

Burrow architecture of the Damaraland mole-rat (*Fukomys damarensis*) from South Africa

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Abstract

The burrow architecture (length, internal dimensions, fractal dimension of tunnel systems, number of nesting chambers and surface mounds) was investigated in the Damaraland mole-rat (*Fukomys damarensis*). A total of 31 animals were caught from five different colonies and their burrow systems were excavated in their entirety. The mean and SD colony size was 6 ± 3.3 , with a range of 2-10 mole-rats. The sex ratio was male biased 1.21:1. Males had a body mass of 80.5 ± 33.8 g, but were not significantly different to those of females which had a mean body mass of 83.4 ± 24.9 g. The burrow system of the Damaraland mole-rats follows the same general architectural plan as recorded for other species of mole-rat with either one or two more centrally based deeper more permanent burrows which often connect to a nest area, which is used for resting and rearing offspring. The burrow systems contained several more superficial secondary tunnels at a shallower depth. The secondary tunnels accounted for up to 80% of the total burrow

system. The mean length of the burrow system was 130.4m and covered an area of 1403m². The mean number of secondary branches in a burrow system was 10. The mean fractal dimension was 1.154 which implies the mole-rats do not explore their surrounding environment particularly efficiently when compared to that of other mole-rat species, but this may relate to the size of the main food resource, the Eland bean (*Elephantorrhiza elephantina*) which is randomly distributed and fed on *in situ*. Our study showed that colony size influences the size and complexity of the burrow system with larger colonies having a longer burrow system covering a greater area with more secondary tunnels than that of smaller colonies.

Keywords

Burrow system, *Fukomys damarensis*, fractal dimension, mole-rat, foraging

Introduction

African mole-rats (Bathyergidae) are subterranean rodents that exhibit varying degrees of social complexity ranging from strictly solitary species (*Bathyergus*, *Georychus* and *Heliophobius*) through to eusocial species (*Fukomys* and *Heterocephalus*) (Jarvis and Bennett, 1990, 1991). The solitary species generally occur in more mesic regions compared to the eusocial species which occur in arid areas (Jarvis *et al.*, 1994). Two theories support the social evolution of mole-rats; Aridity Food Distribution Hypothesis (AFDH) (Jarvis *et al.*, 1994; Faulkes *et al.*, 1997; Bennett and Faulkes, 2000) and the Phylogenetic Constraints Hypothesis (PCH) (Burda *et al.*, 2000, Lovy *et al.*, 2012). The AFDH predicts the evolution of a eusocial lifestyle driven by an arid environment with unpredictable, sporadic rainfall and clumped food resources with a low digestibility (Bennett and Jarvis, 1988). Whereas the PCH considers eusociality to be a precursor to surviving in harsh environments (Burda *et al.*, 2000). Both conflicting hypotheses conclude

that social subterranean species would be able to live in harsher environments than solitary species.

Lovegrove and Wissel (1988) posited that solitary foraging by specialist feeders such as bathyergids in areas where geophyte densities are low (often arid regions) is uncommon as the risk of unproductive foraging is high. This was based on the concept that increased foraging efficiency often results in increased fitness of individuals within foraging groups of animals ranging from herbivorous (Jarman, 1974), omnivorous (Crook, 1972) and carnivorous mammals (Schaller, 1972) through to birds (Cody, 1971; Krebs, 1974).

Eusociality is characterized by three features namely, 1) a clear division of labour with reduced reproduction by some colony members (mutualism) (Lin and Michener, 1972); 2) there are generally two or more generations present in a family group (Wilson, 1975); 3) there is cooperative care of the young with subordinate individuals taking care of offspring (Crespi and Yanega, 1995). The Damaraland mole-rat is one of the few eusocial species of subterranean rodent (Jarvis and Bennett, 1993) and exhibits a complex colony structure in comparison to the mole-rat genus *Cryptomys*. Colonies normally comprise a single breeding female and up to two reproductive male consorts (Bennett, 1990; Burland *et al.*, 2002; Šumbera *et al.* 2012). Body mass for adult females range from 88-145g, whereas adult males range from 103 – 202g. Reproductive females are identified by a larger body size than non-reproductive females and they have clearly defined nipples and a perforate vagina (Jarvis and Bennett, 1993). Only 11% of animals disperse to form new colonies (Jarvis and Bennett, 1993). In intact colonies of the Damaraland mole-rat there is a primary reproductive division of labour and a secondary work related division of labour into frequent and infrequent workers (Bennett & Jarvis, 1988).

