

# Variations in the Foraging Behaviour and Burrow Structures of the Damara Molerat *Cryptomys damarensis* in the Kalahari Gemsbok National Park

B.G. LOVEGROVE and SUZANNE PAINTING

Lovegrove, B.G. and Suzanne Painting. 1987. Variations in the foraging behaviour and burrow structures of the Damara molerat *Cryptomys damarensis* in the Kalahari Gemsbok National Park. — *Koedoe* 149 – 163. Pretoria. ISSN 0075 – 6458.

Aspects of two habitat-specific foraging behaviours of the social subterranean rodent *Cryptomys damarensis*, are discussed in terms of burrow structure, resource dispersion patterns, sand moisture content, burrow temperature regimes, and predatory pressures, in the Kalahari Gemsbok National Park, South Africa.

Key words: Molerats, subterranean rodents, burrow structure, foraging behaviour, Kalahari, geophytes, energetics.

*B.G. Lovegrove and Suzanne Painting, Department of Zoology, University of Cape Town, Rondebosch, 7700 Republic of South Africa.*

## Introduction

Much recent attention has been focussed on the metabolism and energetics of the bathyergid molerats (McNab 1979; Jarvis 1978; Withers & Jarvis 1980; Du Toit, Jarvis & Louw 1985; Haim & Fairall 1986; Lovegrove 1986a, 1986b, 1987). Generally it has been found that the bathyergids display resting metabolic rates (RMR) considerably lower than those measured for other subterranean rodents and above-ground rodents. The arid-habitat species of subterranean rodents have the lowest RMRs (Lovegrove 1986a). Furthermore, the seven bathyergids that have been investigated to-date, namely *Bathyergus suillus* (Schreber, 1782), *B. janetta* Thomas and Schwann, 1904, *Georychus capensis* (Pallas, 1779), *Cryptomys hottentotus* (Lesson, 1826), *C. damarensis* (Ogilby, 1838), *Heliophobius argenteocinereus* Peters, 1846, and *Heterocephalus glaber* Rüppel, 1842, scale metabolism virtually independent of masses between 39 – 1 000 g (Lovegrove & Wissel 1987). In other words, a 39 g molerat has virtually the same mass-specific resting metabolic rate as that of a 1 000 g animal.

Mass-independent scaling of metabolism does not occur in other subterranean rodents, such as the geomyid pocket gophers (Hayssen & Lacey 1985), but it has been observed in the heteromyid rodents apparently in response to the difficulty of balancing a water and energy budget (McNab 1979). Concurrent with the

unusual metabolism of the bathyergids, is the fact that, unlike the other families of subterranean rodents, the bathyergids display a gradient of sociality ranging from strictly solitary molerats (*Bathyergus suillus*, *Georchus capensis* and *Helio-phobius argenteocinereus*), through colonies with a group size of 10–20 animals (*Cryptomys*; *pers. obs.*), to the eusocial (Jarvis 1981) naked molerat *Heterocephalus glaber*, which has a colony size of about 60 animals (Jarvis 1981; Brett 1986). At present, indications are that the social status and metabolism of the bathyergids have been selected for in response to the high energetic costs and low probabilities involved in locating widely dispersed geophytes (plants with underground storage organs) by random burrowing (Jarvis 1978; Vleck 1979, 1981; Brett 1986; Lovegrove 1986a, Lovegrove & Wissel 1987). Consequently, current attention is being focused on the foraging behaviours and burrow structures of the bathyergids. In this paper we present data on the foraging behaviour and burrow patterns of the Damara molerat *Cryptomys damarensis* in the Kalahari Gemsbok National Park (KGNP), Republic of South Africa.

### *Study animals*

*Cryptomys damarensis* is a social subterranean rodent (De Graaff 1972, 1981) karyotypically distinct from the other cryptomids (Nevo, Capanna, Corti, Jarvis & Hickman 1986). Although a distinct species status for *C. damarensis* has not been taxonomically formalised, based on the recent work of Nevo *et al.* (1986), we tentatively elevate this molerat to species rank in this study. Lovegrove (1986a) gives a mean mass of 125 g for *C. damarensis*, but Jarvis (*pers. comm.*) has recently trapped animals in Namibia with masses of 200–250 g, so it is likely that a mass of 125 g might not be the best estimate of the mean population mass of *C. damarensis*.

