter Three), body temperatures would be elevated even further, supporting the suggestion (Chapters Three and Four) that hyperthermia may restrict the time that is spent burrowing.

Data for the bathyergids obtained during the damp sand trials can be compared with data for other subterranean rodents and insectivores (Table 9) which were also measured in damp, compacted sand (Vleck 1979, Du Toit *et al.* 1985, Vleck & Kenagy 1987). In particular, one important trend is evident. The metabolic scopes of burrowing for the bathyergids were 5.02 - 5.25 times RMR, the highest for all the subterranean mammals (Table 9). This is most likely due to the low RMRs of the bathyergids (Chapter Six), and their tendency to scale RMR independently of the influence of mass (Chapter Nine). Furthermore, for all eight species studied todate (Table 9), there was a significant ($p < 0.01$, $r^2 = 0.78$) relationship between burrowing (digging) metabolic rate (DMR) and RMR given by the power curve (Fig. 27):

$$\text{DMR} = 3.76(\text{RMR})^{0.471} \qquad .....(2)$$

When considered in terms of daily energy expenditures, the relationship given by equation (2) can be of crucial importance to subterranean mammals which could potentialy fail to maintain a positive energy balance through problems of limiting resources, poor quality food (Chapter Two), or problems in locating and aquiring widely dispersed food resources (Chapters Two, Nine and Eleven).

The following simple, hypothetical example, illustrates this point. Let us arbitarily assume that all subterranean rodents spend 70 % of the day resting, and 30 % of the day burrowing, and consider a 35 g mesic-adapted subterranean

Table 9. The metabolic scope of burrowing for subterranean rodents and insectivorous moles. References: 1) This study, 2) Du Toit *et al.* 1985, 3) Vleck (1979) and 4) Vleck & Kenagy (1987).

Species	class	Body mass (g)	VO_2 rest ($cm^3g^{-1}h^{-1}$)	VO_2 digging ($cm^3g^{-1}h^{-1}$)	Ratio digging /rest	Ref.
Georychus capensis	Rodent	197	0.59	3.41	5.80	2
Cryptomys damarensis	Rodent	152	0.57	2.86	5.02	1
Heterocephalus glaber	Rodent	32	0.64	3.36	5.25	1
Thomomys bottae	Rodent	143	0.84	4.10	4.80	3
Thomomys talpoides	Rodent	75	1.65	4.08	2.47	4
Scapanus townsendii	Insectivore	148	1.17	2.46	2.10	4
Scapanus orarius	Insectivore	59	1.78	5.73	3.20	4
Neurotrichus gibsii	Insectivore	10	6.30	10.00	1.60	4

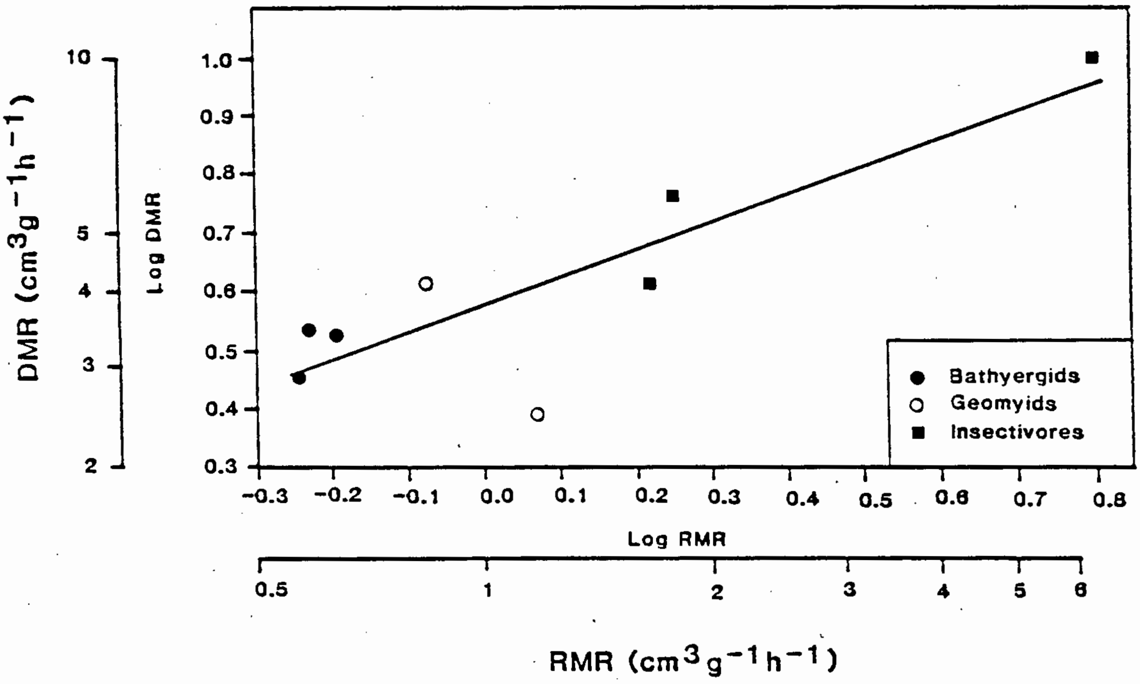

Fig. 27. A log-transformed regression of burrowing metabolic rate (DMR) as a function of resting metabolic rate (RMR) for subterranean rodents and insectivorous moles. Data from Vleck (1979), Vleck & Kenagy (1987), and this study.

rodent other than a bathyergid. Then the RMR of this animal, predicted by the curve for the RMR of mesic-adapted subterranean rodents (RMR = $10.62M_b^{-0.467}$; Chapter Six), would be 2.02 $cm^3.g^{-1}.h^{-1}$. Equation (1) predictes a DMR of 5.24 $cm^3.g^{-1}.h^{-1}$, and therefore a daily energy expenditure of 2508.24 cm^3O_2, or, assuming 19.94 $J.cm^{-3}O_2$ (see Vleck 1979), an expenditure of approximately 50 $kJ.day^{-1}$. Now consider the bathyergids which scale RMR according to the equation RMR = $1.00M_b^{-0.107}$ (Chapter Nine). A 35 g bathyergid would have a RMR of 0.68 $cm^3.g^{-1}.h^{-1}$, and from equation (2) a DMR of 3.14 $cm^3.g^{-1}.h^{-1}$, giving a daily energy expenditure of approximately 23.8 $kJ.day^{-1}$. This is less than half of that for non-bathyergid mesic-adapted species. The point I wish to emphasise is that, although the bathyergids display low RMRs, they are capable of a large metabolic scope for burrowing which enables them to achieve metabolic capacities during burrowing almost consistent with those of other subterranean mammals. This energy is essential for the large power output required for burrowing (Vleck 1979). Once again, this example illustrates the adaptive significance of a low RMR in terms of energy conservation, rather than in terms of McNab's (1979) overheating hypothesis.

It is not clear why three of the four burrowing trials gave data trends that deviated from the predictions of Vleck's (1979) model. The trends imply that burrowing becomes more efficient with distance. At this point there is no obvious factor which can account for these trends, and at the same time account for the data which did fit the model. Nevertheless, one could speculate on various possibilities. The one factor common to these three trials was that more time was spent shearing soil than pushing soil, compared with the *C. damarensis* trial in damp sand. Therefore, the efficiency of shearing over extended periods of time appears to be the dominant component of the model. One possibility could be that the cost of shearing a given mass of soil is not a linear function of shearing speed. Taylor *et al.* (1970) have shown that the total cost of running 1 km by rodents and dogs decreases as speed increases. If this trend were to apply to shearing speed, it is possible that molerats steadily increase shearing speed as they burrow. This effect would not be apparent in loose soils e.g. such as *C. damarensis* in damp sand and Vleck's (1979) trials, because of the dominance of the K_p coefficient. There may be other possibilities, such as anaerobic metabolism, but whatever the case, this aspect of burrowing energetics, and therefore the cost-of-burrowing model, requires further investigation. In fact, a closer examination of Vleck's (1979) original data for clay soils, and presumably therefore the hardest of the soils he investigated, reveals a similar deviance from his prediction of a positive polynomial trend in the cost of burrowing.

One aspect of the cost of burrowing comparisons (Table 8), was that although the cost of burrowing 20 cm by *H. glaber* in damp soil was greater than that for *C. damarensis*, *H. glaber* used 32 % less energy than *C. damarensis* to burrow the same distance in dry sand. This confirms Vleck's (1981) observation on the advantage of small body size during burrowing. In fact he found that body size is inversely proportional to soil hardness in the Geomyidae. It also assists in explaining the body size trend shown by the bathyergids. The largest bathyergids, *Bathyergus* (600 - 1500 g), are restricted to soft, calcereous sands (De Graaff 1981, Davies & Jarvis 1986), intermediately sized molerats *G. capensis* and *Cryptomys*, inhabit harder gravelly soils and compacted sands (De Graaff 1972, 1981; Davies & Jarvis 1986, Lovegrove & Jarvis 1986), whereas the smallest bathyergid, *H. glaber*, is found in soils that become extremely hard (Jarvis 1985, Brett 1986).