Frequent workers are characterised by a smaller body mass in comparison to infrequent workers. Non-reproductive members of the colony show altruistic cooperative behaviour by helping to raise and look after pups until they are of 3 months of age (> 45g) and are capable of independent feeding and tunnel excavation (Bennett, 1990; Jarvis and Bennett, 1993).

Burrowing in African mole-rats has been described by Genelly (1965) and Jarvis and Sale (1971). The substrate is pushed along the burrow and either pushed to the surface to create a mound or deposited into an old tunnel (Jarvis *et al.*, 1998) depending upon the soil moisture content. In arid regions, when the substrate becomes dry, it becomes increasingly difficult and energetically costly to excavate and extend the tunnels of the burrow system and to produce mounds (Vleck, 1979). Therefore in the dry season the mole-rats tend to backfill previously excavated and disused tunnels instead. Burrow excavation and subsequent extension generally follows a period(s) of good rainfall, when the soil is moist resulting in linear burrows (Jarvis *et al.*, 1998) enabling the colony to forage optimally. Burrowing was believed to be random and suspected that mole-rats forage “blindly” without being able to sense the location of food resources (Jarvis *et al.*, 1998). It is now believed that mole-rats can sense kairomones produced by the roots of plants, but these chemo-signals only operate over a short distance (Heth *et al.*, 2002). Once a food resource has been located it will either be taken back to a food storage area or if the geophyte is too large to be stored the colony eats parts of the geophyte *in situ*. It has been posited by Heth (1989) that once a large food resource has been located the burrowing technique changes from digging linear to a more reticulate pattern that explores the area more efficiently with numerous foraging branches (Lovegrove and Painting, 1987), as the likelihood of encountering another food resource is high (Heth, 1989; Brett 1991; Spinks *et al.*, 2000). This

area restricted search strategy has been suggested to be an adaptation to the clumped distribution of geophytes (Heth, 1989).

Burrow systems of mole-rats are based on the same general design comprising of up to 90% shallow foraging tunnels (Miller, 1957; Jarvis and Bennett, 1991) located at an approximate depth of 15 – 35cm (Thomas *et al.*, 2009). The shallow foraging tunnels usually terminate at the roots of tubers and geophytes which constitute the main food resources. These shallow foraging tunnels connect to a deeper more permanent tunnel architecture including numerous chambers that are used for nesting, food storage (Lovegrove and Painting, 1987), sanitization and retreat (Bennett & Faulkes, 2000; Škliba *et al.*, 2009). Tunnel dimensions vary with the species, number of individuals, sex, and local habitat conditions (Romanach *et al.*, 2005). There is very limited data available on the burrow architecture of eusocial species. Home range data for the Damaraland mole-rat burrow system has been suggested to cover an area of up to 10 000m² based upon the presence of mole mounds on the ground surface (N.C. Bennett and J.U.M. Jarvis, unpublished data), and Lovegrove (1988) found a burrow home range of 13 000m² based on radio telemetry for a large colony of 20 animals at Nossob, in the Gemsbok Kalahari National Park. Lovegrove and Painting (1987) excavated Damaraland mole-rat burrow systems in two geographically different locations in the Kalahari (sand dune and grassland) and found similar burrowing patterns in both environments. Burrow systems both contained deeper more permanent primary burrows that were generally straight and had shallower secondary foraging branches. These two tunnel types represent a compromise between predatory pressures, environmental factors and food resource dispersal patterns (Lovegrove and Painting 1987). More recently, Voigt (2014) investigated colony formation and dispersal in Damaraland mole-rats. The release of three unrelated mole-rats resulted in the construction of a burrow system of

approximately 100m based on mound production. The mound production indicated similar burrow construction to that of Lovegrove and Painting (1987) with a single linear burrow with star like branching at the most southern point of the main burrow. The branching was suggested to be due to the location of food resources (Voigt, 2014). The three introduced animals were joined by a dispersing animal and colony formation has been suggested to be by pairs and small groups (Jarvis and Bennett, 1993; H. Thomas per. obs). It has been suggested that smaller colonies and dispersing animals will have home ranges that are reduced and may be affected by a different scale of resource clumping than those of larger colonies (Jarvis *et al.*, 1998).