The species is restricted to the Kalahari desert, occurring throughout north-western Namibia and Botswana (De Graaff 1972). It is common and fairly abundant in the sand dunes between the Nossob and Auob rivers in the KGNP (De Graaff 1972), but can also be found along the riverine zones of the Nossob River, especially in the north of the KGNP (*pers. obs.*). •

### *Study sites*

Field work was undertaken at two sites near Nossob camp during January and August 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 Nossob camp.

The Nossob site was generally flat, bordered in the east by red sand dunes, and in the west by the riverine *Rhigozum* plant communities. The vegetation at this site is well described by Leistner (1967) for “compact pink and white sands”. The virtual geophytic monoculture of *Dipcadi gracillimum* Bak., together with the



Figure 1. Nossob site showing *Dipcadi gracillimum* setting seed, the lack of grasses due to overgrazing, and mole-hills from the primary burrow system of *C. damarensis*. Photo: B.G. Lovegrove.

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. 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. gracillimum* (Fig. 1).

The Dune site comprised a number of dune valleys in close proximity (< 2 km) to each other. The vegetation at this site is described by Leistner (1967) for "non-calcareous red sands and dune slopes". The tubers of the gemsbok cucumber *Acanthosicyos naudinianus* (Sond.) C. Jeffrey (Fig. 2), were by far the most common geophytes at this site.

## 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 per day), but this dropped dramatically once most of what we presumed to be the sub-dominant animals in the colony, had been caught. No reproductively active females were caught. All trapped animals were subsequently used to measure metabolic rates in the laboratory at Cape Town University.

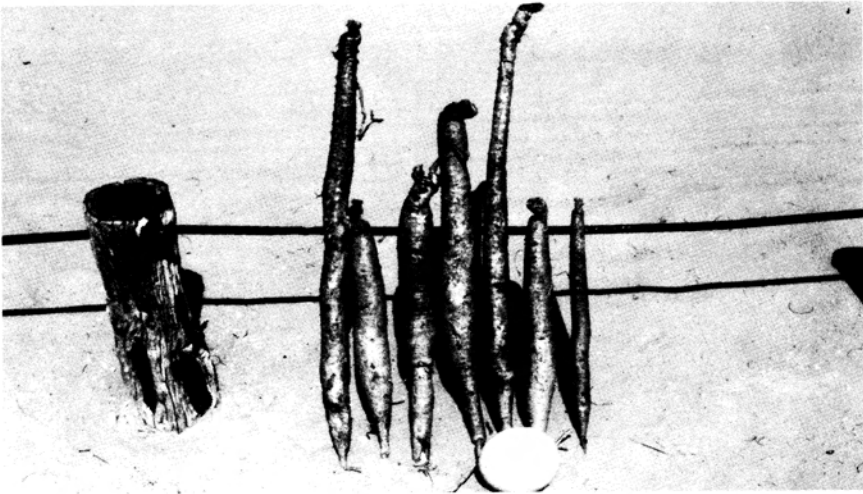


Figure 2. The tubers of the Gemsbok cucumber *Acanthosicyos naudinianus* excavated at the Dune site showing the range of tuber sizes. Ostrich egg for scale. Photo: B.G. Lovegrove.

The depths and diameters of mole rat 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. Extensive sampling of geophyte abundances at each site was also undertaken, but these results will only briefly be discussed as they are being published elsewhere. Similarly, only brief mention will be made of burrow temperatures recorded at the Nossob site.

## 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 mole-hills, forms the main artery of the burrow system, and is generally the straightest and largest section of the system (Figs. 3 and 4). For example, the total length of an unblocked primary burrow excavated from one system was 82 metres. The mean depth of the primary burrow from the surface was 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 1). The mean distance between mole-hills was 122,5 cm (Table 1). It is assumed that this mean distance closely approximates the mean distance between the lateral burrows leading off from the primary burrows to the mole-hills (Fig. 3).

