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Food availability and foraging by wild colonies of Damaraland mole-rats (*Cryptomys damarensis*): implications for sociality

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Abstract We investigated some of the ecological determinants of sociality in the Damaraland mole-rat, including the spatial distribution and biomass of resources (geophytes) available to foraging Damaraland mole-rats in partly vegetated sand dunes in the Kalahari and in grasslands near Dordabis, Namibia, and the foraging behaviour and residency characteristics of colonies at Dordabis. In both study areas, the geophytes had a clumped distribution, but the highest coefficients of dispersion and mean biomass occurred in the Kalahari where the principal food was the gemsbok cucumber. However, because the coefficient of digestibility was lower in geophytes from the Kalahari than from Dordabis, and the mole-rats only ate about half of a gemsbok cucumber, there was less energy available to mole-rats in the Kalahari. At Dordabis, large established colonies occur in the areas with the richest resources and remain resident in the same area for many years; within this area they search (blindly) for food during brief periods when the soil, at burrow depth, is moist and easily worked. Initially, long straight burrows are dug and few bulbs are taken; once the soil dries, minor changes are made to the burrow system as the mole-rats exploit the food patches they located immediately after the rain. Our results show that the characteristics of the resources, and the short time interval during which location of new resources is possible, favour group living; however, the constraints imposed by these features affect large and small colonies in different ways. Small colonies are more likely to fail than large ones and some crucial factors in the survival of these newly formed colonies are the richness of the area in which their burrows are located, and the size of the colony work force available to locate the food.

Key words Foraging · Sociality · Bathyergidae · Mole-rats

Introduction

African mole-rats (Bathyergidae) exhibit a number of unusual features, not least of which is the diversity of social organisation. Some genera have a solitary lifestyle, others are colonial and yet others, such as naked mole-rats and Damaraland mole-rats, are eusocial (Jarvis et al. 1994). In contrast, most other subterranean mammals are aggressively solitary and highly xenophobic.

Arid areas, where evaporative water loss is high and, most importantly, rainfall is unpredictable, are characterised by a predominance of social genera of mole-rats (Bennett 1988). When dry, the soils in these regions are difficult to excavate, greatly increasing the costs of burrowing. Consequently, most burrowing occurs after rain, when the soil is most easily worked. The sporadic rainfall and high evaporation rates in arid regions mean that the mole-rats are restricted to short periods (Fig. 1) during which conditions for burrowing and foraging are optimal (Bennett 1988; Jarvis and Bennett 1991). Even during these periods, however, there are limits to the absolute distance a single mole-rat can dig each day. These are associated with the energetic costs of burrowing, the maximal rate of incisor growth (their digging tools) and heat load (McNab 1979; Jarvis and Bennett 1991). Moreover, in arid habitats, the food resources (geophytes) tend to be larger but of poorer quality than in mesic regions and food is often clumped or widely dispersed (Lovegrove and Painting 1987; Bennett 1988; Lovegrove and Knight-Eloff 1988; Brett 1991; Jarvis and Bennett 1991).

It has been suggested that under these ecological conditions, selective pressures related to the high energetic costs and the low probability of locating widely

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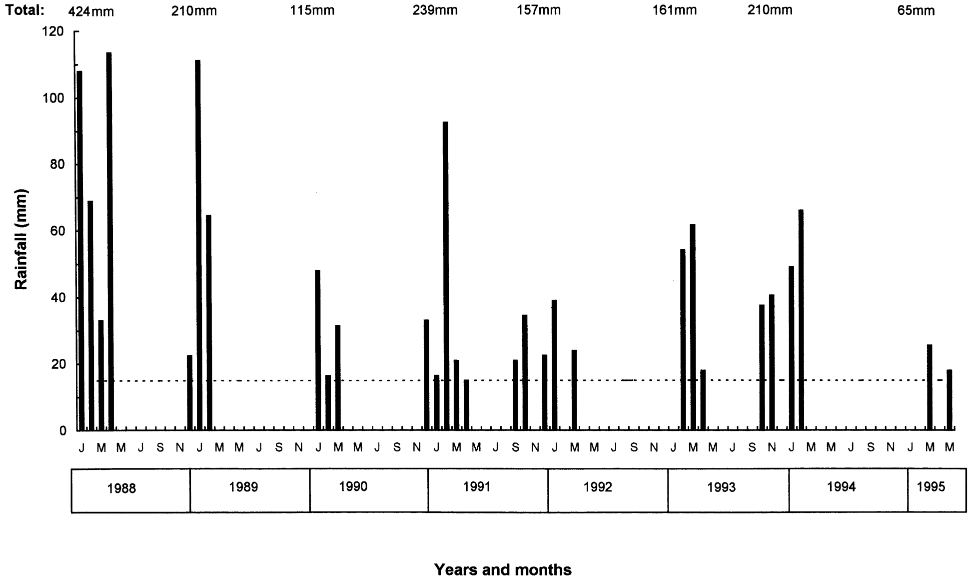