The large differences in the cost of burrowing 50 cm in dry and damp sand by *C. damarensis* and *H. glaber* has important consequences for both species. The sands in the arid habitats of these molerats remain dry for many months of the year. Using Vleck's (1979) model to predict burrowing costs under these conditions would result in underestimates of 150 - 370 %. *H. glaber* reduce these costs as far as possible by maintaining a small body size and low RMR at the expense of homeothermic ability (McNab 1966, Withers & Jarvis 1980), particularly the workers. *C. damarensis* however, must maintain the minimum body size and RMR capable of maintaining endothermy during winter (Chapters Three, Four, Six), and consequently incurs a slightly higher cost of burrowing. This also explains why *C. damarensis* engages in intensive burrowing in the Kalahari immediately after rain. Besides avoiding the physical problems involved in constructing a molehill in dry sand, they would use 3.7 times less energy to extend the primary burrow (Chapter Three) when the sand is damp. The cost of burrowing 50 cm by *C. damarensis* in damp sand was the lowest of all of the subterranean mammals (Table 8).

Conclusions

This study has highlighted various aspects of the energetics of burrowing in the bathyergids. It has, for example, shown that molerats are capable of a large metabolic scope for burrowing, and that their low RMR means that their daily energy expenditure should theoretically be considerably lower than that for non-bathyergid, mesic-adapted species. It has also shown that the cost of burrowing and burrowing speed, is heavily dependent on the rate at which soil is sheared loose. Dry soils required 1.5 - 3.7 times more energy per unit distance burrowed than damp soils. It has provided good evidence suggesting that soil hardness may be one of the most important natural selection pressures selecting for body size. Finally, it has shown that whereas Vleck's (1979) model predicted the cost of burrowing fairly well in soft (damp) soils, his model does not account for unexplained factors, which alter the behaviour of the model in harder (dry) soils.

CHAPTER NINE

Sociality of the Bathyergidae: Metabolic Scaling and the Role of Risk-Sensitivity: A Model

Introduction

Increased foraging efficiency is important in enhancing the fitness of individuals within foraging groups of birds (Fisher 1954, Horn 1968, Crook 1970, Cody 1971, Siegfried 1971, Krebs *et al.* 1972, Ward & Zahavi 1973, Krebs 1974, Thompson *et al.* 1975), mammalian carnivores (Kuhme 1965, Schaller 1972, Caraco & Wolf 1975), ungulates (Jarman 1974) and primates (Crook 1972). The recent development of the concept of "Risk-Sensitive Behaviour", or RSB (see Weissburg 1986), suggests that the survival benefit to individuals foraging within groups is not necessarily the maximisation of mean energetic returns, but rather, a reduction in the risk of poor returns while foraging alone (Krebs 1974, 1980; Caraco & Wolf 1975; Thompson *et al.* 1975; Caraco 1980; Caraco *et al.* 1980; Real *et al.* 1982; Caraco & Lima 1985). I follow Caraco's (1981) definition of risk to mean "...the chance of doing poorly while foraging due to the stochastic nature of energetic rewards...".

In short, these studies infer that individual foragers are sensitive to the probability distribution of foraging risks, such as the time or distance between successive resource encounters. So far however, the hypothesis considers only 'decisions' made by individual foragers on a day-to-day basis as to whether or not to join foraging groups. These decisions supposedly are based upon daily assessments of the individual's physiological status.

Considerations of the ecological correlates of sociality in the endotherms have to-date, however, not included the most social of all of the endotherms, the bathyergid molerats. The family presents an unusual opportunity to investigate ecological correlates and possible causes of sociality. This chapter examines various hypotheses which suggest that although RSB concerns grouping and foraging decisions on a day-to-day basis, the relative risks associated with different habitat-related foraging patterns could be a principal factor determining group size in the bathyergid molerats. In addition, it will examine if the existence and maintenance of groups of various species-specific sizes represents an optimum long term solution to risk. I shall also argue that the random nature of subterranean foraging imposes such stringent energetic constraints on the bathyergids, particularly on those occurring in arid regions, that virtual mass-independent scaling of resting metabolic rate (RMR) is the most effective physiological adaptation to overcome these constraints. To present this argument, I shall conduct a short background review and then develop a model which investigates foraging risk as a function of group size and resource dispersion characteristics. I consider the implications of the model with regard to selective influences on body size, the allometry of mass-specific resting metabolic rates, and the group sizes of the bathyergids.

Background review

Foraging and diet

For the purposes of this study, the foraging behaviour of the following bathyergids has been considered: *B. suillus, G. capensis, C. damarensis, C. hottentotus*, and *H. glaber*. These molerats display two distinct types of foraging behaviour. The largest bathyergid, *B. suillus*, is a generalist feeder which eats a significant proportion of aerial vegetation (Table 10) which it obtains by pulling entire plants underground by the root system (Davies & Jarvis 1986). The diet of the smaller bathyergids is more specialised, consisting almost entirely of geophytes (Table 10). These molerats locate geophytes by burrowing at species-specific depths (Jarvis & Sale 1971, Davies & Jarvis 1986, Lovegrove & Jarvis 1986). Thus, although generalist feeding was assummed to be the general pattern for subterranean rodents in habitats with low production and food quality (Nevo 1979), this is not the case for the small, mostly social bathyergids. These animals capitalise on the temporal reliability of geophytes, thereby avoiding the necessity to venture to the surface to find food. Therefore, irrespective of overall habitat productivity,

Table 10. The percentage occurrence of four food categories in the stomach contents of five bathyergids. References: 1) Beviss-Challinor (1980), 2) Broll (1981), 3) Pers obs.

Species	Body mass (g)	Subterranean Geophyte (%)	Subterranean Root (%)	Aerial Leaf (%)	Aerial Stem (%)	Other (%)	Ref.
B. suillus	635-1500	15.2	21.5	29.1	32.7	1.6	2
		47.5	10.0	7.0	35.0	0.0	1
G. capensis	181	83.8	7.6	1.9	3.1	3.4	2
		91.6	1.3	0.0	5.2	1.6	1
C. hottentotus	60-90	94.6	2.2	0.4	2.7	0.0	2
		100.0	0.0	0.0	0.0	0.0	1
C. damarensis	100-200	100.0	0.0	0.0	0.0	0.0	3
H. glaber	25-32	57.1	42.2	0.0	0.0	0.0	2

these molerats can be considered to be specialists, feeding predominantly on geophytes.

Size and dispersion characteristics of geophytes are reflected in variations in the body size and the degree of sociality of the specialist bathyergids (Table 11). Large solitary molerats (*G. capensis*) occur in mesic habitats characterised by abundant, small geophytes, whereas smaller social species (*C. damarensis, H. glaber*) occur in arid habitats where geophytes (mostly tubers and tubiferous roots) are large and widely dispersed (Table 11, Fig. 28).

Energetic constraints of foraging

Vleck (1979, 1981) has shown that the body size and metabolism of subterranean rodents is heavily dependent on habitat productivity and the energetic cost of foraging by burrowing in soils with different physical properties. He has shown that the energy cost of burrowing varies with soil density, cohesiveness, burrow size, and burrow structure. His argument is that energy conservation is important to subterranean rodents, and that "...the low basal metabolic rates and thermal conductances can be viewed as adaptations to conserve energy, rather than adaptations to heat stress..." (Vleck 1979). Chapter Eight confirmed these arguments and also showed that soil moisture has a profound influence on the cost of burrowing, body size, and the metabolic rate of the bathyergids.

Table 11. Geophytes comprising the diets of three bathyergids. Data for *H. glaber* from Brett (1986) are the means of values for the tuber *Pyrenacantha*. Data for *C. damarensis* from Chapter Two are for the tubers of *A. naudinianus*. Data for *G. capensis* from Du Toit *et al.* (1985) are for various similar-sized corms of different species. Colony size for *H. glaber* from Jarvis (1985) and Brett (1986), for *C. damarensis* from Chapter Four and Bennett & Jarvis (1987), and for *G. capensis* from De Graaff (1981).

Species	Body mass (g)	Colony size	Geophyte wet mass (g)	Geophyte density (No.m^{-2})	Mean NN dist. (m)	Disp. pattern
H. glaber	25-32	60	5280	0.059	2.22	Random
C. damarensis	100-200	25	670	0.165	0.94	Random
G. capensis	181	1	0.23	< 500	>0.02*	Random?

* Calculated assuming a random distribution.

NN = Nearest neighbour.

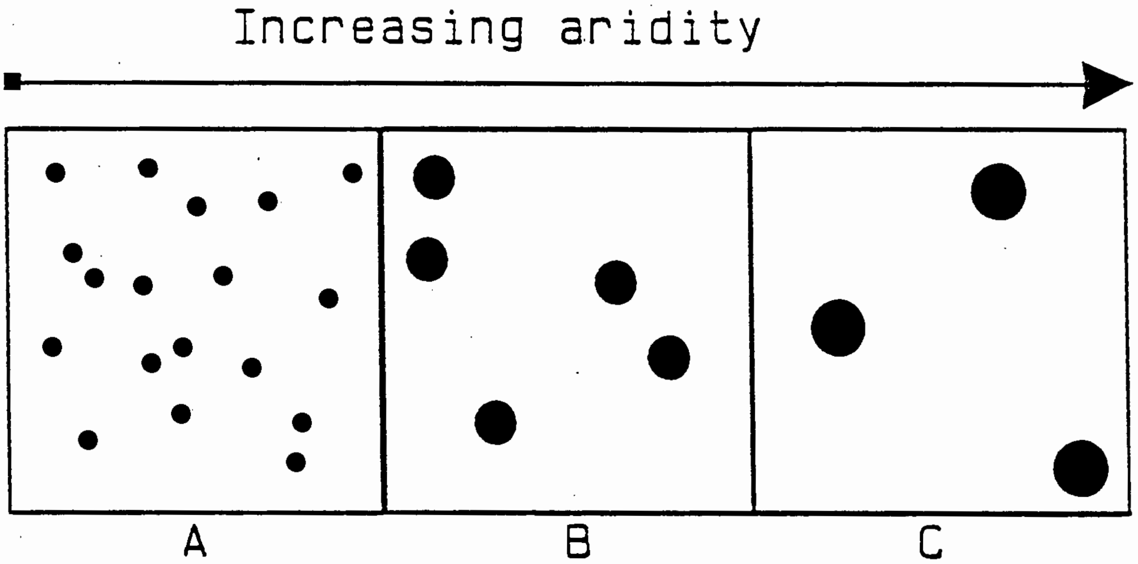

Fig. 28. Diagramatical representation of the general trend, with increasing aridity, of increasing geophyte size, and increasing geophyte nearest-neighbour distance. Geophyte distributions are random for the situations depicted in B and C, but are unknown for the mesic situation depicted in A.