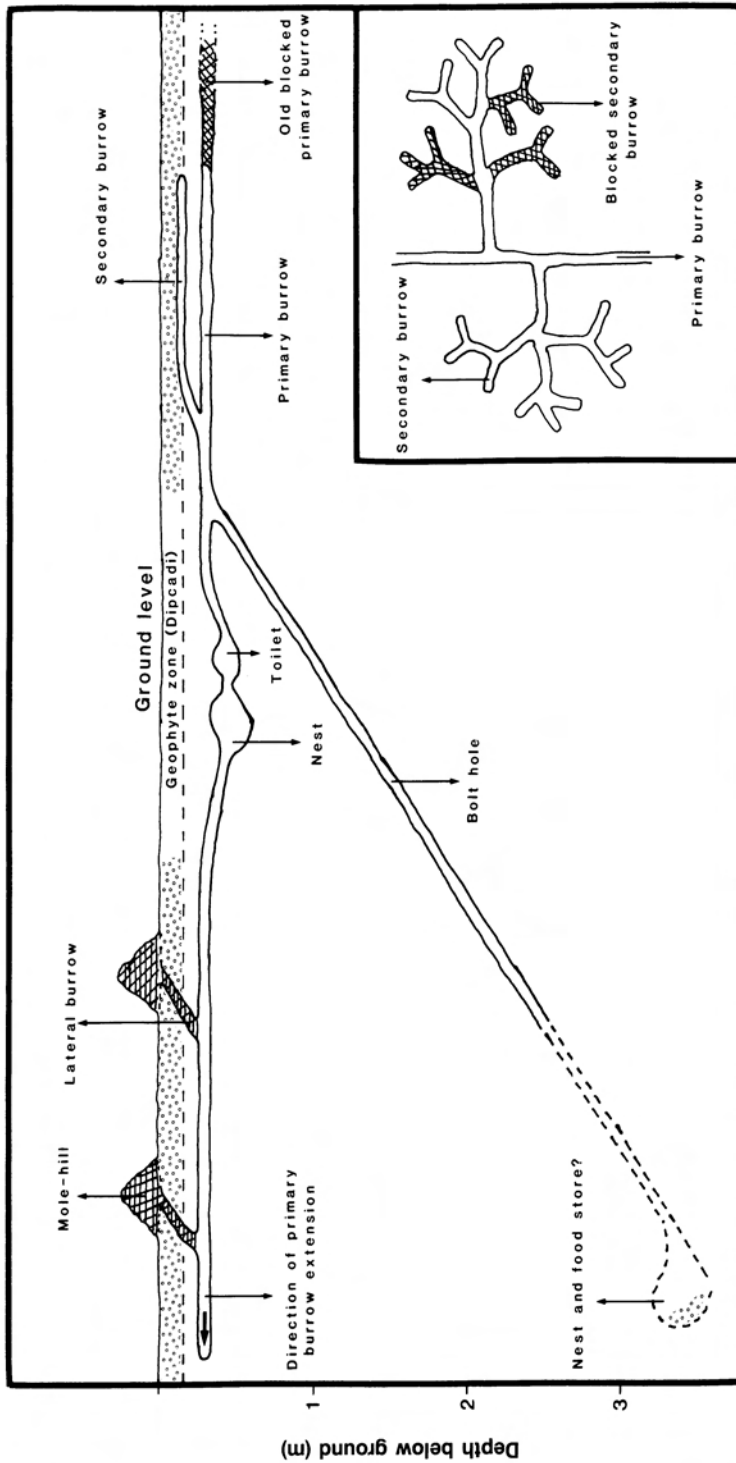


Figure 3. A schematic diagram showing the burrow types and various structures comprising the burrow system of *C. damarensis* at the Nossob site. Broken lines indicated parts of the system that were not excavated. Inset shows detail of the secondary burrows viewed from above. Vertical axis to scale only.