Due to this assumption we test the hypothesis that larger colonies will have a larger burrow system that is more complex in structure indicated by a higher fractal dimension value than those of smaller colonies. This study may provide additional evidence for the assumptions of the foraging model of Lovegrove and Wissel (1988): that larger group size offer adaptive benefits in terms of how thoroughly the surrounding area is explored. The main objective of this study was to investigate and describe the architecture and structural characteristics of five Damaraland mole-rat burrow systems as part of recent ongoing research into foraging behaviour of subterranean rodents (Herbst and Bennett, 2006, Sichilima *et al.*, 2008, Škliba *et al.* 2009, Šumbera *et al.*, 2012, Thomas *et al.*, 2009, 2012a, 2012b, 2013) and foraging efficiency (Le Comber *et al.*, 2002, 2006).

Methods

Study site

The study was undertaken in March 2013 near the town of Blackrock in the Northern Cape province, South Africa (27°07'50S, 22°50'50E). The site comprised of natural land used for

grazing cattle. The land was sparsely vegetated with grasses (*Aristida*, *Eragrostis* and *Schmidtia* species), bushes (*Acacia mellifera*, *Grewia flava* and *Lycium cinereu*), trees (*Acacia erioloba* and *Acacia haematoxylon*), legumes (*Elephantorrhiza elephantina*) and cucurbits (*Acanthosicyos naudinianus*). The soil surface was loose for the top 5cm and then became compact. The soil largely consisted of compacted medium (1-1.5mm) and coarse (1.5 – 2mm) sand particles (37% and 60% respectively) ranging to a depth of 1m, determined by the passing of soil through a graded series of sieves.

Study animals

A colony of animals was defined as a group of two or more individuals caught from the same burrow system comprising of at least a single male and a single female. Typically all colony members were caught from a single trap, but occasionally two traps were located at a single site. Active burrow systems were identified by the location of rows of fresh mounds on the surface. Animals were captured using modified Hickman live traps (Hickman, 1979) (length: 30 cm, diameter: 7 cm) baited with sweet potato. Traps were checked every 2-3 h during daylight to prevent heat stress in captured animals and left open overnight. On capture, mole-rats were sexed, weighed (± 0.1 g Sartorius balance, Epsom, Surrey, UK) and kept in a secure ventilated plastic container (1 x 0.5 x 0.5m) until the entire colony was caught. Animals were defined as either being adult (> 90 g), sub-adult (>45 g and <90 g) or juvenile (<45 g) based on body mass (Bennett and Faulkes, 2000). The mole-rats were kept on a natural sand substrate and given paper toweling as nesting material. The animals were fed twice a day on sweet potato and carrot, but were not provided with free water as their entire water intake is obtained from the food provided. The animals were then transported to the University of Pretoria for use in further

studies (University of Pretoria ethics number ECO75-12). Animals were cared for in accordance with the regulations stipulated by the ethical committee of the University of Pretoria and permits for capture, export and import were obtained from the Northern Cape Department of Nature Conservation and Gauteng Directorate of Nature Conservation.

Excavation of burrow systems

Upon removal of the entire colony, active burrow systems were excavated manually with hoes to expose the tunnels along their entire length. An active burrow system was defined as being the open burrow system excluding the excavation of back-filled tunnels. A total of 5 burrows were excavated. The lengths of the burrows and their dimensions were recorded *sensu* Thomas *et al.*, (2009; 2012a; 2013) for *B. suillus*, *G. capensis* and *C.h. hottentotus* respectively. The depth from the ground surface to the top of the burrow; height and width of the burrow were measured using a tape measure (± 0.1 cm). Tunnels were defined as either being deep, semi-permanent (> 25 cm deep) or shallow, secondary foraging (< 25 cm deep) tunnels. A map of each burrow system was recorded relative to magnetic north and later digitised. Tunnel depths were recorded approximately every metre and the location and dimensions of any nests, bolt-holes and latrines were also noted. Nests were defined as chambers with single or multiple entrances filled with nesting material (Thomas *et al.*, 2009). Large food resources (*Eland bean*, *E. elephantina*), which had been partially consumed *in situ* were noted. A food resource that was being eaten *in situ* was defined as a large geophyte passing through the tunnel system in which parts of the tuber had clearly been eaten. Bolt-holes were steep-angled tunnels (almost vertical) that were greater than 50cm in length. Latrines were defined as being blind-ended tunnels packed with soil and faeces. The positions of fresh mounds were recorded as in Thomas *et al.*, (2009). Fresh

mounds were determined by clear casting. The burrow area was determined by creating a convex polygon around the system as in Thomas *et al.*, (2009; 2012a; 2013).