Similarly, Jarvis (1978) and Brett (1986) have suggested that the low mas-specific RMR of *H. glaber* (see McNab 1966; Withers & Jarvis 1980) can be attributed to the need to maintain a low energy budget for the colony in response to widely dispersed and patchy food resources, and to the high cost of burrowing in very hard soils. In Chapter Six I proposed that the predictions of Jarvis (1978) and Vleck (1979, 1981) are mutually supportive.

McNab (1979a) on the other hand, maintains that the low RMR of subterranean rodents is primarily an adaptation to reduce heat stress, an hypothesis which has recieved little support (Jarvis 1978; Vleck 1979, 1981; Withers & Jarvis 1980; Chapters Six, Seven and Eight).

In considering the "energy conservation" hypotheses in terms of the foraging behaviour of the bathyergids, I propose that a) the specialist bathyergids, feeding exclusively by burrowing, incur greater costs during foraging than the generalist feeders, which feed partly off the surface and b) the location of resources by the specialists is considerably more random than is the case for the generalist feeders (see model assumptions later).

The model

Based on the above discussion, I develop a model which investigates the foraging risks of the specialist bathyergids based on the following assumptions (discussed in detail later): Molerats locate randomly distributed geophytes with density (No.m^{-2}), d, by random foraging involving burrowing only. When a geophyte is encountered by any one of a number, n, of equally cooperative molerats within a group, the geophyte is shared with the other foragers in the group, and the effective encounter distance burrowed by all foragers is simply the distance (m), s, burrowed to the first, or next, encounter. If the radius (m) of the burrow is r_b, and the radius of the geophyte (assumed to be spherical) is r_g, then molerats can locate geophytes if the distance between the centres of the burrow and geophyte < $r_b + r_g = R$.

Starting from the last encounter with a geophyte (s = 0), the probability that none of the n individuals encounters a geophyte after burrowing a distance, s, is (see appendix):

$P(s) = e^{-2Rnds}$ ...(3)

The mean distance, $\bar{s}$, between two consecutive encounters is

$\bar{s} = (2Rdn)^{-1}$ ...(4)

so the mean number, $\bar{g}$, of geophytes found per individual per distance is:

$\bar{g} = 2Rnd$ ...(5)

Equation (3) quantifies risk as the probability of unproductive foraging, such that an increase in n (Fig. 29) d or R decreases the risks of unproductive foraging. For instance, at constant d and R the risk of no encounter after say 3 m for the case n = 1 is 0.66, which is 41 times greater than that for the case n = 10 where the risk = 0.016 (Fig. 29). In habitats such as those of *H. glaber* where geophyte density is very low ($d = 0.059.m^{-2}$; Table 11), the model predicts that a solitary forager would have a 50 % risk of no encounter after burrowing a distance of 84 m. Simultaneous cooperative foraging therefore reduces the distances an individual must burrow before any one individual in the colony encounters a geophyte, thereby reducing the risk of unproductive foraging. Geophyte density influences risk in exactly the same way as colony size.

One of the most significant aspects of the model is that, although equation (4) shows that the mean encounter distance per indidividual decreases with increasing n at constant d and R, equation (5) shows that, compared with solitary foragers, there is no energetic advantage to the individual by foraging cooperatively in groups. I discuss the important implications this has on the energetics of group foraging later and in Chapter Eleven.

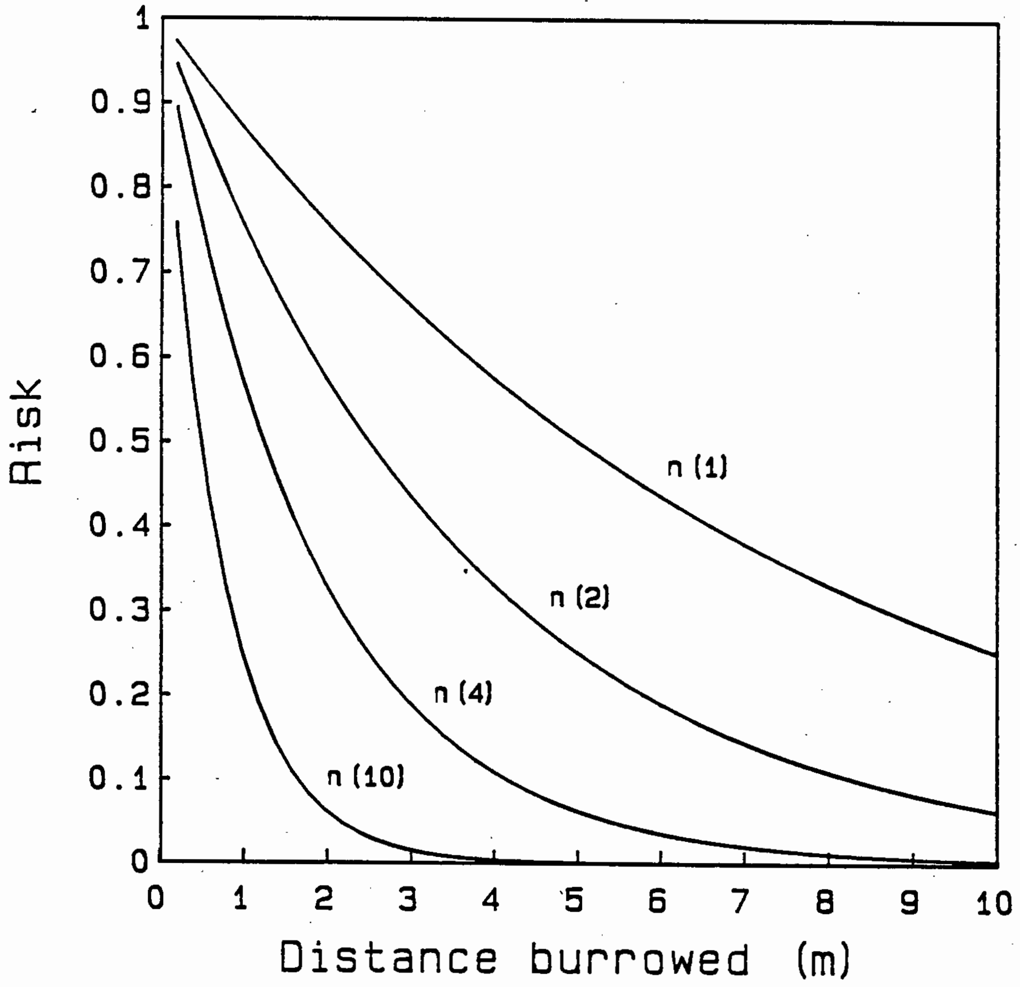

Fig. 29. The curves of foraging risk, quantified as the probability of unsuccessful geophyte encounters, as a function of distance burrowed for different group sizes (n) of cooperatively foraging molerats. The constants in equation (3) were d = 1 and R = 0.069.

Thus far, the major implications of the model are that a) the benefit of cooperative foraging is that it greatly decreases the risks of unproductive foraging, and b) group size does not increase individual energetic benefits. The model therefore supports similar models such as those of Thompson *et al.* (1975). Consequently, the first hypothesis I propose is that solitary foraging by specialist bathyergids is precluded in habitats where geophyte densities are low, simply because the risks of unproductive foraging are too great. The cost of burrowing long unproductive distances is not energetically viable for solitary foragers. A similar argument has been proposed by Brett (1986). As habitats become more arid, geophytes are more widely dispersed, and cooperative foraging becomes a more stable alternative to a solitary existence. This hypothesis is examined further in Chapter Eleven.

Evaluation of Assumptions

For cooperative foraging to function successfully, the assumption that individuals share their finds with the colony must hold. It is known that the social bathyergids bring geophytes to a common food store if the geophytes are small enough to be carried by single individuals (Davies & Jarvis 1986, Lovegrove & Jarvis 1986). If, however, the geophyte is very large, the colony feeds on the tuber *in situ* (Jarvis & Sale 1971, Brett 1986, Chapter Two).

The assumption that all geophytes are spherical does not always hold. This may be an important factor influencing foraging risks because from equation (3) it is evident that there would be a smaller probability of locating long thin tubers with a relatively small radius:volume ratio, than there would be for spherical tubers. In the case of the *Pyrenacantha* tubers which formed the principal diet of *H. glaber* in Brett's (1986) study, the tubers are approximately spherical in shape. On the other hand, the principal food item of *C. damarensis*, the tubers of *A. naudinianus*, are long and carrot-shaped (Chapter Two). This assumption would therefore be an important consideration in quantifying foraging risks for any particular habitat and social system, but for the purpose of comparing the relative foraging risks of group versus solitary foraging within a particular habitat, the assumption is not important. The same argument applies to the assumption that all geophytes must lie at the same depth as the burrow. For mesic areas this assumption does not hold, because geophytes are spread throughout the top 20 cm of the soil column and are not all located at any particular burrow depth (Lovegrove & Jarvis 1986, Chapter Two). In arid areas however, tubers are so large or long and carrot-shaped, that encounters would be made even if the burrow was at depths above or below an optimum encounter depth (Chapter Two). Again, this assumption would only be important when quantifying the foraging risks of particular habitats.