Fig. 1 The rainfall at Dordabis over the study period to show the few instances during which extensive burrow excavation was possible. Only rainfall exceeding 15 mm over a 7-day period, and therefore penetrating to burrow depth and triggering burrowing, is shown as *bars*. The 70-year mean for the study area is 275 mm denotes 15 mm rainfall

dispersed geophytes may have promoted the evolution of group living in the Bathyergidae (Jarvis 1978, 1985; Lovegrove and Painting 1987; Bennett 1988; Lovegrove 1988; Lovegrove and Wissel 1988; Jarvis and Bennett 1991)

The Damaraland mole-rat *Cryptomys damarensis* occurs in arid regions of southern Africa in colonies of up to 41 individuals (mean = 18). In each colony, a single female and, usually, one male reproduce (Bennett and Jarvis 1988; Jarvis and Bennett 1993). The non-reproductive colony members are the offspring of the breeding pair and are reproductively quiescent (Bennett et al. 1993, 1994; Bennett 1994; Jarvis et al. 1994). They constitute a work force that performs a pivotal role in provisioning the colony.

This paper draws on data from two study areas to examine some of these ecological aspects in more detail. In particular we make (1) an inter-habitat comparison of resource characteristics, to investigate regional variation and to obtain an indication of the importance of resources in shaping bathyergid life history traits, including sociality, and (2) a detailed investigation of foraging behaviour in the Damaraland mole-rat, again to provide insight into the significance of sociality in mole-rats.

Materials and methods

Distribution, biomass and nutritional value of geophytes in two study areas

Kalahari Gemsbok National Park

Our study area was in vegetated dunes approximately 1 km from the Twee Rivieren rest camp. The predominant geophyte in the area was the gemsbok cucumber *Acanthosicyos naudinianus* (over 95% of the biomass of geophytes), whose position could be determined by following its above ground trailing vine. In parts of two burrow systems, the distribution of all visible gemsbok cucumber tubers growing in the neighbourhood of a length of foraging burrow was mapped using strip quadrats (5 × 20 m). Each of these strips extended 10 m on either side of the burrow (Fig. 2). In one system, 14 strips were mapped (an area of 1400 m^2), and in the other 16 (1600 m^2). The coefficient of dispersion of the tubers was calculated (Zar 1984).

In each strip, two gemsbok cucumber tubers, chosen at random, were dug up, weighed and their lengths measured. Weighed samples of entire tubers were dried to determine their water content. Their energy content (kJ) was assessed by bomb calorimetry (CP500 macro-bomb calorimeter) as described by Bennett and Jarvis (1995). The mean mass and energy content of these tubers was then used to estimate the total biomass and energy potentially available to the mole-rats. One of the burrow systems was partially excavated to examine the amount of each tuber eaten by the mole-rats.

Nearest-neighbour distances of geophytes were measured within two of the clumps and in two geophyte-poor areas. This provided an estimate of the minimum distance a mole-rat would have to travel from one geophyte to another.

Dordabis, Namibia (*120 km south-east of Windhoek*)

The study area consisted of a gently sloping dune and a valley of more consolidated soil abutting a dry river bed. Nine species of geophyte eaten by mole-rats occurred in the study area: *Dipcadi glaucum*, *D. marlothii*, *D. bakeranum*, *D. platyphyllum*, *Eriospermum rautenenii*, *Ledebouria rerduta*, *L. undulata*, *Ornithogalum stapffii* and the tuber *Talinum arnotii*. The most abundant of these was the wild onion, *D. glaucum*. Many geophytes are difficult to identify unless in bloom and, consequently, in this study, all these bulbs and corms were lumped together.

After rainfall when the geophytes had sprouted, the depth below ground of 228 bulbs was measured; all of them occurred within the top 12.5 cm of soil. The distribution of geophytes within the study area was then determined using randomly placed quadrats. Fifty-four 0.50 × 0.50 m quadrats were dug to a depth of 25 cm. The soil was sieved and all the geophytes counted, weighed and their diameters measured. The number of geophytes in each quadrat was used to calculate the coefficient of dispersion of the geophytes in the study area (Zar 1984). The density of geophytes present in eight areas inhabited by mole-rats (five small, and three large colonies with > 18 animals) and in three areas lacking mole-rats was assessed by counting the number of sprouting geophytes within at least 20 2 × 2 m quadrats, selected at random in each area. In addition, nearest-neighbour distances of geophytes were measured in 30 1-m^2 plots.

Foraging by the mole-rats at Dordabis

Analysis of a food store

To assess whether the mole-rats selectively stored certain sizes of bulbs and corms, the diameters of geophytes in the immediate vicinity of a 9-m section of burrow were compared with the diameters of geophytes found in the food store of the same burrow system. For additional comparisons, the diameters and masses of 481 geophytes collected in the 54 random quadrats were measured.