Analysis of burrow structure

Fractal dimension is an independent measure of burrow complexity (Le Comber *et al.* 2002; 2006). A fractal dimension is essentially a measure of the degree to which a one-dimensional structure fills a plane, and thus reflects the thoroughness with which mole-rat burrows explore the environment (Le Comber *et al.*, 2002). For this reason, fractal dimension is a more natural measure of burrow architecture than other approaches to analysing what is effectively a foraging path (for a review of methodologies for analysing animal movement see Turchin 1993). An increasingly complex burrow system is characterised by possessing numerous side branches which run in different directions and thus has a higher fractal dimension value than that of a simple blind-ended tunnel with no side branches. The fractal dimensions for all five burrow systems in this study were calculated using the Fractal Dimension Calculator V 1.2 2010 program as used in Thomas *et al.* 2009; 2012a; 2013 which is designed to assist with the application of the ‘box counting’ method as in Le Comber *et al.*, (2002) for determining the fractal dimension of a structure.

Statistical analysis

A Mann Whitney U Test was used to analyse differences in body mass between males and females. Spearman’s rank correlation coefficients were used to analyse the relationship between colony sizes and burrow characteristics. All statistical analysis was conducted in Minitab 16

(Minitab 16 Statistical Software, 2010). All values given in the text are mean \pm Standard Deviation (SD) unless stated otherwise.

Results

Colony composition

In total, 31 Damaraland mole-rats were captured from five colonies, comprising 6 adult males and 5 adult females, 6 sub-adult males and 7 sub-adult females, 5 juvenile males and 2 juvenile females. Colony size ranged from 2 to 10 animals (6.2 ± 3.35). The ratio of males to females varied ranging from a 1:1 to 1.21:1 ratio (male/female). The mean body mass of males was not significantly different to that of the females, $U = 0.27$ $P = 0.843$ 80.5g [(SD=22.7 g) $n = 17$], 83.4g [(SD=15.5 g) $n = 14$] for males and females respectively) (Table 1). Juveniles were present in three out of five colonies and represented 16.1% of the total population caught. Colony size positively correlated with burrow size ($R=1$, $P < 0.001$ and $R=0.9$, $P=0.037$, for burrow length and area respectively) and complexity ($R=0.975$, $P=0.005$ and $R=1$, $P=0.001$, for number of branches and fractal dimension value respectively). Colony size also positively correlated with the number of geophytes located, but did not correlate with the overall geophyte mass ($R=0.949$, $P=0.014$ and $R=-0.1$, $P=0.873$ for the number and mass of geophytes found within the system).

The burrow systems

The burrow length ranged from 43 – 257m with a mean home range of $1403 \pm 1113\text{m}^2$ (Table 2). Burrow systems generally comprised one or two main deep central tunnels that connected to the nest area in 66 % of the systems and a varying number of shorter shallow secondary tunnels (Fig

Table 1: Colony composition and body mass of five colonies of Damaraland mole-rats (n=31) (*Fukomys damarensis*) from Blackrock, Northern Cape, South Africa.

Colony	No. of animals	Adult males	Adult females	Sub-adult males	Sub-adult females	Juvenile males	Juvenile females	Male mass (g)± SD	Female mass (g) ± SD
1	2	1	1	0	0	0	0	110	99
2	10	6	4	3	2	1	1	87.3±30.8	86±27.6
3	9	6	3	1	2	4	0	54±31.8	77.3±21
4	4	2	2	1	1	0	0	98.5±14.8	107.5±26.2
5	6	2	4	1	2	0	1	107±29.7	69.5±25

Table 2: Burrow characteristics for the Damaraland mole-rat burrow systems ($n=5$) (mean and SD)