The most critical assumption of the model is the assumption that molerats forage randomly and do not locate food using cues. Because it is difficult to imagine how any sense other than olfactory could be utilised to detect subterranean food items within a dense medium such as soil, I have assummed that, if anything, this acts over very short distances and that burrowing is therefore random. Jarvis (1985) and Brett (1986) have shown that the burrow patterns of *H. glaber* appear to follow a random course, and do not lead directly to individual geophytes. Some plants had vegetative tuber systems which formed large patches of smaller tubers. *H. glaber* located these patches by random searching, but once the patch was located they apparently switched to non-random searching by digging a network of foraging burrows in the immediate vicinity of the first encounter. These plants, however, formed only a small proportion of the diet of *H. glaber* in Brett's (1986) study area, and invariably were very widely dispersed compared with unitubiferous plants. My observations of *C. damarensis* foraging for *A. naudinianus* tubers in the Kalahari Desert, suggest that tubers are not located by sensory cues from an appreciable distance because the foraging burrows often passed within 2 - 3 cm of undetected tubers. Until this aspect of foraging behaviour is investigated further, the model and its implications should be viewed within the constraints of this assumption. My intuitive impression, is that, at least for the specialist bathyergids, random foraging is a realistic assumption.

The last assumption to be evaluated is that all individuals within a group partake equally in foraging, i.e. they are all actively involved in searching for geophytes at different sites (digging faces) somewhere within the burrow system. This assumption has severe limitations. Firstly, in the case of *H. glaber*, the non-workers, which include the breeding female, do not forage (Jarvis 1981, Brett 1986). Consequently, the colony supports not only the daily energetic requirements of the non-workers, but also the costs of reproduction of the non-workers, specifically those of the breeding female. Secondly, it has been shown that *H. glaber* do not burrow individually at digging faces, but form cooperative "digging chains" (Jarvis & Sale 1971). Therefore, the number of digging faces in the burrow system does not necessarily correspond with the number of available workers. As discussed in Chapter Eleven, there are benefits to having a caste system which has survival significance beyond the risks of foraging.

These two observations suggest that unless social groups can compensate for the effective reduction of digging faces, for a given group size supporting infrequent and non-workers (i.e. n = n - x, equation 3, where x = non-workers), individual energetic benefits are lowered, and foraging risks are enhanced (equations 4 & 5), when compared with solitary foragers. The principal indirect way of compensating for these added energetic and risk constraints, would be to reduce the total energy expenditure of the colony, including that of burrowing. Theoretically, there are at least three ways in which this can be achieved; namely a) reducing body size, b) reducing thermoregulatory costs through huddling in the nest, and c) reducing mass-specific RMR.

Body size

There is a clear trend of decreasing body size with increasing colony size, increasing aridity, decreasing geophyte density (Table 11) and, as the model suggests, decreasing foraging risks. These trends support the hypothesis that a decrease in body size might represent a means of decreasing the absolute energy expenditure of a colony of molerats. Ordinarily, the mass-specific metabolic rates of small animals are much higher than those of larger animals, but the absolute metabolism of smaller animals is lower. It has already been suggested that factors such as soil type and soil moisture are important determinants of body size (Vleck 1979, 1981; Chapter Eight), nevertheless, in the case of the specialist bathyergids I feel confident that energy conservation must play an important role as well.

Nest-huddling

Concerning thermoregulatory costs, Withers and Jarvis (1980) have shown that *H. glaber* conserves significant amounts of energy by huddling in the nest. Heldmaier (1975) also showed that in mice there was an effective improvement in thermal balance during nest-huddling. Therefore, compared with solitary species, huddling must act to lower individual energy expeditures and therefore the total energy expenditure of the colony.

Resting metabolic rate

Data on the mass-specific RMR and body masses of seven bathyergid species were taken from Chapters Six and Seven. Least-squares-fit regressions (Zar 1974) were performed on the log-transformed mass-specific RMRs and body masses (M_b), yielding the linear relationship (Fig 30):

$$\log RMR = 0.089 + (-0.138)\log M_b \qquad ...(6)$$

or the power curve:

$$RMR = 1.23M_b^{-0.138} \qquad ...(7)$$

The regression was not significantly different from a horizontal line ($F = 5.743$, $p > 0.05$, $r^2 = 0.53$). The datum point for *H. argenteocinereus* fell outside the 95 % confidence limits of the regression and there is reason to believe that it is suspect. Firstly, the mass-specific RMR of this species was calculated from measurements taken from only two individuals (McNab 1966), and secondly, the mean body mass of these two animals (89 g) was nearly half that

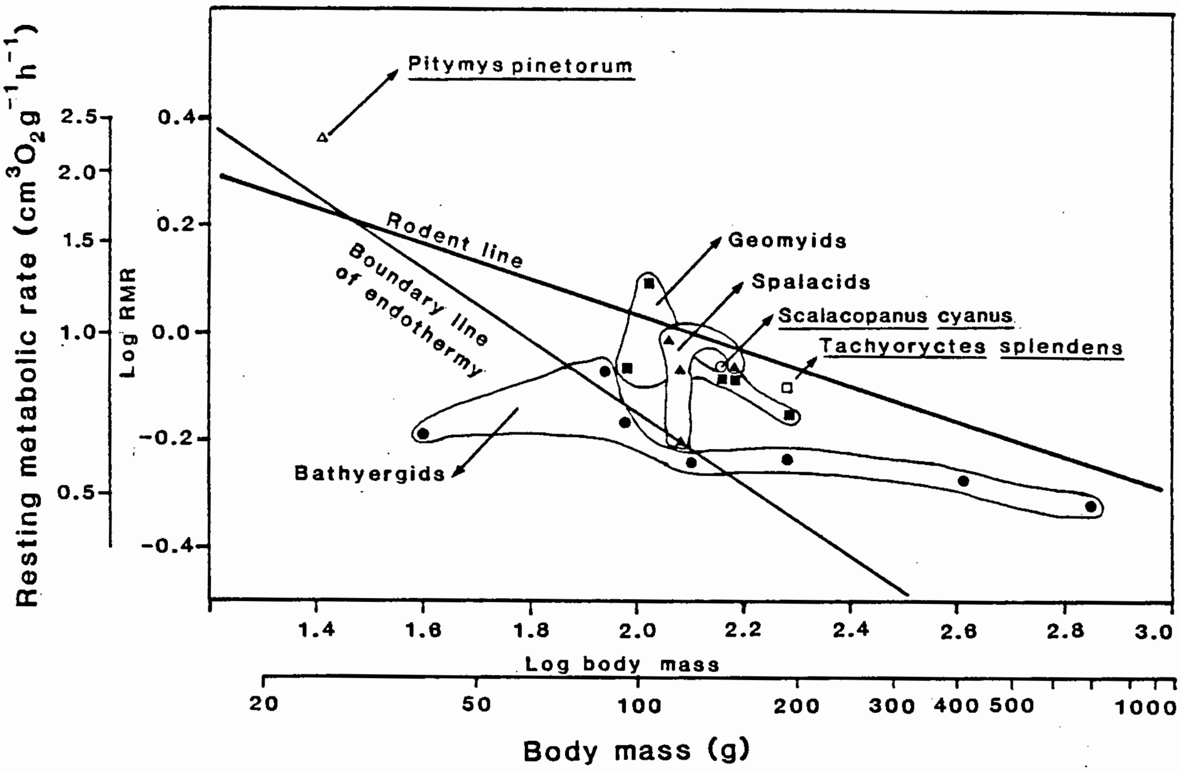

Fig. 30. Log-transformed regression of mass-specific resting metabolic rate as a function of body mass for various families of subterranean rodents. The "rodent" line represents the log-transformed power curve of 122 rodent species calculated by Hayssen & Lacey (1985). The "boundary line of endothermy" represents the postulated minimum mass-specific RMR required to maintain endothermy without the use of torpor (McNab 1979b). Data from Hayssen & Lacey (1985) for the Geomyidae and Spalacidae, Contreras (1986) for *Spalacopus cyanus*, Chapter Seven for the bathyergids, and McNab (1979a) for all other species.

of the mean adult mass (160 g) reported by Jarvis and Sale (1971) and Jarvis (1973). Therefore the reported mass-specific RMR of *H. argenteocinereus* is probably an overestimate of the adult mass-specific RMR of the species. When this datum point is discarded from the log-transformed regression, the regression is significant ($F = -3.723$, $p < 0.05$, $r^2 = 0.78$), and the slope of the representative curve is lower:

$$RMR = 1.00M_b^{-0.107} \qquad ...(8)$$

In any event, the scaling of mass-specific RMR of the bathyergids is virtually independent of the influence of mass.

The slopes of equations (7 & 8) were both significantly lower ($p < 0.05$, comparison of slopes) than those calculated for the geomyids (-0.493) and non-subterranean rodents (-0.331) by Hayssen & Lacey (1985) (Fig. 30).* The allometry of bathyergid metabolism is however very similar to the mass-independent scaling of metabolism of the burrowing heteromyid rodents (Hayssen & Lacey 1985), a trend that has been attributed to the need to conserve water and energy (McNab 1979b).