Foraging behaviour

On two occasions, we visited our study site approximately 2 months after the first heavy rain of the season. This rain resulted in widespread burrowing activity and also stimulated the geophytes to sprout. The foraging activity of the mole-rats during this period was assessed as follows.

Estimates of burrowing activity. All fresh mounds thrown up by a colony of 16 mole-rats in the 2-month period following a single heavy rainstorm (40 mm rain) were counted. These mounds were clearly distinguishable from older mounds by their unweathered appearance. The volume of soil from 25 of these mounds was measured and the total volume of soil excavated by the colony was calculated as the product of mean mound volume and total number of mounds. The diameters of the burrows at the various capture points were measured and, together with the estimates of the total volume of soil thrown up as mounds, used to estimate the length of burrow excavated by the colony. To determine the extent of the burrow system, the colony was captured, marked, released and recaptured at the extremities of long rows of mounds radiating from their nest area.

Examination of foraging behaviour. To examine the dynamics of foraging – from the initial digging of foraging burrows to the harvesting of resources – the number of harvested geophytes adjacent to two ages of mounds were examined. The first set of mounds were new (formed within the previous week), and the second set were more weathered and were approximately 2 months old. Ten rows (all but one at least 10 m long) of each age of mound were selected in the study area. Using the line of mounds as the central axis, the distribution of all sprouting geophytes for at least 2 m on either side of the axis was plotted. In the plots with new mounds, the position of each geophyte was plotted to scale on a map, whereas only the total number of geophytes in each 1 m^2 was noted in the plots with old mounds. Additionally, all harvested geophytes (evidenced by wilting of the aerial portion of the geophyte) were noted. The total area surveyed was 500 m^2 for new mounds and 590 m^2 for old mounds.

The ten rows of new mounds were also used to assess whether there was any evidence of directed (versus random or blind) burrowing towards geophyte-rich areas. For this, the number of geophytes in 1-m^2 quadrats sited at least 1 m from the path of the burrow was compared with the number in quadrats surrounding mounds. Excavations have shown that no freshly dug foraging burrow is situated more than 50 cm from its mound, therefore, to ensure that the actual foraging burrow was included in the quadrat, the mound was centred in the square, which was orientated towards the next mound.

Estimate of distance that has to be dug to encounter a geophyte. We estimated the average distance a mole-rat would have to dig to encounter successive geophytes. We used the ten plots of freshly dug mounds and, based on the pattern of molehills, assumed that after encountering a geophyte, the mole-rat searched for the next geophyte by moving forwards within a 45° arc (i.e. the burrowing was blind but directional). Each 5° of the arc was assigned a number (0–10). Using randomly generated numbers, a 5° arc was selected and the distance to the next geophyte within the 5° segment measured. The distance between 149 geophytes was measured in this manner.

Results

Distribution, biomass and nutritional value of the geophytes

Kalahari Gemsbok National Park

The gemsbok cucumber tubers had a mean mass of 409 g (n = 32) and were up to 100 cm long. Visually, the spatial distribution was one of large, relatively dense, clumps of tubers interspersed with areas with few tubers. The coefficients of dispersion (CD) for the geophytes in the two systems showed that the tubers were indeed clumped (CD = 15.3 and 24.9). The density of the tubers ranged from 0.63 tubers · m^{-2} within the clumps to 0.03 tubers · m^{-2} between the clumps (Fig. 2, Table 1). The available biomass ranged from 257.7 g · m^{-2} within

Fig. 2 The distribution of gemsbok cucumbers adjacent to portions of a burrow system at Twee Rivieren. The area was surveyed in 16 5 × 20 m rectangular strips, running approximately 10 m on either side of the burrow (*small circle* position of a tuber, *large circle* mound indicating the position of the burrow, *open arrowhead* the 10-m midpoint of the next surveyed strip). The densities and digestible energy values of the tuber-rich (A, B) and tuber-poor (E) areas are given in Table 1

Table 1 Numbers and available digestible energy of gemsbok cucumber tubers, in and outside tuber-rich patches, at Twee Riveren. *A* and *B* refer to the patch areas, and E to the inter-patch area, depicted in Fig. 2

Area	Number of tubers (tubers · m^{-2})	Available digestible energy (kJ · m^{-2})
Tuber-rich areas		
(A)	0.63	311.2
(B)	0.29	146.8
(C)	0.55	137.2
(D)	0.39	97.9
Tuber-poor areas		
(E)	0.06	30.5
(F)	0.16	40.6
(G)	0.03	7.5

Table 2 Densities of geophytes in three areas occupied by large *Cryptomys damarensis* colonies (>18 individuals), five areas occupied by small colonies and three areas lacking mole-rats. The mean number of geophytes differed significantly between the 3 areas ($F_{(2,218)}$ = 31.106, P < 0.00001)