Colony	Colony size	Burrow length (m)	Burrow area (m ²)	Branch number	Fractal dimension	Mound number	Burrow depth (cm)	Nests
1	2	43	193.6	5	1.02	5	18.8	No
2	10	257	2800	17	1.28	9	25.4	No
3	9	183	2265.1	15	1.21	10	27.1	Yes
4	4	79	1232	5	1.05	8	23.1	No
5	6	89.9	525	9	1.21	9	24.8	Yes
Mean	6.2	130.4	1403.1	10.2	1.15	8.2	23.8	
SD	3.4	87.6	1113.3	5.6	0.11	1.9	3.2	

1a-e). Secondary tunnels generally lead off from the main deeper tunnels at right angles. There was 10.2 ± 5.6 tunnel branches present accounting for 48 – 80% of the burrow system (Table 2) and had a mean diameter of 5 ± 0.1 cm. Secondary burrows had a depth range from 11.5 – 15.5cm, whereas the main central tunnels had a depth range of 37.6 – 46.5cm. There were 8.2 ± 1.9 fresh mounds produced per burrow system and the systems had a fractal dimension value of 1.154 ± 0.11 (Table 2). There were no food stores present within the burrow systems instead the secondary tunnels led to a food resource (Eland bean) which was eaten *in situ*. All burrow systems contained at least one food resource and the mean food mass was 614.6 ± 182.3 g (Table 3). Burrow systems had a varying number of nest chambers and bolt-holes (Table 3). Three burrow systems (1b, c and e) contained one nest and two burrow systems did not have any nest chambers (1a and d). Nests were either located at the centre of the burrow system or on the periphery with one or more tunnels connecting it to the rest of the burrow system (Fig 1a-e). The largest nest belonged to the burrow system that contained 9 animals and its dimensions were 43x38x40cm. Nests were filled with dried husks of bulbs and grass and were located slightly deeper than the main tunnels. All but one burrow had at least one bolt-hole present and this was