Another important consequence of this scaling pattern is that the mass-specific RMRs of the three social bathyergids, *H. glaber, C. hottentotus* and *C. damarensis*, fall below the values predicted by the "minimal boundary line for endothermy" (McNab 1974) (Fig. 30). This is significant, because although *H. glaber* is virtually incapable of maintaining endothermy (McNab 1966, Withers & Jarvis 1980), *C. hottentotus* (Haim & Fairall 1986) and *C. damarensis* (Chapter Six) are good thermoregulators. As yet, there is no evidence to suggest that the cryptomyids employ torpor. This observation suggests that despite low body temperatures and low mass-specific RMRs, a normal-to-low conductance ensures that the cryptomyids maintain endothermy over a fairly wide range of ambient temperatures below the lower limit of thermoneutrality. This implies that the conductance of *C. damarensis* and *C. hottentotus* has evolved in response to cool burrow temperatures rather than warm burrows (*cf.* McNab 1979a), and that the low mass-specific RMR of these two species may have little to do with potential hyperthermia hazards *per se*.

The unusual scaling of mass-specific RMR in the bathyergids comfirms the suggestions of various authors (Brett 1986; Jarvis 1978; Vleck 1979, 1981; Withers & Jarvis 1980; Chapters Two - Eight) that ecological constraints associated with balancing an energy budget, such as the high cost of burrowing, low habitat productivity, and resource dispersion characteristics, are likely to be more important determinants of the metabolic rate of subterranean rodents than the constraints associated with heat stress.

Although exceptionally low mass-specific RMRs would lower the absolute energy expenditure of the colony, they also indirectly permit a reduction in foraging risks by increasing group size. The savings in energy of individuals can simply be channelled into increasing the group size of the colony, and consequently further decreasing the encounter distances between geophytes, and the associated foraging risks. This concept is illustrated in Table 12. The largest bathyergid, *B. suillus* is used as a standard, because it has a mass-specific RMR, and consequently an absolute metabolism which is most similar to the predicted value for rodents. Note that for *H.glaber*, a reduction in the mass-specific RMR from the predicted value of 1.47 $cm^3g^{-1}h^{-1}$ to the observed value of 0.64 $cm^3g^{-1}h^{-1}$ (44% of expected), means that the number of these molerats with absolute metabolism equivalent to one *B. suillus* is more than doubled from 5.9 animals to 13.5 animals. Note also that although the greatest benefits of mass-independent scaling of metabolism occur in the social bathyergids i.e. those that deviate most from the expected metabolism, the smaller solitary bathyergids also benefit considerably. (Table 12). In short, the principle I am advocating is that instead of a solitary large-sized animal coping with high foraging risks, it is a better proposition to have numerous smaller animals with the same mass-specific RMR as the larger solitary individual, and consequently the same combined absolute metabolism as the larger animal. As an

Table 12. The observed and predicted mass-specific and absolute metabolic rates of seven bathyergids.

Data from Chapter Seven.

Species	Body mass (g)	Observed mass-sp. RMR	Predicted mass-sp. RMR*	Observed absolute RMR	Predicted absolute RMR	A	B	A/B	Social status
H. *glaber*	39.5	0.64	1.47	25.3	58.1	13.5	5.9	2.3	Social
C. *damarensis*	125.0	0.57	1.01	71.3	126.3	4.8	3.2	1.5	Social
C. *hottentotus*	95.0	0.68	1.10	64.6	104.5	5.3	3.8	1.4	Social
G. *capensis*	191.0	0.59	0.88	112.7	168.1	3.0	2.4	1.3	Solitary
H. *argenteocinereus*	88.0	0.85	1.13	74.8	99.4	4.6	4.0	1.2	Solitary
B. *janetta*	406.0	0.54	0.68	219.2	276.1	1.6	1.4	1.1	Solitary
B. *suillus*	712.0	0.48	0.56	341.8	398.7	1.0	1.0	1.0	Solitary

A: The number of mole-rats that would use the same observed absolute metabolism as one B. *suillus*.

B: The number of mole-rats that would use the same predicted absolute metabolism as one B. *suillus*.

* Predicted by Hayssen & Lacey (1985) equation for rodents.

RMR = Resting Metabolic Rate in $\text{cm}^3.\text{g}^{-1}.\text{h}^{-1}$

analogy, it is equivalent to cutting up a large animal into say 13 pieces, and sending each piece off to look for food.

These observations strongly suggest that the allometry of the mass-specific RMR of the bathyergids, termed here Risk-Sensitive Metabolism (RSM), effectively reduces the risks of unproductive foraging in solitary and social molerats by a) decreasing the mass-specific RMR and therefore, the cost of burrowing (Chapter Eight), b) reducing the total costs of foraging of a colony of animals, and c) achieving a group size related to the mean resource abundance which minimises the risks of non-productive burrowing.

Predation and Kin Selection

I maintain that the principal factors selecting for RMR and group size in the bathyergids are the relative risks and energetic constraints involved in foraging for widely dispersed food resources, but I acknowledge that at least in terms of group size, other factors such as predation may play an important role as well. De Graaff (1981) and Brett (1986) report various forms of predation on *C. damarensis* and *H. glaber*. If, however, the degree of sociality is determined largely as a consequence of foraging risk reduction and energy conservation, this suggestion needs to be put into the context of an individual's relative reproductive potential, or fitness, in a group versus solitary existence. Many, if not most members of *H. glaber* and *C. damarensis* colonies are never afforded the opportunity of reproducing (Jarvis 1981, Brett 1986, Bennett & Jarvis 1987), whereas solitary bathyergid species may breed every year. This could imply that although the risks of foraging are considerably reduced by remaining in permanant foraging groups, these individuals sacrifice reproductive fitness. This is not necessarily true.

Inbreeding in *H. glaber* colonies appears to be extensive (Brett 1986, Jarvis pers. comm.). This is probably due to the many problems associated with dispersal (see Chapter Eleven). As the model suggests, the risks of resource procurement that a solitary individual faces in habitats where resources are very widely dispersed, are high. The average distance between colonies of *H. glaber* in undisturbed habitats in Kenya was 1 km (Brett 1986). Even if *H. glaber* were to attempt to promote outbreeding by dispersing between colonies, the risks involved in such behaviour would be high. Likewise, surface dispersal over such vast distances is not a viable proposition for a small (25 - 32 g) hairless and blind animal, which is behaviourally, morphologically, and physiologically adapted to an obligate subterranean existence.

Inbreeding leads to "inbreeding depression", namely a decrease in offspring size, fertility, and fitness (Crow and

Kimura 1970). Under certain conditions however, it may actually promote the fitness of an individual. Chesser and Ryman (1986) suggest that species which inbreed regularly probably have reduced inbreeding depression as a result of selection against deleterious alleles. Furthermore, the low incidence of random environmental pertubations of subterranean habitats (Nevo 1979), should result in deleterious alleles being less important than would be the case for aboveground habitats. It has also been suggested that inbreeding individuals will contribute more of their genes to the next generation than do outbreeding individuals if the fitness loss in dispersal is greater than the inbreeding depression in fitness (Bengtsson 1978, Chesser and Rymen 1986). As long as the presence of the individual within the molerat colony promotes foraging efficiency by decreasing foraging risks, that individual's fitness is ensured through the successful breeding of close relatives. This argument is of course speculative, but I feel confident that when the genetic relatedness of these species is investigated the argument will hold.

Summary

This study proposes that the foraging behaviour and extent of dietary specialisation of the bathyergid molerats has an important influence on foraging efficiency and the degree of sociality. I have presented a simple model which investigated the risks of unproductive foraging as a function of group size, resource dispersion, and resource size. The behaviour of the model indicated that the risk of poor performance during foraging could be the principal cause of sociality in the bathyergids. Cooperative foraging reduces the risks of unproductive foraging, and represents a more stable long term behaviour in arid habitats where resources are widely dispersed. However, energetic benefits of sociality can only be realised if the total energy expenditure of the colony is minimised by reducing body size, mass-specific RMR, and thermoregulatory costs. I regard the trend towards mass-independent scaling of mass-specific RMR in the bathyergids to be important in promoting sociality as a solution to risk, and have termed it Risk-Sensitive Metabolism.

CHAPTER TEN

Daily Energy Expenditure of *Cryptomys damarensis*: An Activity Time Budget Estimate

Introduction

Currently the most popular method of measuring the energetic cost of free existence, is the the estimation of CO_2 production by the doubly labelled water ($^3HH^{18}O$ and $^2HH^{18}O$) method (Lifson & McClintock 1966). In the laboratory it has been shown that the accuracy of this method is approximately 8 % (Nagy 1980). Nagy (1980) investigated the six assumptions on which the method is based, and found that in the field some of the assumptions are violated, resulting in some instances, in errors in the estimate of CO_2 production as high as 80%. He found that one of the largest sources of error occured when CO_2 and H_2O entered isotopically labelled animals across respiratory or skin surfaces. Typically, this error occurs in an unstirred or confined area, such as a burrow. He suggested that the error would be "...significant in gregarious animals that communally inhabit enclosed spaces such as burrows, dens, or enclosed nests, where CO_2 from unlabelled animals can accumulate" (Nagy 1980). This error can only be avoided if ambient H_2O and CO_2 have specific activities of H and O equal to those in the body water of the labelled animal (Lifson & McClintock 1966). The group size (20 - 25) and gregarious nesting behaviour of *C. damarensis* (Bennett & Jarvis 1987, Chapter Four) therefore pose serious potential sources of error in the use of the doubly labelled water method.