Colony size	Total number of plots	Mean number of geophytes (bulbs · 2 m^{-2})	SD	Range
Large	62	60.68	33.53	7–127
Small	97	49.30	26.89	5–121
No mole-rats	60	22.28	22.28	0–78

clumps to 12.7 g · m^{-2} between clumps (mean for whole area 140.5 ± 24.5 g · m^{-2}). Food trials in the laboratory revealed that the percentage of digestible energy (coefficient of digestibility) of gemsbok cucumbers was 52.5% (Bennett and Jarvis 1995). Excavation of the foraging burrows indicated that the mole-rats did not eat entire tubers but ate up and down the tuber in the vicinity of the burrow, such that the mole-rats consumed the section of the tuber exposed by the burrow and also approximately one burrow diameter above and below the burrow. In so doing, they ate approximately 48% of the tuber. If 48% of each tuber is consumed and the coefficient of digestibility is 52.5%, the amount of digestible energy available to the mole-rats ranged from 31.6 to 42.1 kJ · m^{-2} in tuber-poor areas and from 101.5 to 610 kJ · m^{-2} in tuber-rich areas (mean 73.8 kJ · m^{-2}).

As an indication of the minimum distances mole-rats would have to dig to find a tuber, the mean nearest-neighbour distances between tubers located in two regions of high tuber density (one from each burrow system) were 0.98 ± 0.62 m (n = 224) and 1.52 ± 1.0 m (n = 295). Whereas the mean nearest-neighbour distance outside the clumps in the two systems was 2.38 ± 1.2 m (n = 46) and 4.0 ± 4.6 m (n = 47).

Dordabis, Namibia

The geophytes had a mean mass of 5.6 ± 12.3 g and a mean diameter 1.59 ± 0.95 cm (range 4.4–0.34, n = 481). They occurred at a mean depth of 8.76 ±1.75 cm (range 4.1–12.5 cm, n = 228). Using the 54 randomly selected quadrats, the geophytes in the study area were found to have a clumped distribution (CD = 10.56). The density of geophytes in the plots varied from 4 to 160 · m^{-2}.

If a mole-rat had been able to use cues to burrow directly to the next geophyte, the minimum distance it would have had to burrow to encounter the next bulb (mean nearest-neighbour distance) in 25 1 × 1 m plots was 15.23 ± 12.89 cm. The mean biomass was 98 g · m^{-2} (range 0.72–431 g · m^{-2}). In terms of energy obtainable from the geophytes, the study area had a mean of 345 kJ · m^{-2} (range 2.5–1517 kJ · m^{-2}) of which 330 kJ · m^{-2} (range 2.4–1450 kJ · m^{-2}) could be utilised by the mole-rats, assuming a coefficient of digestibility of 95.6% (Bennett and Jarvis 1995) and that the mole-rats consume the entire bulb.

There were significant differences between bulb densities in the neighbourhood of the three areas sampled: areas inhabited by large colonies, by small colonies and areas devoid of mole-rats (one-way ANOVA $F_{(2,218)}$ = 31.186, P < 0.00001). The areas containing no mole-rats were poorest in geophytes; the large colonies occurred in the richest geophyte areas and the smaller colonies tended to occupy slightly poorer areas (Table 2).

Foraging by the mole-rats at Dordabis

Analysis of food store

In the partially excavated burrow system, a food store was found close to the nest, at a depth of 2.4 m. It contained 106 bulbs with a total mass of 1456 g. The geophytes were stored in loose soil within the chamber. The mean diameter of the geophytes in this store was 2.49 ± 0.4 cm (range 1.6–3.4 cm). In contrast, 77 bulbs collected during excavation of an adjoining 9 m of foraging burrow had a mean diameter of 1.9 ± 0.8 cm (range 0.5–3.6 cm), a figure comparable to the larger randomly collected sample of 481 geophytes (1.59 ± 0.95 cm, range 0.3–4.5). Frequency distribution plots (Fig. 3) further show that the mole-rats selectively store the larger bulbs.

Foraging behaviour

Estimate of burrowing activity by a colony. The total biomass of the 16 mole-rats in this colony was 2.2 kg. Following the rainstorm of 40 mm, they dug more than 700 m of tunnels and pushed onto the surface 2.6 metric tons of soil to form 365 mounds.

Examination of foraging behaviour. The geophytes occurring in the path of the foraging tunnel were not more abundant than elsewhere in the strip of ground on either

Fig. 3 Size-frequency distribution plots for geophytes taken from a food store and from around 9 m of burrow