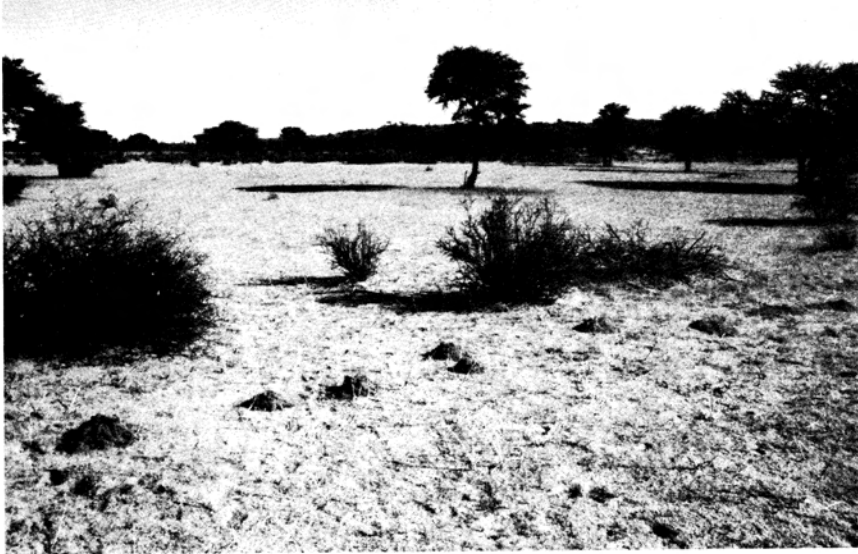


Figure 4. The characteristic mole-hills associated with the extension of the primary burrow system at the Nossob site. The indentations in the foreground are caused by ungulates trampling and collapsing the shallow secondary burrows. Photo: B.G. Lovegrove.

Table 1  
*Mean measurements of the depths, diameters, and segment lengths, of the burrows of *Cryptomys damarensis* in the Kalahari Gemsbok National Park. Sample sizes in parentheses*

Site	Burrow type	Depth to top (cm)	SD	Depth to bottom (cm)	SD	Burrow diameter (cm)	SD	Segment length (cm)	SD
Nossob	Primary	25,1 (38)	2,8	31,7 (38)	2,9	6,6 (38)	0,8	122,5 (54)	52,1
Nossob	Secondary	10,3 (50)	2,1	16,1 (50)	2,3	6,0 (50)	1,1		
Dunes	Primary	29,8 (30)	6,4	36,5 (30)	6,6	6,7 (30)	0,9	151,1 (75)	62,0

Generally, the secondary burrows lead off at right angles to the primary burrows, invariably branching after 0,5 m – 2 m into a number of hand-like burrows (Fig. 3). The mean depth of the secondary burrows from the surface was 10,3 cm to the top of the burrow, and 16,1 cm to the bottom, resulting in a mean burrow diameter of 6,0 cm (Table 1). When the system was excavated in winter, all of the secondary burrows were solidly blocked with sand. However, during summer many of the secondary burrows were found to be open, or only partially blocked. These burrows are not associated with mole-hills, and their presence can only be detected where trampling by ungulates has collapsed these shallow burrows (Fig. 4). When the secondary burrow system is exposed, the mole-rats 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, 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 bolt hole was located leading off from the primary burrow at a depth of 27 centimetres. This burrow descended for 5 m at an angle of 23° to a depth of 2,2 metres. At this point, further excavation of the bolt hole had to be terminated to avoid the risk of the excavation collapsing on top of the authors. 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 bolt hole at > 3 metres.

During the course of all excavations at the Nossob site, the only geophytes encountered were the bulbs of *D. gracillimum*. On average the bulbs were found at a depth of 10 cm, but were never found deeper than 14 cm below the surface.

#### Dune site

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

The mean depth of the primary burrow from the surface 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 1). The mean distance between mole-hills (segment length) was 151,1 cm (Table 1). 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 mole-hills at the Dune site revealed two distinct types. The first type represents the mole-hills 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 mole-hill is typically either a single mound larger than the primary burrow mole-hills, or, two or three mounds pushed up in very close proximity to each other. These latter mole-hills are associated with feeding, as they are always located next to an *Acanthosicyos naudinianus* tuber which has been eaten by the mole-rats (Fig. 5). When these tubers are excavated, an arrangement of burrows can be found surrounding the tuber (Figs. 6 and 7). 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







Figure 5. A 'feeding' mole-hill situated immediately above a *A. naudinianus* tuber at the Dune site. Note the runners from the tuber leading out of the centre of the mole-hill. Photo: B.G. Lovegrove.