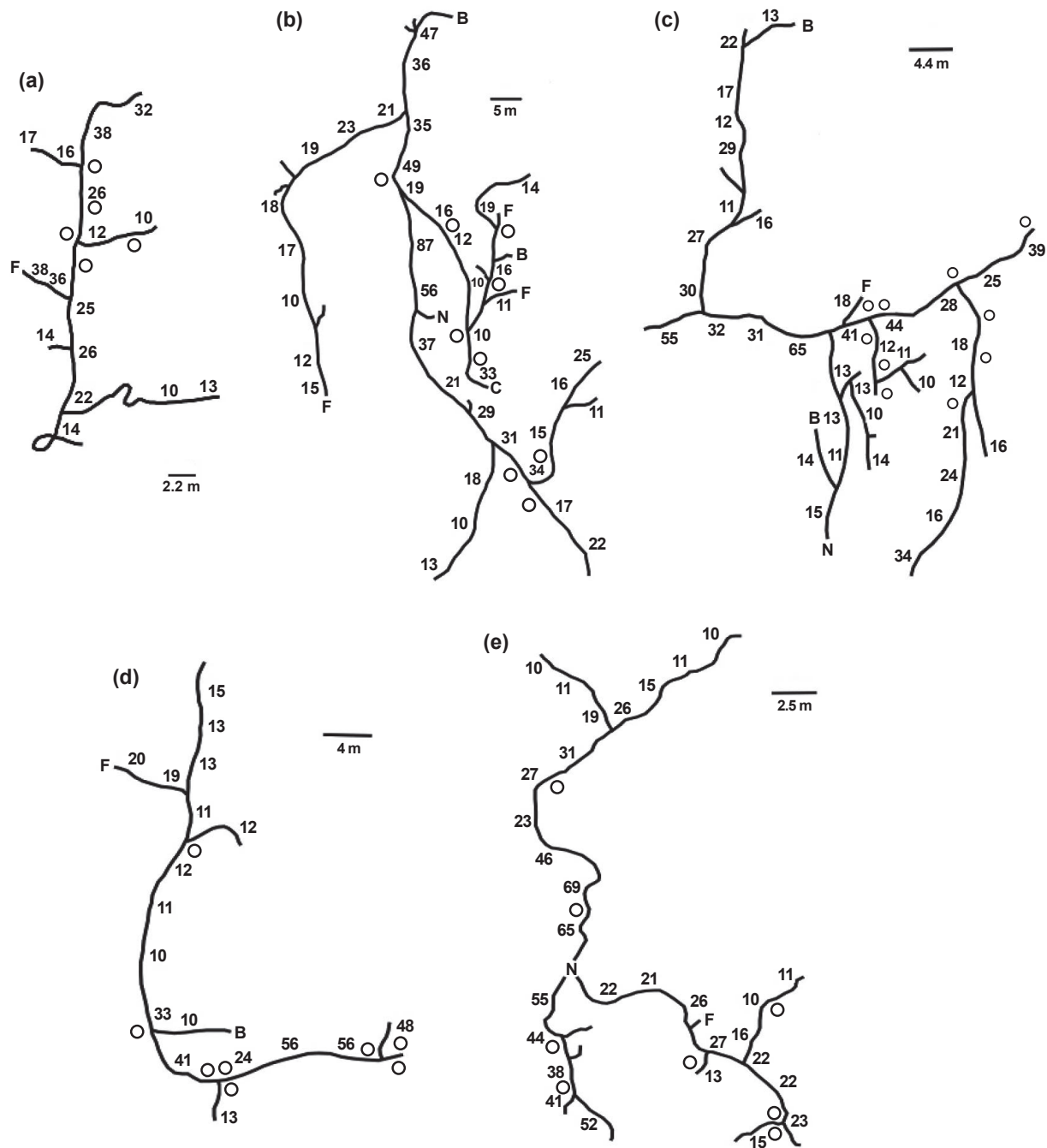


Figure 1: Burrow systems of five colonies of Damaraland mole-rats at the study site in Blackrock, Northern Cape, South Africa (a = two animals, b = 10 animals, c = nine animals, d = four animals, e = six animals). Numbers indicate burrow depth (in cm). Circles indicate mounds, F indicates location of a food source, N indicates a nest site, B indicates a bolt-hole and C indicates an empty chamber

Table 3: Type and number of chambers present in five burrow systems of Damaraland mole-rat (*Fukomys damarensis*) from Blackrock, Northern Cape, South Africa

Burrow system	Food resources	Food weight (g)	Nest	Nest dimensions (cm)	Nest depth (cm)	Bolt-hole	Depth at bolt-hole location (cm)	Other
a	1	652	0			0		0
b	3	664	1	38 × 34 × 42	64	2	45	1
c	2	449	1	43 × 38 × 40	31	2	67	0
d	1	876	0			1	53	0
e	2	432	1	30 × 28 × 36	57	1	66	0

often located on the periphery of the burrow system (Fig 1a-e). Colony two had an empty chamber with the dimensions 29 x 30x 22cm (Table 3).

Discussion

It has been suggested that a very large burrow system is not always advantageous (Herbst and Bennett, 2006) and that when comparing burrow lengths the optimum working length and cost of maintenance of the burrow must be considered (Herbst and Bennett, 2006). We predicted that, larger colonies would occupy larger burrow systems which, in turn, would cover greater areas. Our results support our prediction as there was a positive correlation between colony size, burrow size and area covered by the burrow. Our results support the work of Thomas *et al.*, (2013) for the social *C. h. hottentotus* in that the burrow systems of larger colonies were correlated with a larger burrow length and covered a greater area than that of the smaller colonies. The burrow area covered in our study was significantly smaller than others reported for the Damaraland mole-rat in the central Kalahari (Lovegrove, 1988). Lovegrove (1988) reported a burrow area of approximately 13 000 m² for a colony of 20 individuals. The reason for this may be that the burrow area was an approximation based on radio telemetry and the burrow systems were not excavated. The difference in burrow area may be due to locality and environmental constraints as the study was conducted further north than our study in a more arid region (Gemsbok National Park) where food resources may be more sporadically distributed in comparison and therefore it would be necessary to have a longer burrow system covering a larger area. Differences in burrow characteristics within the social *C.h. hottentotus* has previously been shown to be due to locality and environmental constraints (Thomas *et al.*, 2013). Also our maximum colony size was ten animals, whereas Lovegrove's (1988) colony size was 20 animals.