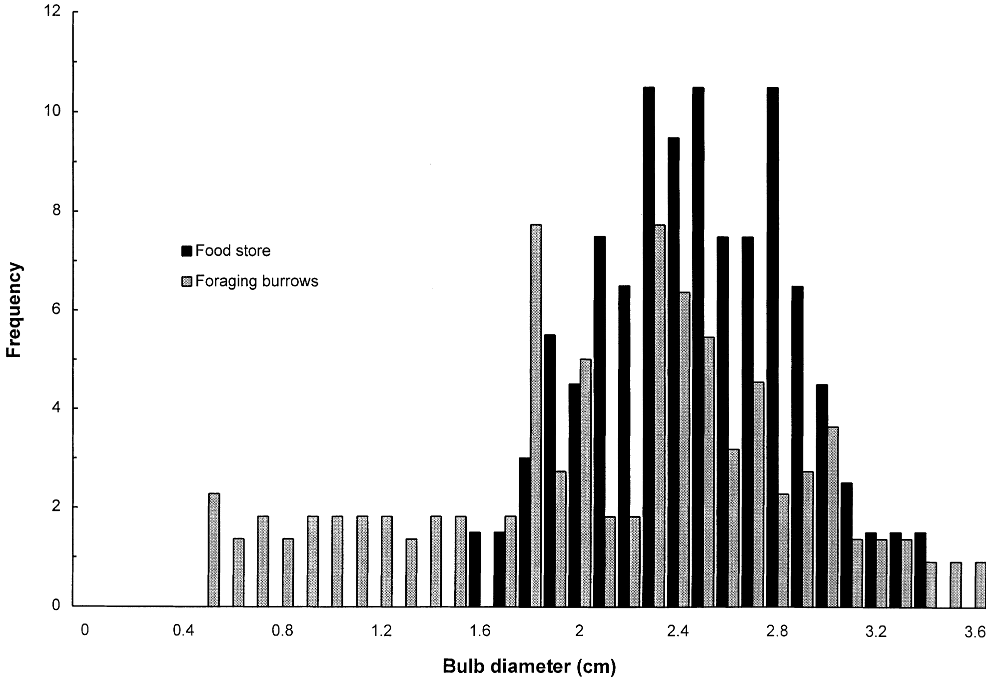

Table 3 Examination of whether mole-rats selectively forage towards resource-rich areas. A comparison of the number of geophytes adjacent to mounds/burrows with the number away from mounds. Results are presented as the mean ± SD (*n* in parentheses). No significant differences were found between the two sets of quadrats in ten transects (Student's *t*-test)

Plot	Number of geophytes		*P*-value
	Near mounds	Away from mounds	
1	6.89 ± 1.29 (9)	5.33 ± 2.57 (18)	>0.3
2	4.50 ± 1.29 (4)	9.20 ± 6.61 (35)	>0.1
3	4.22 ± 5.38 (9)	2.88 ± 3.64 (33)	>0.3
4	22.25 ± 15.52 (4)	23.20 ± 11.14 (10)	>0.8
5	3.92 ± 2.43 (12)	2.41 ± 2.49 (27)	>0.08
6	7.30 ± 3.09 (10)	5.68 ± 3.23 (22)	>0.1
7	5.60 ± 4.62 (10)	5.56 ± 4.67 (18)	>0.09
8	14.83 ± 4.79 (6)	12.60 ± 10.10 (10)	>0.6
9	12.77 ± 6.42 (13)	12.53 ± 8.64 (19)	>0.9
10	13.11 ± 5.71 (9)	14.85 ± 11.71 (13)	>0.6
All	8.79 ± 7.22 (86)	7.77 ± 8.11 (205)	>0.3

side of the burrow (Fig. 4a, b, Table 3). There was therefore no evidence that the mole-rats were able to detect and burrow towards geophyte-rich areas.

Examination of the foraging pattern of the mole-rats showed that the first burrows dug after rainfall had relatively few branches. Furthermore, only 14% of the geophytes that the mole-rats encountered (i.e. that were growing less then 1 m from a mound) were removed by them. Many clumps of geophytes near the burrow were not harvested by the mole-rats during this initial phase of foraging (Fig. 4a). In contrast, there was evidence of more extensive harvesting of geophytes (42%) by mole-rats in the vicinity of the older burrows (Fig. 4b).

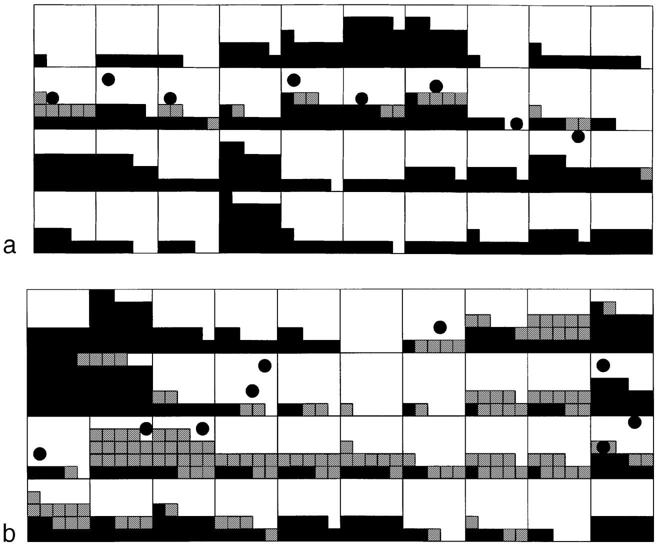

Fig. 4 Examples of transects taken at Dordabis along freshly dug foraging burrows (**a**) and ones dug approximately 2 months before the survey (**b**) to show the path taken by the mole-rats in relation to numbers of geophytes, and the number of geophytes harvested by the mole-rats. The actual positions of the geophytes within each 1-m^2 block are not shown. Each *large square* is 1 m^2. One *small black square* is an uneaten geophyte (a maximum of 25 can be shown per square metre), a *stippled small square* is a harvested geophyte, and a *black circle* denotes the position of a mound