Consequently, I decided that the use of the method would be futile and not very cost-efficient.

The benefit of obtaining some estimate of the daily energy expenditure of free-ranging *C. damarensis* will be clear in the next chapter. It simply provides a value with which the behaviour and significance of the model presented in Chapter Nine can be illustrated. The procedure I have used and the estimates I have obtained are, however, also potentially erroneous. These errors should not detract from the empirical data presented in other Chapters and this Chapter should be evaluated on its own. I have calculated a daily energy expenditure based on the RMR (Chapter Six), the metabolic cost of burrowing (Chapter Eight), and the activity budget (Chapter Four) of *C. damarensis*.

Methods

Assumming a linear increase in metabolism between resting and burrowing activity, the following equation:

$$Y = 0.57 + 0.201X \qquad \text{...(9)}$$

where Y = mass-specific metabolic rate and X = activity state (0 - 10), gives the metabolic rate of the different activity states of *C. damarensis* in dry sand. The absolute metabolism (cm^3O_2) of these activity states were then calculated for a 152 g animal from the percentage time spent in each activity state while in the nest and active (Chapter

Four). Then, I have used an RQ value of 0.77 calculated for *Thomomys bottae* by Vleck (1979) to calculate an energy conversion factor of 19.94 $J.cm^{-3}$. Once again, for comparative purposes that will be clear in the next chapter, I have also calculated the daily energy expenditure of *H. glaber* and *G. capensis* assumming that these two species would have the same activity budget as that of *C. damarensis*. These estimates of the daily energy expenditure are given in Table 13.

Using estimates of burrowing speed in dry sand for all three species (Du Toit *et al.* 1985, Chapter Eight), and assumming that all molerats spend 3.06 $hrs.day^{-1}$ burrowing (Chapter Four), I have calculated the daily distance that individual molerats would burrow. The study of Du Toit *et al.* (1985) used sand that was dry but not 'bonded' and compacted. Nevertheless, I have used the highest burrowing speed that they obtained, 0.5 $m.h^{-1}$, despite the fact that this speed would probably be slower in dry compacted sand. Burrowing speeds are given in Table 14 and will be discussed again in the next Chapter.

Results and discussion

A 152 g *C. damarensis* was calculated to have a daily energy expenditure of 76.48 $kJ.day^{-1}$. The daily metabolism was therefore 1.84 times RMR. Of this estimate, 31.3 % was used

Table 13. The absolute energy expenditure of a 152 g *C. damarensis* at various activity states while in the nest, and out of the nest (foraging). Activity state data from Chapter Four.

		In nest		Out of nest	
Activity state	Metabolic rate ($cm^3g^{-1}h^{-1}$)	Time in activity state (hours)	Absolute metabolism (cm^3)	Time in activity state (hours)	Absolute metabolism (cm^3)
0	0.58	12.98	1144.3	0.37	32.6
1	0.77	2.04	238.8	0.29	33.9
2	0.97	1.26	185.8	0.40	59.0
3	1.17	0.61	108.5	0.26	46.2
4	1.37	0.45	93.7	0.12	25.0
5	1.58	0.21	50.4	0.26	62.4
6	1.78	0.19	51.4	0.20	54.1
7	1.98	0.09	27.1	0.16	48.2
8	2.18	0.11	36.4	0.39	129.2
9	2.38	0.07	25.3	0.16	57.9
10	2.58	0.32	125.5	3.06	1200.0
Totals		18.33	2087.2	5.67	1748.5

Assuming 19.94 $J.cm^{-3}$, daily energy expenditure = 76.48 $kJ.day^{-1}$.

Table 14. Resting metabolic rates (RMR), Burrowing metabolic rates (DMR), daily energy expenditures (E_d), burrow radii (r_b), and the daily distances burrowed (S_d), of three bathyergids. Data from Chapters Three, Six, Seven, and Eight, and from Du Toit *et al.* (1985) and Brett (1986).

Species	Body mass (g)	Burrowing speed ($m.h^{-1}$)	RMR ($cm^3g^{-1}h^{-1}$)	DMR	E_d (kJ)	r_b (cm)	S_d (cm)
H. glaber	32	0.30	0.64	2.78	17.70	2.2	0.92
C. damarensis	152	0.92	0.57	2.58	76.48	3.3	2.82
G. capensis	197	0.50	0.59	3.41	110.08	5.0	1.53

CHAPTER ELEVEN

Conclusions: An Exercise in Fitness and Survivorship Potential

Introduction

This chapter takes the form of an exercise which draws together all data presented or reviewed in earlier chapters, with the foraging model presented in Chapter Nine. Throughout the exercise several hypothetical situations will be presented which illustrate how, in my opinion, energetic constraints can account for most of the behavioural, physiological, and morphological characteristics of the bathyergid molerats. I have chosen the southern Kalahari (Dune site) as representing the general intermediate habitat for the species comparisons, mainly because of its relative homogeneity, and simplicity with respect to subterranean resource distributions.

First, a few considerations. As pointed out in Chapter Nine, I fully appreciate the limitations involved in attempting to model nature exactly, particularly considering the many assumptions made. I also appreciate that *C. damarensis* is the only molerat suitably adapted to the Kalahari, and should therefore display a greater fitness potential there, than any other bathyergid. Nevertheless, a comparative approach provides the best insight into the factors responsible for the evolution of characteristics such as body size, group size, and metabolic capabilities. Furthermore, considering the universal simplicity and constancy of the physical features of subterranean microhabitats, greater credibility can possibly be attributed to these comparisons than, for example, to those made between aboveground species. What follows therefore, is my own interpretation of the energetic constraints and foraging risks responsible for the evolution of sociality and eusociality in these subterranean rodents. Because it is impossible to design controlled field experiments which would succeed in definitively isolating the causes of sociality, I feel that the ecophysiological modelling approach I have adopted, is the most suitable alternative.

The object of the exercise is to evaluate the survivorship and fitness potential in the Kalahari, of the three bathyergids for which energetic data is available, namely *C. damarensis*, *H. glaber*, and *G. capensis*. It is equivalent to asking the simple question; how would *C. damarensis* survive in the KGNP if it were to have the same physiological and morphological features as those of *H. glaber* and *G. capensis*? Why not be bigger or smaller, more furry or less furry, or live alone instead of in groups? The procedure will be to estimate the costs and benefits of burrowing between successive tuber encounters, for different group sizes and tuber densities.

Methods

The cost of burrowing between two succesive tuber encounters (E_b) can be calculated from the mean distance ($\bar{s}$) that would have to be burrowed between tubers (equation (5), Chapter Nine), divided by the daily distance burrowed (S_d), and multiplied by the daily energy expenditure of the molerats (E_d) such that $E_b = E_d(2RdnS_d)^{-1}$, where $R = r_b + r_g$; $r_g = 2.2$ cm (Chapter Two) and r_b are from Table 14 (Chapter Ten).

Solitary existence

Consider the Dune site in the KGNP during summer, where tubers occur in densities ranging from 0.017 - 0.407 tubers.m^{-2} with a mean of 0.165 tubers.m^{-2} (Chapter Two), and where soil temperatures and burrow depths are the same as those described in Chapter Three. Consider first a molerat that has located a tuber with an energy availability of 2002 kJ (Chapter Two), would a solitary animal of each species obtain sufficient energy from this tuber to enable it to burrow the mean distance to the next tuber encountered? Let us also assume that if it does not have sufficient energy, it either dies of starvation, or, is forced to the surface where it is eaten by a predator.

Based on the respective energy requirements of each species and the mean tuber density, *C. damarensis* and *H. glaber* survive showing profits of 508 kJ and 677 kJ respectively, but *G. capensis* incurs a loss of 1026 kJ and dies. If we consider E_b to be an index of the survivorship potential for all three species, then *H. glaber* and *C. damarensis* would have a 2.29 and 2.09 times greater suvivorship potential than *G. capensis* at the mean tuber density. Now, if *C. damarensis* and *H. glaber* were then to encounter a patch within the macro-clump with a lower tuber density of 0.110 - 0.130 tubers.m^{-2}, neither species would survive. So far, the exercise shows that a solitary *G. capensis* would not survive the probabilistic and energetic constraints of foraging even at the mean tuber density, primarily because its body size is too large, and its daily energy expenditure too high (Chapter Eight). On the other hand, *C. damarensis* and *H. glaber* can exist as solitary individuals, but only at the mean tuber density, and if they immediately commence burrowing after having located a tuber.

In the next situation, we consider viable breeding pairs of all three species. The distance that any one individual of the pair has to burrow before either one of the pair locates a tuber is now halved, and consequently the costs are halved. However, the same density-dependent profits enjoyed as solitary molerats are now shared by the pair. The exercise once again shows that at the mean tuber density, the pairs of *H. glaber* and *C. damarensis* would survive showing lower individual profits, but that a pair of *G.*

capensis would not. We now eliminate *G. capensis* from the exercise. Even as a pair it could not survive. It is simply too big.