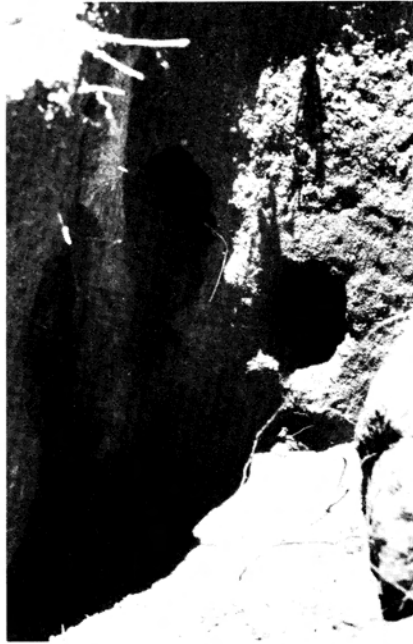


Figure 7. An excavation of a *A. naudinianus* tuber that has been eaten by mole-rats. The burrow on the top left is the primary burrow. The spiral burrow (blocked with sand) leads down and around the tuber from the primary burrow. Note that only the bark of the tuber has been eaten in this instance. Burrow diameters are 6–7 cm. Photo: B.G. Lovegrove.

sand from these spiral excavations is pushed up close to the tuber to form the 'feeding' mole-hills. From a sample of 40 eaten tubers that were excavated, it was found that only the outer bark was eaten from the older larger tubers, whereas the younger, thinner, tubers were often completely eaten with only the top 10 cm of the tuber remaining. The remains of some of these eaten tubers, whether large or small, are capable of recovering from this herbivory, and will sprout and grow during the next growing season (Fig. 8). During the six months separating the January and August field work, no additional mole-hills had been pushed up at two colonies where a note was made of the original arrangement of mole-hills.

## Discussion

Two foraging patterns can be identified by the burrow structures of *Cryptomys damarensis* in the Kalahari Gemsbok National Park. These patterns appear to represent a compromise between predatory pressures, microclimatic factors, and most importantly, species-specific resource dispersion patterns. Although geophytes

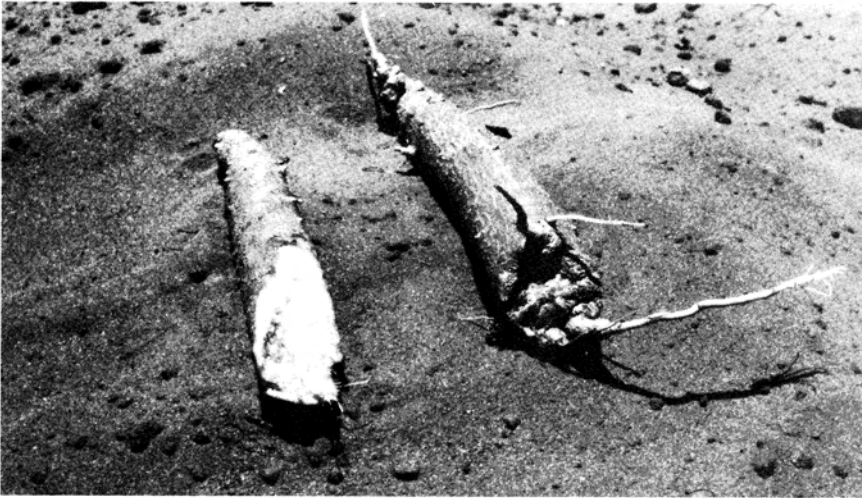


Figure 8. Tubers of *A. naudinianus* eaten by free-ranging mole-rats. The tuber on the left has been freshly eaten by mole-rats. The tuber on the right was eaten one or two years previously. Note that this tuber subsequently recovered and initiated further growth. Photo: B.G. Lovegrove.

appear to be the exclusive food items at both sites, the dispersion patterns of the two main geophytes concerned varies quite considerably (*unpubl. data*). In short, *Acanthosicyos naudinianus* tubers were found to have a random distribution around mole-rat colonies at the Dune site, with a density of 0,26 tubers per square metre. The mean mass of these tubers was 670 g (n = 53). At the Nossob site, the mean density of *Dipcadi gracillimum* bulbs ranged from 40–120 bulbs per square metre in the immediate vicinity of burrow systems. The mass of these bulbs is very variable, ranging from 0,4–5,2 grams.