Mean distance that had to be dug between geophytes. Using the 45° arc and measuring the distance from one geophyte to the next within randomly selected 5° segments, we estimated that a mole-rat at Dordabis would have to dig a mean of 1.79 ± 1.18 m (*n* = 149 geophytes) to encounter the next geophyte.

Discussion

Resource characteristics

It has been postulated that resource characteristics have played an important role in shaping the evolution of sociality in the Bathyergidae (Jarvis 1978; Lovegrove and Wissel 1988; Jarvis and Bennett, 1991, 1993; Jarvis et al. 1994) However, there is a paucity of field data to support this hypothesis.

Most investigations of resource characteristics have focussed on a single site, and consequently regional variation in these characteristics has not been considered. The very considerable inter-habitat differences revealed in this study highlight the danger of making species-level generalisations from a single habitat. Regional and local variability make it difficult to determine the scale of clumping of resources that is biologically significant to the mole-rats. Furthermore, large and small colonies will be affected differently by the size of a patch, the distribution of geophytes within a patch and the distance between patches. Long-term recapture data from our site at Dordabis have shown that the home range of large colonies of Damaraland mole-rats may exceed 10 000 m^2 (N.C. Bennett and J.U.M. Jarvis, unpublished data), and Lovegrove (1988) recorded a home range of 13 000 m^2 in an area with gemsbok cucumbers at Nossob in the Kalahari Gemsbok National Park. If large colonies of mole-rats forage over scales of this magnitude, the distribution of small clumps may be far less important to them than the spacing of large clumps. On the other hand, dispersing animals, or small colonies, with small home ranges, may be more affected by a different scale of clumping.

In both our study areas, the geophytes had a clumped distribution. However the two areas differed in the size of the geophytes, the size and spacing of the clumps, in the depth at which the geophytes occurred and in the energy available to the mole-rats. The mole-rats in the two areas may therefore be exposed to different selective pressures.

Even within the same dune systems in the Kalahari Gemsbok National Park, appreciable differences in resource characteristics were found. Thus at Twee Rivieren, we found that gemsbok cucumbers occurred in clumps of roughly 25 m^2 spaced 20–25 m apart. Rows of mounds pushed onto the surface by the mole-rats clearly indicated that they had dug through areas with very few tubers as they searched for a new patch (Fig. 2). In contrast, in their study area in the dunes near Nossop, Lovegrove and Knight-Eloff (1988) noted that the gemsbok cucumbers occurred randomly within very large patches (0.25 km^2) separated from each other by distances of more than 0.5 km. They also mention that mole-rat colonies were rarely found in these 'suboptimal' interclump areas. In our study area therefore, interclump distances may be important to a colony as it forages and also during dispersal and colony-founding events, whereas at the Lovegrove and Knight-Eloff site, a colony could probably survive within the confines of a single large patch. In this latter case, inter-clump distances may only be crucial when individuals attempt to disperse.

At Dordabis, the clumps of geophytes were smaller and much closer together than those of gemsbok cucumbers in the Kalahari Gemsbok National Park. Nevertheless, clumping of these resources means that these mole-rats are still having to dig through good and lean areas as they forage for food. It would however appear that, because of the nature of the resource, foraging at Dordabis incurred considerably less risk of not encountering the next clump of geophytes than in the Kalahari Gemsbok National Park. Presumably in the former locality, lone dispersers and small colonies have a better chance of finding sufficient food to survive during this critical period than in the Kalahari.

Differences were also apparent in the energy available to the mole-rats in the Kalahari and at Dordabis. Mature gemsbok cucumbers have a fibrous central core which is avoided by the mole-rats (Lovegrove and Painting 1987). Consequently, our estimates of available energy, in which whole tubers were used, were probably overestimates. Additionally, previous studies have shown that the coefficient of digestibility for the gemsbok tuber (52.5%) is much less than for the bulbs and corms at Dordabis (95.6%) (Bennett and Jarvis 1995). The site at Dordabis thus provides a richer supply of food than that in the Kalahari, again making the former a less precarious habitat for mole-rats than the Kalahari.