Our results for burrow length are smaller than the social *F. anseli* burrows (Škliba *et al.*, (2011). This may be due to a difference in excavation method, as we only excavated active burrow systems and did not excavate backfilled burrows. Excavating backfilled burrows does not give a true representation of an active burrow length since mole-rats disperse both above and below ground (Voigt, 2014) thus creating the possibility of linking a dispersing mole-rat burrow system with the colony it was dispersing from. Thomas *et al.* (in preparation) used the same excavation and data capture method as in this study, but found *F. anseli* burrows to be longer than those of *F. damarensis*. This may be due to a small sample size or relatively newly formed colonies indicated by one or two litters in this study (n=5) compared to that of *F. anseli* (n=33; Thomas *et al.*, in preparation). In more arid regions Damaraland colonies may contain up to 41 individuals with a modal size of 12 animals (Bennett and Jarvis, 2004), whereas our maximum colony size was 10 animals suggesting that our colony sizes were smaller although not significantly different ($U = 32.5$, $P = 0.346$). Our small colony sizes suggest that the majority of our colonies were newly formed which may occur after the rains as this allows for easier tunnel extension and a greater likelihood of finding new mates and maintaining genetic diversity. Although our colonies may have been newly formed, each colony had a queen present with a perforate vagina and visible nipples.

The burrow system of the Damaraland mole-rat follows the same general architecture as observed in other species of mole-rat (Nevo, 1999, Busch *et al.*, 2000). The burrow system generally comprises of one or two main deeper more permanent tunnels with numerous secondary branches. It has been reported that secondary branches account for 90% of the total burrow, but in this study the secondary tunnels accounted for between 48 – 80% of the burrow

system. This may be as a consequence of thermoregulatory requirements since subterranean daily temperature fluctuations decrease especially below 30cm (Bennett *et al.*, 1988; Thomas *et al.*, 2009) and the burrow systems were excavated in the summer season. Food resources namely the Eland bean (*E.elephantina*) were located at a greater depth than most of the secondary tunnels. This suggests that the secondary burrows may be dual purpose for example allowing access to the surface for gas exchange (Roper *et al.*, 2001) or for thermoregulatory capacities. *Fukomys anselli* burrows differ from the general design as they appear to have no distinct division of tunnel usage (Škliba *et al.*, 2012). One hypothesis that may explain the larger percentage of deeper tunnels is the Risk Sensitivity Behaviour hypothesis (RSB), which posits that social groups can compensate for a given group size supporting infrequent and frequent workers by reducing the total energetic expenditure by reducing the energetic constraints (Lovegrove and Wissel, 1988). One method of reducing the energetic constraints of foraging is by having a smaller percentage of the burrow system at a shallow depth making it less susceptible to temperature fluctuations both seasonally and daily.

The burrow systems of both social and solitary mole rats do not show any seasonal differences in the burrow complexity as indicated by the fractal dimension value (Spinks and Plaganyi, 1999; Šumbera *et al.*, 2003; 2012; Sichilima *et al.*, 2008; Thomas *et al.*, 2009; 2012). Our results show that larger colonies explore the surrounding environment more efficiently than smaller colonies indicated by a positive correlation between fractal dimension value and colony size. Our results support the concept of a foraging strategy changing once a food resource has been located (Heth, 1989, Voigt 2014) as each of the colonies had a food resource that had been eaten *in situ*, with numerous secondary tunnels around it. In mesic regions fractal dimension values have been

reported as being closer to one for the social *C. h. hottentotus* (Thomas *et al.*, 2013), this also appears to be true for the semi-arid regions that the Damaraland mole-rat inhabits indicating a less complex burrow system than other social mole-rats such as *F. mechowii* and *F. anelli* (Sichilima *et al.*, 2008, Sumbera *et al.*, 2012),

Many studies investigating burrow characteristics have examined differences between seasons (Sichilima *et al.*, 2008; Thomas *et al.*, 2009; 2012a; 2013) or between sexes (Thomas *et al.*, 2012a). If Damaraland mole-rats exhibit similar burrow characteristics as other species, then the results of this study should highlight the minimum habitat excavation and exploration as our study was conducted at the end of the dry season when the soil is least friable, just before the beginning of the annual rains. Burrow systems of both solitary (*B. suillus*, *G. capensis*, Thomas *et al.*, 2012a; 2012b) and social species (*F. mechowii*, Sichilima *et al.*, 2008) of mole-rats have been found to be longer and cover a greater area during the rainy season, suggesting that Damaraland mole-rat burrow systems would also be longer and cover a greater area in the rainy season.