The secondary burrows at the Nossob site quite obviously represent foraging burrows excavated at a depth optimally suited to harvest *D. gracillimum* bulbs. The non-association of mole-hills 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 *Heterocephalus glaber* (Jarvis & Sale 1971; Brett 1986), *Heliophobius argenteocinereus*, *Tachyoryctes spendens* (Jarvis & Sale 1971), *Cryptomys hottentotus* (Genelly 1965; Davies & Jarvis 1986), and *Bathyergerg 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 Kalahari Gemsbok National Park. As discussed below, this factor may be one of the most important physical constraints faced by *Cryptomys damarensis* in the Kalahari, having a profound influence on the ecology and behaviour of the species.

Observations on the production of mole-hills by other bathyergids such as *Georychus capensis*, *Bathyergerg suillus* and *Cryptomys hottentotus*, have shown

that mole-hills can only be produced in aggregated soils, or soils, even sandy uncompacted 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 explains why no mole-hill production has been observed during dry periods in the KGNP, whereas good rainfalls are immediately followed by intense mound production (M. Knight *pers. comm.*).

We believe this post-rain burrowing activity is associated with the extension of the primary burrow system into new unharvested areas adjacent to the main colony. Provided that sufficient resources are available to maintain the mole-rats during this important digging period (stored food in the case of *D. gracillimum* bulbs, or reliable *in situ* food in the case of previously located *A. naudinianus* tubers), the excavation of a long straight primary burrow would be the optimal strategy for ensuring future access to a large unforaged area on each side of the primary burrow. 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. Under this hypothesis it is likely that the 'feeding' mole-hills discussed earlier, are probably only produced after rains.

Besides the cooperative foraging effort required to locate widely dispersed food resources, the massive 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 factors selecting for group size and sociality in this species. The energetic costs and benefits of cooperative foraging and digging are being investigated by author BGL at present.

The similarity in depths between the primary burrows of the Nossob and Dune site colonies suggests that this depth has been selected for by factors other than those associated with the optimal procurement of resources, as is the case with the secondary burrows. Factors such as the risk of predator-access associated with burrow collapse due to trampling, and soil compactness, are likely to be the important determinants of primary burrow depth. At a depth of 25 cm – 29 cm the primary burrows can withstand intense trampling above ground, and will even withstand the weight of an off-road vehicle. In addition, at depths above 25 cm the sand may not be compacted enough to ensure a permanent open burrow system. The higher costs of establishing the primary burrows at deeper depths (Vleck 1981) probably sets the lower depth limit.

One of the most interesting features of the burrow systems of *C. damarensis* is the great depth to which the bolt hole descends. Whereas the bolt holes of the burrow systems of other bathyergids are primarily regarded as escape routes or points of safe refuge from predators that have invaded the burrow system (Jarvis & Sale 1971; Brett 1986; Davies & Jarvis 1986), a strong argument can be developed suggesting that the bolt holes in *C. damarensis* burrow systems play an important thermoregulatory role as well.

The mean temperature of the primary burrows at the Nossob site during January, the hottest month in the KGNP, was 33,4 °C (*unpubl. data*). This mean temperature is consistent with the mean maximum temperatures for January (33,6 °C) recorded at a depth of 30 cm by the South African Weather Bureau at Upington (400 km south of Nossob) over six years (1980 – 1985). The same data base gave mean maximum temperatures of 33,3 °C and 32,1 °C for soil depths of 60 cm and 120 cm respectively. The soil temperatures recorded for Upington are therefore fairly good estimates of soil temperatures in the KGNP, and can be used to estimate the mean burrow temperatures for July, the coolest month in the Kalahari. From the same data base, the mean minimum soil temperatures for July were 14,8 °C, 16,0 °C and 17,8 °C for soil depths of 30 cm, 60 cm and 120 cm respectively. Generally, soil temperatures are coolest in summer, and warmest in winter, at soil depths below 1,2 metres.