Reproduction

Let us now assume that the total accumulated profits from successive tuber encounters are sufficient for the female in the pair to breed, and that she uses 100 % of these profits to successfully raise say five molerats to reproductive age. The exercise shows that a group of seven molerats survive successfully at the mean density, but that as individuals they now only enjoy a 14.3 % share of the same profit enjoyed as solitary individuals. Assuming that selection acts at the level of the individual (e.g Dawkins 1976), and that each individual will strive to reproduce itself, they remain in the colony and a brother-sister pair will mate and conceive simultaneously with the original breeding pair. The accumulated profits now have to be shared between the two females, so each gets a 50 % share of the accumulated profit. However, these shares prove to be insufficient to maintain the pregnant females, and the dominant female successfully intimidates the sub-dominant female to the point where she spontaneously aborts, or, dies. The breeding female then successfully raises say another four molerats.

At least for *C. damarensis* in the Kalahari, this situation implies that only one pair of molerats can breed in the colony. The suggestion of inbreeding is realistic, and has been discussed in Chapter Nine. There is a very small possibility of a receptive female being able to locate and conceive with a non-related con-specific male. The same argument would apply to *H. glaber* in Kenya.

Dispersal

During the following breeding season, the process is repeated. Another brother-sister pair and the original breeding pair successfully conceive. However this time, the younger breeding female responds to the intimidation by the dominant female by leaving the burrow system to establish her own. This she does by blocking a blind-ending burrow behind her, somewhere in the burrow system, and continues to burrow as fast as possible to get away from the parent burrow system. Now let's be generous and assume that she can survive at full burrowing capacity for four days without food i.e. a burrowing capacity equivalent to 306 kJ for *C. damarensis* and 70.8 kJ for *H. glaber*. At the mean tuber density neither species would survive the time period and effort required to locate the next tuber. In fact the density of tubers would have to be as high as 0.85 $tubers.m^{-2}$ and 3.2 $tubers.m^{-2}$ for *C. damarensis* and *H. glaber* respectively, before dispersal could be successfully accomplished. These densities are 2.1 - 7.8 times greater than the highest tuber density measured at the Dune site. In this situation *C. damarensis* would have a 3.8 times greater chance of survival than *H. glaber*. By virtue of its larger body size it can withstand longer periods of starvation, and therefore burrow further than *H. glaber* before starving.

Even if both individuals in this breeding pair attempted to disperse together, remembering that burrowing distances would be halved, they would not survive. Of course, at tuber densities lower than the mean, a more realistic situation, the situation would be worse. It is highly likely that in the Kalahari, where the tubers of *A. naudinianus* appear to form large macro-clumps each invariably inhabited by a well established colony of molerats (Chapter Two), dispersing molerats would have to burrow through sub-optimal habitat in the hope of aquiring an uncolonised macro-clump. The density of tubers in these sub-optimal habitats will be equal to, or, below the lowest density of the marco-clumps, say between 0.005 - 0.017 tubers.m^{-2}. The only way that these breeding pairs could successfully locate the next tuber at a tuber density of 0.017 tubers.m^{-2}, would be to disperse in groups of 48 and 180 for *C. damarensis* and *H. glaber* respectively. Besides the fact that these group sizes are larger than the observed group size, they would totally defeat the object of dispersal in the first place.

Earlier it was argued that a dispersing solitary individuals would succeed at the mean tuber density if a tuber had already been located. Dispersing females could therefore locate a tuber somewhere in the parent burrow system before breaking contact with the parent burrow system. Once again, at tuber densities less than $0.110.m^{-2}$, or those assummed for sub-optimal habitats, these females would not survive. These situations highlight one of the most important aspects of this thesis, namely that solitary molerats can not survive dispersal from parent colonies in habitats where resources are widely distributed. The probabilities of locating tubers are too low, and therefore the risks of foraging too great. In short, a solitary existence represents an extremely unstable alternative to living in groups.

Colony size

A further aspect that requires discussion concerns the optimal group size of a species given a particular resource distribution. For instance, the exercise shows that at the mean tuber density in the Kalahari, *C. damarensis* could theoretically maintain a colony of 200 molerats, which is much greater than the observed colony size. What therefore, is the disadvantage of having a large group size? I suspect that one important constraint concerns the total biomass and renewal rate of resources within macro-clumps.

Assumming no reproductive costs, 20 molerats would have a daily energy expenditure of approximately 1530 $kJ.day^{-1}$, whereas a colony of 200 molerats would have an expenditure of 15300 $kJ.day^{-1}$. The larger colony would therefore exploit the macro-clump ten times faster than the smaller colony. My observations of individual colonies in the Kalahari suggest that over a two year period, colonies remain in particular macro-clumps for this entire period. This implies that the daily energy expenditure of these smaller colonies is probably lower than, or at best equal to, the rate at which resources are renewed. However, the energy expenditure of a colony of 200 molerats is probably much greater than the renewal rate, which would require that a colony of this size frequently has to locate uncolonised macro-clumps. Furthermore, heavy exploitation of the macro-clump, not only by the molerats, but also by large ungulates, such as the gemsbok *Oryx gazella* (Williamson 1987, pers. obs), would lower the mean tuber density therby lowering the probabilities of tuber encounters and increase the enrgetic constraints of foraging. This, incidently, implies possible competion between gemsbok and molerats. For many obvious reasons this situation represents a less stable alternative to remaining as long as possible in an established macro-clump. I would hypothesise therefore, that the optimal group size of social bathyergids is largely a function of the spatial pattern, biomass, and renewal rate, of distributions of geophytic resources.

Differentiation of labour

In Chapter Nine I presented an argument suggesting that inbreeding, through close genetic relatedness among all molerats in a colony, ensures that all individuals achieve at least the minimum level of fitness, simply by assisting the breeding pair to breed successfully. Minimum fitness can be regarded as the passing on of 50 % of an individual's genes, which would be achieved if they were able to outbreed successfully. If we consider the lack of data concerning genetic relatedness in the molerats and we accept the above argument, it is not difficult to hypothesise on the energetic basis for the selection of a worker caste, and ployethism.

Let us now assume that, instead of the mean body size of 152 g, 50 % of the colony maintain the smallest body size capable of ensuring maximum burrowing efficiency, say 100 g (SC3 in Chapter Four). From Chapter Eight, we know that smaller molerats burrow more efficiently in hard soils, so this is a reasonable assumption. The daily energy expenditure of a 100 g molerat would then be about 50 kJ.day^{-1}, which is 35 % lower than that for a 152 g molerat. To a colony of 20 molerats this represents a daily saving of 266 kJ, or 18 % of the daily energy expenditure of the colony. These savings can be chanelled into a number of areas which would further enhance the efficiency and fitness of the whole colony. Firstly, they could be channelled into supporting and maintaining an additional five worker molerats of the same body size. Secondly, they could be channelled into three soldier molerats with a body mass of 200 g, whose function would be the defence of the burrow system. Thirdly, they could support not only the breeding female, but also the dominant breeding male(s), so that these molerats need not partake in foraging but concentrate their activities exclusively on successful reproduction. These are just three of the possibilities that could theoretically occur for the same daily energy expenditure of 20 molerats with a body mass of 152 g. I propose therefore that the smaller body size of the worker caste and polyethism have evolved primarily for a) increasing burrowing efficiency and reducing the risks of foraging, b) decreasing the daily energy expenditure of the colony, and c) inreasing the versatility of the colony by promoting the existence and maintenance of specialist castes, such as workers, breeders, and possibly soldiers. Although this argument presents a strong case for the factors favouring the evolution of ployethism, it does not provide any clues as to the as yet unexplained mechanism of polyethism. In this respect, however, I would suggest that male dominance by the larger molerats must be involved.

Thermoregulation

So far, we have only considered the Kalahari habitat during summer. We have seen that once a tuber has been located, *H. glaber* actually show a slightly better survivorship potential than *C. damarensis*. This is due entirely to their smaller body size, and therefore their lower daily energy expenditure. The pertinent question then, is why have smaller body sizes not evolved in *C. damarensis*? The answer probably concerns the maintenance of endothermy. During winter, the mean temperature of the primary burrows are between 18 - 19°C (Chapter Two). At this temperature *C. damarensis* maintains body temperature at an elevated metabolic rate of approximately 2.6 times RMR (Chapter Six). This metabolic scope is approximately half of that incurred while burrowing (Chapter Eight), suggesting that thermoregulatory costs during foraging are not an important consideration to *C. damarensis* during winter. When not foraging, *C. damarensis* need simply nest in the deeper galleries of the burrow system, such as the bolthole, where temperatures are higher (Chapter Three). In addition, thermoregulatory costs can be further reduced by huddling in the nest. Nevertheless, a smaller body size in *C. damarensis* would increase energetic costs of thermoregulation appreciably and thus upset the present thermal equilibrium which this species marginally maintains in its habitat. However, the situation for *H. glaber* at these temperatures is entirely different. Below 20°C, solitary individuals, as well as individuals within huddling groups, rapidly become hypothermic (McNab 1966, Withers & Jarvis 1980). Furthermore, Chapter Eight showed that even at 27°C in damp sand, individuals showed a significant tendency towards hypothermia over a period of less than an hour. I feel therefore, that *H. glaber* would not survive the thermal stress of the primary burrows and nest sites in the Kalahari Desert during winter. Because of their very low mass-specific RMR and small body size they would not be able to maintain thermal equilibrium. They do not experience these constraints in their natural habitat in Kenya, because the seasonal variation of the mean burrow temperatures (Brett 1986) is considerably lower than in the Kalahari burrows.