Foraging underground imposes high energy demands on the mole-rats and they exhibit dietary and physiological modifications to enable them to fully exploit the resources available to them. Buffenstein and Yahav (1994) have shown that gemsbok cucumbers have a very low protein and high fibre content. This is similar to the nutritional content of poor-quality grasses that can usually only be consumed by specialized ruminants. Despite this poor-quality food, the Damaraland mole-rats derive sufficient energy from the tubers by having highly efficient caecal fermentation. Lovegrove and Knight-Eloff (1988) note that the caecum comprised 26% of the total hind gut length; this is larger than for most southern African rodents (3.7–20.2%, Perrin and Curtis 1980) and is only exceeded by another mole-rat, *C. hottentotus* (29.1%, Perrin and Curtis 1980). Their habit of autocopophagy also enables Damaraland mole-rats to further utilise the energy released from the fibre by microbial action. Most of the species of geophytes at Dordabis are toxic to livestock (Kellerman et al. 1990) but are eaten with apparent impunity by the mole-rats. *C. damarensis* must possess mechanisms to detoxify these geophytes and this again enables it to exploit a wider range of food resources than many other animals in the area. Mole-rats do not drink free water and in both areas the geophytes provided them with all the moisture they need.

In metabolism cages in the laboratory, mole-rats required between 0.75 and 1.41 kJ · g^{-1} body mass per day (Bennett and Jarvis 1995). An inactive 130-g mole-rat (mean mass of mole-rats at Dordabis) would therefore require 98–183 kJ daily. In terms of wet mass of food, a caged 130-g mole-rat consumed an average of 40 g of gemsbok cucumber and 34 g of *D. glaucum* each day. We do not have information on the energy requirements of free-living mole-rats but Lovegrove (1987) found, in laboratory studies, that the energy cost of burrowing in *C. damarensis* was about five times that of the resting metabolic rate.

Our calculations show that a mole-rat at Dordabis, digging blindly but in a directional way, would burrow on average 1.79 m to encounter the next geophyte. A 130-g mole-rat would therefore have to burrow on average 10.74 m to find 34 g of geophytes simply to meet its resting metabolic requirements, the distance dug would be considerably more to meet the energy requirements of an active animal. Thus, even in the more favourable habitat at Dordabis, mole-rats have to dig considerable distances to meet their daily energy requirements. This distance would be lowest in geophyte-rich areas monopolised by large colonies (see below) and further reduced if the mole-rat could recognise that it was entering a patch of food and changed its searching pattern to explore the area more thoroughly. Indeed Jarvis and Sale (1971) and Brett (1991) found evidence of this change in foraging behaviour in the naked mole-rat in Kenya; their burrow pattern changed, from long relatively straight tunnels to a network of tunnels, when they encountered patches of small tubers.

From our long-term study at Dordabis, it would appear that within the area contained by their burrow system, the energy available to the large established colonies of mole-rats is sufficient to maintain the colony more or less indefinitely. Colonies have remained resident in the same home range for many years (> 7 years) and have not simply exploited an area and then moved on (Fig. 5).

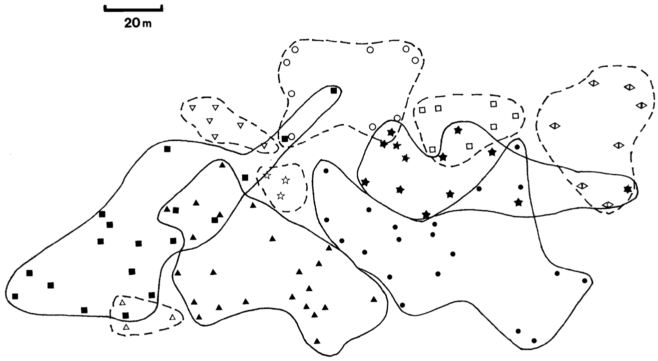

Fig. 5 The capture sites (*symbols*) over time for selected colonies of mole-rats at Dordabis to demonstrate site fidelity (--- + *open symbols* = home ranges of small colonies; — + *black symbols* = home ranges of large colonies, each of the latter being recaptured in the depicted area for at least 6 years)

The resource characteristics at Dordabis have important implications for the formation of new colonies. Our data have shown that many, but by no means all, of the small newly founded colonies occur in areas poorer in geophytes than those occupied by large well-established colonies. This may be one of factors contributing to the failure of small colonies. It would, however, appear from an ongoing long-term demographic study at the site (J.U.M. Jarvis and N.C. Bennett, unpublished work) that competition with larger well-established colonies may also play a role in the success or failure of a nascent colony. These factors would be even more compounded in the Kalahari dune systems where patches of geophytes are widely spaced and dispersing mole-rats would either have to dig through large, geophyte-poor inter-patch areas or compete with well-established colonies for space within patches.