These temperatures are physiologically significant because the mean maximum and minimum soil temperatures of the primary burrows are above and below the upper and lower limits of thermoneutrality for *C. damarensis* (Lovegrove 1986a) during summer and winter respectively. Presumably therefore, molerats should avoid these energetically costly temperatures if possible, simply by moving down the soil column to depths where temperatures remain very constant, and are closer to the upper and lower thermoneutral temperatures during both seasons. One way of achieving this, would be to nest somewhere near the deepest part of the bolt hole where temperatures are physiologically less stressful. Although we predict that this is probably what happens, this supposition can only be substantiated with careful radiotelemetry.

Brett (1986) has used radiotelemetry in Kenya to show that *H. glaber* thermo-regulates 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). *Cryptomys damarensis* on the other hand, is exposed to a considerably wider seasonal range of environmental temperatures than occurs in Kenya, and consequently has a relatively low thermal conductance, and a good thermoregulatory ability to ambient temperatures of 10 °C (Lovegrove 1986a).

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 for weeks at a time when temperatures are suitable.

At this stage, we are not yet sure whether *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 should take place. Author BGL intends investigating this possibility in the immediate future.

In closing, it is worthwhile speculating on the different behaviours of *C. damarensis* at the two sites. It is interesting that the foraging behaviour and burrow structure (with the possible exception of the deep bolt hole) 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.

One hypothesis proposed by Lovegrove & Wissel (1987), is that the group size of molerat societies is a positive function (probably exponential) 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 Kalahari Gemsbok National Park, where 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. gracillimum* bulbs (i.e. at Nossob site). 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.

It is also interesting to speculate whether the two foraging behaviours and presumed group sizes of *C. damarensis* in the KGNP, can partially account for the chromosomal speciation evident in this species (Nevo *et al.* 1986). This suggests that the behaviours of *C. damarensis* may be innate functions of habitat type in the Kalahari. The test of these hypotheses can only really be achieved through careful radiotelemetry, much additional trapping, and further karyotyping of chromosomes.

## Conclusions

The burrow systems and foraging behaviours of *C. damarensis* in the KGNP are structured in a manner which (a) optimises access to monogeophytic food resources, (b) reduces the risk of predatory invasions of the burrow system, and (c) probably enables a certain degree of behavioural thermoregulation to take place. Furthermore, the energetic costs of establishing, maintaining, and extending such vast burrow systems is unlikely to be achieved by solitary animals, suggesting that cooperation and sociality is fundamental to the survival of *C. damarensis* in an arid region like the Kalahari desert. Rainfall, more specifically sand moisture content, plays a major role in the burrowing and foraging activity of this species.

## Acknowledgements

Author BGL is grateful to his supervisor, Prof. G.N. Louw, for invaluable encouragement and assistance. He is indebted to Dr. A. Hall-Martin, Dr. V. de Vos, Dr. G. de Graaff, and Mr. E.A.N. le Riche, all of the National Parks Board of Trustees, for kindly assisting in his research, and for allowing him to work in the Kalahari Gemsbok National park. We are especially

grateful to Mike Knight (NPB) and Annette Knight-Eloff (Mammal Research Institute), for kindly making research facilities available to us, for sharing in stimulating discussions, for their generous hospitality at Nossob, and lastly, for teaching us how to thermoregulate efficiently in the Kalahari desert. This study was financed by CSIR (FRD) and the University of Cape Town. We thank all concerned.