Nest chambers and bolt-holes were present and located slightly deeper than the main tunnel as found by Lovegrove and Painting, (1987) for the eusocial Damaraland mole-rat and the solitary Namaqua dune mole-rat (Herbst and Bennett, 2006). Nest sites were located centrally and on the periphery of the burrow system as reported for Ansell's mole-rat, *Fukomys anelli* (Thomas *et al.*, in preparation) and the common mole-rat, *C.h.hottentotus* (Thomas *et al.*, 2013). Nests are used for rearing offspring and for resting in therefore a central location offers more protection against predators than a peripheral location. Two of the burrow systems we excavated had no nest chambers present (1a and d). This may be due to the colonies being small in size (2 and 4

animals respectively), newly formed and the burrow systems recently created. The colonies were most likely to be newly formed as there was no presence of juveniles (Table 1) that would require a nest area. It has been shown in *F. anselli* nests are often located next to or close to bolt-holes, latrines and food stores (Skliba *et al.*, 2012), but this was not found in this study. There were no latrines present in the burrows, unlike those reported in *F. anselli* and *F. mechowii* (Skliba *et al.*, 2012; Sichilima *et al.*, 2008).

Food stores were not found in any of the excavated burrow systems in this study, instead it appears that the mole-rats 'farm' the geophytes similar to that of the social *C.h.hottentotus* (Spinks *et al.*, 2000) and is contradictory to solitary species *B. suillus* (Davies and Jarvis, 1986) and *G. capensis* (Thomas *et al.*, 2012) which create large food stores. It has been suggested that the food storage method is dependent upon food size (Spinks *et al.*, 2000) as in the case of Damaraland mole-rats where food supply is scattered and clumped, therefore farming geophytes provides a longer term food supply than storing small geophytes in a food cache. Lovegrove and Painting (1987) found spiralled burrows located around large food resources indicated by a collection of three mounds fairly close to each other. Lovegrove and Painting (1987) also found that secondary burrows presumably used for foraging were not present if the food resources were located at a deeper depth. This did not appear to be true of our study as mole-mounds were produced sporadically and were not clumped. Lovegrove and Painting (1987) found the Damaraland mole-rat feeding on mainly the Gemsbok cucumber (*Acanthosicyos naudinianus*) whereas in our study we found the mole-rats mainly feeding on Eland bean (*E. elephantina*). This suggests that they have a varied diet and do not appear to have a natural preference as they appear to feed on both the gemsbok cucumber and eland bean (Voigt, 2014). Voigt (2014)

noticed branching to occur near food resources as did Lovegrove and Painting (1987) and this appeared to be true for our study. There is evidence to suggest that the Damaraland mole-rats also eat smaller bulbs as husks have been found to be used as nesting material, but no bulbs were present within the burrow system.

Bolt-holes were found in four of the burrow systems and appear to be a very common feature in the burrow systems of most species of mole-rat (Schultz, 1978; Jarvis and Sale, 1971; Sichilima *et al.*, 2008; Thomas *et al.*, in review). Bolt-holes have been reported to go to depths of 2m (Davies and Jarvis, 1986) in solitary and social species and up to 3m in the Damaraland mole-rat burrow systems. The difference in depth of the bolt holes suggests that they may play a role in thermoregulation (Hickman, 1990) rather than only being as an anti-predatory function (Davies and Jarvis, 1986). It has been also posited that boltholes may be used as drainage sumps (Bennett and Faulkes, 2000). In Damaraland mole-rat burrow systems it appears that bolt-holes are used primarily for a thermoregulatory function due to their range of depths throughout localities. It is unlikely that boltholes are used as drainage sumps as rainfall tends to be sporadic and unpredictable.

In conclusion, differences in burrow size and complexity appear to be correlated with the colony size based upon the concept of the RSB and the AFDH. Our results suggest that colony size is one of the influential factors when investigating burrow systems and foraging strategies of mole-rats. Other possible influential factors may include the external environment conditions (season and rainfall) and the presence of food resources. There is a paucity of data relating to burrowing

strategies and burrow architecture in subterranean rodents especially the eusocial species. Further research into the burrow architecture of other eusocial species of mole-rat, especially the naked mole-rat (*Heterocephalus glaber*) would help to elucidate the factors that affect burrowing dynamics and foraging behaviour in eusocial mammals. Seasonal data on the burrow system of the Damaraland mole-rat may help elucidate other factors determining the architecture of their burrows and their foraging behaviour.

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