Foraging behaviour

After heavy rainfall, the soil at burrow depth becomes moist and easily worked by the mole-rats. This triggers a frenzy of burrowing activity; the colony work force is mobilized and long relatively unbranched tunnels are dug by the animals. The effort involved is impressive – 16 animals with a total mass of 2.2 kg excavated and moved 2.6 tons of soil in less then 2 months. Observations at Dordabis show that, during this initial phase, the mole-rats concentrate on enlarging their burrow system and hence their foraging territory, and little harvesting of food items occurs. As the soil dries out, these extensive exploratory tunnels are revisited by the mole-rats and the geophytes are harvested by digging minor lateral excursions from the main tunnel. When the soil is very dry and no mounds can be thrown onto the surface, the mole-rats resort to shunting this excavated soil into portions of the burrow system. At the height of the dry season it is difficult to find open tunnels – nearly all of them have been packed with excavated soil. When it is dry in the Kalahari, the top ±40 cm of soil becomes very loose and unworkable by the mole-rats but their food supply is secure because they can continue to exploit the long gemsbok cucumbers from the deeper burrows by constructing spiralling chambers around the tuber (Lovegrove and Painting 1987). At Dordabis, the upper layers of soil are more compact than in the Kalahari and harvesting of the deeper-lying bulbs and corms can continue even when the soil is dry.

One important aspect that Lovegrove and Knight-Eloff (1988) mentioned as needing study was whether or not mole-rats search and locate tubers on a purely random basis. We found no evidence from our field observations that Damaraland mole-rats know the whereabouts of geophyte-rich clumps and dig towards them. In surveyed plots (Fig. 4a, b), the mole-rats often missed rich areas only a metre away from their tunnel and there was no difference between the densities of geophytes in the path of the burrow system and that more than 1 m away (Table 3). The initial search for geophytes therefore appears to be done blindly. However, because the burrows are relatively straight, there is economy of effort in that the animals do not search the same area twice and therefore the search is not random.

We have observed that small newly founded colonies are sometimes unable to dig tunnels long enough to sustain them through the dry times. Ongoing field studies at Dordabis in Namibia (Jarvis and Bennett 1993) have coincided with a prolonged period of below-average rainfall (1989–1995, Fig. 1). This drought has provided an opportunity to critically examine the survival of both newly founded and well-established colonies under these very harsh conditions. Indeed, during the exceptionally long dry spells experienced in the drought, small colonies were sometimes forced to extend their burrow systems when the soil was dry, presumably because too few resources had been located during the wet spell. Theirs were then the only systems in which mounds of dry, loose, and difficult-to-manage soil were pushed onto the surface. This excavation and disposal of dry soil is energetically costly. It also exposes these small colonies to predation at a time when large colonies are not producing mounds and their burrow systems are tightly sealed off from the surface and therefore largely impenetrable to these predators. At the height of burrowing and mound formation after rainfall, the dilution effect would greatly reduce the risk of predation to any one colony.

It is difficult to study harvesting of food by animals, such as mole-rats, that operate entirely underground. From partial excavations of burrow systems at Dordabis and by us and Lovegrove and Knight-Eloff (1988) in the Kalahari, it is apparent that large food items are left growing and are eaten by the mole-rats in situ. Partly eaten tubers and bulbs are packed with soil and will then regenerate and thus constitute a renewable resource for the mole-rats and may contribute to colonies being able to remain resident in the same area for long periods. This partial consumption of large tubers resembles that of the naked mole-rat (Brett 1991).

It appears, from comparison of bulb diameters in the store with those available to the foraging mole-rats, that the smaller-sized food items are eaten by the mole-rats where they are encountered and that larger bulbs and corms are carried to the communal store. This has been confirmed from laboratory studies on foraging Damaraland mole-rats (N.C. Bennett and J.U.M. Jarvis and S. Telford, unpublished data) and has also been found to be a feature of foraging in the common mole-rat, *C. hottentotus* (Davies and Jarvis 1986; Bennett 1988; A. Spinks, T. Branch and S. Croeser, unpublished data). There are probably energetic advantages in only transporting larger items to the store, which may be >40 m from the foraging area. It is also possible that larger bulbs and corms have a better shelf life than the smaller ones. The function and number of food stores in a burrow system is not known. The store we located close to a deep nest (>2.4 m) would only have been sufficient to support the colony (which contained 25 animals) for a couple of days. If this was the only store in the burrow system, it may have served as a food source for juveniles and for the breeding female when she has pups to feed.

Conclusions

Damaraland mole-rats survive in arid parts of southern Africa because they live communally and are thus able to rapidly mobilise a work force on the few occasions each year when the soil is moist and easily worked. This work force is capable of prodigious efforts and can, within a few weeks, open up large areas, which are later exploited by the mole-rats when the soil is dry and difficult to dig. Critical factors in the survival of colonies are the size of the work force and access to rich patches of geophytes on which to feed. Large colonies are able to survive (indeed they continue to rear young and maintain good body condition) through periods of drought, when rainstorms may be 10 or more months apart, but many newly founded colonies flounder and disappear. It is when environmental conditions are at their most extreme that the advantages accrued by Damaraland mole-rats from living in large cooperative groups are most clearly demonstrated.

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