## References

- BRETT, R.A. 1986. The ecology and behaviour of the Naked mole-rat (*Heterocephalus glaber* Rüppell) (Rodentia: Bathyergidae). Ph.D. dissertation, University of London.
- DAVIES, K.C., and J.U.M. JARVIS. 1986. The burrow systems and burrowing dynamics of the mole-rats *Bathyergus suillus* and *Cryptomys hottentotus* in the fynbos of the south-western Cape, South Africa. *J. Zool., Lond.* 209: 125–147.
- DE GRAAFF, G. 1972. On the mole-rat (*Cryptomys hottentotus damarensis*) (Rodentia) in the Kalahari Gemsbok National Park. *Koedoe* 15: 25–35.
- DE GRAAFF, G. 1981. *The Rodents of Southern Africa*. Pretoria: Butterworths.
- DU TOIT, J.T., J.U.M. JARVIS and G.N. LOUW. 1985. Nutrition and burrowing energetics of the Cape mole-rat *Georychus capensis*. *Oecologia* 66: 81–87.
- GENELLY, R.E. 1965. Ecology of the common mole-rat (*Cryptomys hottentotus*) in Rhodesia. *J. Mammal.* 46: 647–665.
- HAIM, A., and N. FAIRALL. 1986. Physiological adaptations to the subterranean environment by the mole-rat *Cryptomys hottentotus*. *Cimbebasia* 8: 49–53.
- HAYSEN, V., and R.C. LACEY. 1985. Basal metabolic rates in mammals: taxonomic differences in the allometry of BMR and body mass. *Comp. Biochem. Physiol.* 81A: 741–754.
- JARVIS, J.U.M. 1978. Energetics of survival in *Heterocephalus glaber* (Rüppell), the Naked mole-rat (Rodentia: Bathyergidae). *Bulletin of Carnegie Museum of Natural History* 6: 81–87.
- JARVIS, J.U.M. 1981. Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. *Science* 212: 571–573.
- JARVIS, J.U.M., and J.B. SALE. 1971. Burrowing and burrow patterns of east African mole-rats *Tachyoryctes*, *Heliophobius* and *Heterocephalus*. *J. Zool., Lond.* 163: 451–479.
- LEISTNER, O.A. 1967. The plant ecology of the southern Kalahari. *Botanical Survey Memoir* 38.
- LOVEGROVE, B.G. 1986a. The metabolism of social subterranean rodents: adaptation to aridity. *Oecologia* 69: 551–555.
- LOVEGROVE, B.G. 1986b. Thermoregulation of the subterranean rodent genus *Bathyergus*. *S. Afr. J. Zool.* 21: 283–288.
- LOVEGROVE, B.G. 1987. Thermoregulation in the subterranean rodent *Georychus capensis* (Rodentia: Bathyergidae). *Physiol. Zool.* 60(1): 174–180.
- LOVEGROVE, B.G. and J.U.M. JARVIS. 1986. Coevolution between mole-rats (Bathyergidae) and a geophyte, *Micranthus* (Iridaceae). *Cimbebasia* 8: 79–85.
- LOVEGROVE, B.G. and C. WISSEL. 1987. Sociality in mole-rats: metabolic scaling and the role of risk sensitivity. *Oecologia* (in press).
- MCNAB, B.K. 1966. The metabolism of fossorial rodents: a study of convergence. *Ecology* 47: 712–733.
- MCNAB, B.K. 1979. The influence of body size on the energetics and distribution of fossorial and burrowing animals. *Ecology* 60: 1010–1021.
- NEVO, E., E. CAPANNA, M. CORTI, J.U.M. JARVIS and G.C. HICKMAN, 1986. Karyotype differentiation in the endemic subterranean mole-rats of South Africa (Rodentia: Bathyergidae). *Z. Saugetierk.* 51: 36–49.
- VLECK, D. 1979. The energy cost of burrowing by the pocket gopher *Thomomys bottae*. *Physiol. Zool.* 52: 122–125.

- VLECK, D. 1981. Burrow structure and foraging costs in the fossorial rodent, *Thomomys bottae*. *Oecologia* 49: 391 – 396.
- WITHERS, P.C., and J.U.M. JARVIS. 1980. The effect of huddling on thermoregulation and oxygen consumption for the naked mole-rat. *Comp. Biochem. Physiol.* 66A: 215 – 219.