Mesic habitats

This far, I have concentrated on the potential survivorship of molerats in arid habitats where resources are widely distributed. I have also argued that the risks of foraging preclude a solitary existence in arid habitats. However, we also need to consider the opposite situation, namely the fitness of social species in mesic areas, where geophytes are small but occur in high densities. In brief, after excluding *H. glaber* because of their inability to thermoregulate in this habitat, the exercise shows that a species such as *C. damarensis* would display an equal, if not greater fitness potential in mesic regions, compared with solitary species. Nevertheless, according to the model, energetic constraints associated with dispersal are now eliminated, so individuals can theoretically disperse from the colony and locate and mate with non-related conspecifics, as is done by the solitary genera *Georychus* and *Bathyergus*. *C. hottentotus* is a social species which inhabits both mesic and arid regions, and is often found sympatrically with *G. capensis* and *B. suillus* (De Graaff 1981, Lovegrove & Jarvis 1986).

The next question then, is what prevents individuals from dispersing from the parent burrow system? My hypothesis is that the limiting factor is once again body size, and its associated thermoregulatory problems. I have already shown (Chapters Eight and Nine) that for energetic reasons, one of the requirements for the success of social groups is a small body size and Risk-Sensitive Metabolism. Although the thermoregulatory benefits of nest-huddling have only been preliminarily investigated in *H. glaber* (Withers & Jarvis 1980), presumably it is an important aspect when considering the fitness of other small molerats in mesic habitats, such as *C. hottentotus* (90 g). I am suggesting therefore that a solitary *C. hottentotus* would not survive the costs of hypothermia incurred during winter, if it were to maintain a low mass-specific RMR. However, in groups, potential hypothermia in individuals during short foraging periods is unlikely to pose a significant problem, because individuals can rely on the thermoregulatory benefits of nest-huddling. Apart from the problems associated with the costs of burrowing in hard soils, I suspect that cool winter burrow temperatures are an important factor favouring natural selection of larger body sizes of the solitary species. The question of how solitary and social species manage to coexist will probably be found in detailed studies on the avoidance of interspecific competition through species-specific foraging behaviors. There is some evidence (Lovegrove & Jarvis 1986) to suggest that the social species are more selective in their choice of geophytes, concentrating mostly on the larger corms and bulbs.

Generalist feeders

Although this exercise does not concern generalist feeders, the status of the two generalist molerats, *B. suillus* and *B. janetta*, should also be examined. Both species have large body sizes (350 - 1500 g). *B. suillus* inhabits very sandy habitats in mesic regions. *B. janetta* also occurs in sandy habitats, but the habitat is more arid. Considering body size and diet, I would tend to regard *B. suillus* as nothing more than an 'underground rabbit'. Very little is known about the diet of *B janetta*, but I suspect that it feeds on a diet similar to, or perhaps a slightly more specialised one than *B. suillus*. According to my thesis, both species are solitary because the probabilities of locating food resources are not as low as those for the social specialist molerats in arid regions. *B. suillus* has a larger body size than *B. janetta* because of the need to maintain endothermy (Chapter Five), the softer soils in its habitat (Vleck 1979, 1981; Chapter Eight), and the relatively higher productivity of its habitat. *B. janetta* is smaller than *B. suillus* primarily because of the lower productivity of its more arid habitat (Chapter Five).

Risk

For the sake of convenience this exercise has only considered the mean distance that molerats would have to burrow between successive geophyte encounters. This approach is of course the complete antithesis of the philosophy of risk-sensitive behaviour, namely that foragers do no respond to the mean resource characteristics, but rather, to the probability distribution of some aspect of that resource, such as the distance between successive encounters. Attempting to do this excercise using probability distributions is considerably more complicated, and requires the consideration of a time axis, and rates of extinction. I intend this to be one of the subjects of my future research, in collaboration with other researchers. This approach should highlight the causes of sociality more comprehensively and should also throw more light on factors such as optimal group sizes. Nevertheless, by considering the mean distances burrowed, the exercise failed to emphasise sufficiently the role of risk associated with the probability distribution of burrowing distances. What it essentially means to the outcome of the exercise is the following. Wherever the costs and benefits of foraging were considered in marginal situations, such as at low tuber densities, the probability of starvation was greater, simply because of the probability of having to burrow a distance further than the mean distance. This is because the frequency distribution of tuber densities is skewed towards densities lower than the mean (Chapter Two). Also, the fitness of groups was always greater than that for solitary individuals at the same tuber density, because the variation of burrowing distances about the mean burrowing distance decreases with increasing group size (Chapter Nine). In any event, the limitation of not fully considering risk does not affect the general utility of the exercise.

Final summary

Not surprisingly, *C. damarensis* emerges as the sole survivor of this exercise. Its body size is large enough to maintain thermal equilibrium despite a low mass-specific RMR. The large seasonal variation in burrow temperature necessitates the ability to thermoregulate, particularly during winter, so *C. damarensis* cannot increase conductance as predicted by McNab (1979a). On the other hand, body size is small enough to ensure the lowest possible daily energy expenditure while achieving the highest possible burrowing efficiency. This is particularly relevant to the smaller molerats in the colony, which, as I have suggested, probably represent a worker caste. A low RMR profoundly decreases the daily energy expenditure, whereas a large metabolic scope for burrowing, ensures that *C. damarensis* can meet the huge energetic demands of burrowing. Individuals are obliged to remain in groups because, as solitary individuals, the energetic constraints and low probabilities of locating widely dispersed food resources are too great. *C. damarensis* do not necessarily sacrifice genetic fitness by remaining in inbred groups. The group size of the colony is probably a function of the biomass and renewal rate of subterranean resources and possibly also predation pressures.

If we accept the foregoing arguments, the survival of the other bathyergids can also be explained in terms of foraging risks, burrowing energetics, and consequently, Risk-Sensitive Metabolism. The group size of *H. glaber* is larger than in *C. damarensis* because of the lower probabilities involved in locating more widely dispersed geophytes in the habitat of the former species. An exceptionally low RMR in *H. glaber* is a consequence of the need to reduce the energy expenditure of large group sizes, and together with small body sizes, the evolution of worker differentiation and polyethism has been favoured by the same constraints as those outlined for *C. damarensis*. *H. glaber* do not need to maintain an efficient thermoregulatory ability because of the low seasonal variation in burrow temperature, the diel constancy of burrow temperatures and the thermoregulatory benefits achieved from nest-huddling and behavioural thermoregulation.

In mesic regions molerats can be either solitary or social. However, if individuals from social groups have body sizes large enough to maintain thermal equilibrium as solitary individuals during winter, they theoretically would have a higher fitness potential by outbreeding with other solitary individuals. Apart from the other factors which select for body size, such as the cost of burrowing, this explains why, as a general trend, the solitary species are larger than social species. The risk of foraging in mesic regions is considerably less than in arid regions because geophytes, although small, occur in high densities.

Finally, I conclude that there is considerable evidence to suggest that certain physiological features of the

Bathyergidae e.g. Risk-Sensitive Metabolism, have evolved in response to energy conservation considerations. These considerations have, however, tended to highlight relevant factors such as the cost of burrowing and habitat productivity, whereas the probabilities involved in locating food resources are undoubtedly the most important factors. I therefore consider McNab's (1966, 1979) overheating hypothesis to be premature, not very comprehensive, and untestable. It failed to consider all energetic constraints faced by subterranean rodents, such as the Bathyergidae, and should therefore be used with caution. I feel fairly confident therefore that many of the physiological characteristics of other subterranean rodents, such as the Geomyidae and Spalacidae, particularly those in arid habitats, will be best explained by adopting the ecophysiological modelling approach used in this thesis.

CHAPTER TWELVE

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APPENDIX

Consider a solitary molerat burrowing an infinitesimal small distance δs within a large area A containing G geophytes. Thereby, an area $2R\delta s$ is searched for geophytes. Since the geophytes are randomly distributed the probability that a particular one is encountered in $2R\delta s$ is $\frac{2R\delta s}{A}$. Therefore the probability of not encountering any of the G geophytes is:

$$\left(1-\frac{2R\delta s}{A}\right)^{G} \xrightarrow[\delta s \to 0]{} 1-\frac{2RG\delta s}{A} = 1-2Rd\delta s \tag{A1}$$

where $d=\frac{G}{A}$ is the density of the geophytes. Let $P(s)$ be the probability that a solitary individual has not found a geophyte having burrowed a distance s from the last encounter. Then using (A1) we get:

$$P(s+\delta s) = P(s)(1-2Rd\delta s)$$
$$P(s+\delta s) \xrightarrow[\delta s \to 0]{} P(s)+\frac{dP(s)}{ds}\delta s\,.$$

Equating $P(s+\delta s)$ in both of these equations gives:

$$\frac{dP(s)}{ds} = -2RdP(s) \tag{A2}$$

Since $P(0)=1$ we get from (A2):

$$P(s) = e^{-2Rds}. \tag{A3}$$

Consider the case where n individuals are burrowing simultaneously with the same velocity. The probability that none of them encounters a geophyte, having burrowed a distance s , is:

$$P(s) = (e^{-2Rds})^{n} = e^{-2Rnds} \tag{A4}$$

Because of (A1) the probability that any one of the n individuals finds a geophyte in a distance δs is $n\cdot(2Rd\delta s)$. Therefore the probability that any one of the n individuals encounters the first geophyte in the interval $(s, s+\delta s)$ is:

$$P(s)\, n2Rd\delta s. \tag{A5}$$

Thus the mean distance to the first encounter is

$$\bar{s} = \int_0^\infty P(s) sn2Rd\delta s = (2Rnd)^{-1} \qquad (A6)$$

and the mean number of geophytes found per distance is

$$\bar{g} = \bar{s}^{-1} = 2Rnd. \qquad (A7)$$