

**Seasonal changes in burrow geometry of the common mole-rat (Rodentia:
Bathyergidae)**

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Abstract

Sociality in mole-rats has been suggested to have evolved as a response to the widely dispersed food resources and the limited burrowing opportunities that result from sporadic rainfall events. In the most arid regions, individual foraging efficiency is reduced and

energetic constraints increase. In this study, we investigate seasonal differences in burrow architecture of the social *Cryptomys hottentotus hottentotus* in a mesic region. We describe burrow geometry in response to seasonal weather conditions for two seasons (wet and dry). Interactions occurred between seasons and colony size for the size of the burrow systems but not the shape of the burrow systems. The fractal dimension values of the burrow systems did not differ between seasons. Thus, the burrow complexity was dependent upon the number of mole-rats present in the social group.

Keywords

Burrow systems, seasonality, *Cryptomys hottentotus hottentotus*, fractal dimension

Introduction

African mole-rats (Bathyergidae) are endemic to sub-Saharan Africa, occurring in a range of habitats with diverse plant species (Bennett & Faulkes, 2000), a range of soils from sandy loams to hard clays and over a broad range of altitudes with varying levels of precipitation (Bennett & Faulkes, 2000). Of the two subfamilies, the Bathyerginae comprises a single genus *Bathyergus* and the Georychinae comprises five genera: *Georchus*, *Fukomys*, *Heterocephalus*, *Heliophobius* and *Cryptomys* (Faulkes *et al.*, 2004). The common mole-rat, *Cryptomys hottentotus hottentotus* has a wide distribution in South Africa and occurs sympatrically with *Bathyergus suillus*, *Bathyergus janetta* and *Georchus capensis* (Bennett & Faulkes, 2000).

The common mole-rat (*C. h. hottentotus*) occurs over the widest habitat range for any bathyergid. They are found in both arid and mesic environments and excavate burrow

systems in a range of soils from sandy loams through to heavier more compact stony soils. Generally they tend to prefer granitic soils in addition to sandy alluvium (Bennett & Faulkes, 2000). The common mole-rat is a small social rodent with a mean body mass of 77g for males and 57g for females and has a fawn pelt without the presence of any form of head patch (Ellerman, 1940) (as in other species of bathyergid). The common mole-rat occurs in colonies of up to nine individuals in arid regions (Spinks, *et al.*, 2000) and up to 16 animals in mesic regions (Davies & Jarvis, 1986). It is a co-operative breeder and has a division of labour with reproduction typically being restricted to the largest dominant male and female within the colony who inhibit the reproduction of subordinates (Bennett 1989, 1992; Rosenthal *et al.* 1992; Spinks *et al.* 1997). It is herbivorous, feeding upon corms, bulbs and tubers of a range of geophytes which it finds “blindly” whilst constructing elaborate burrow systems (Reichman & Jarvis, 1989). Blind foraging behaviour in a unidirectional fashion is a reasonable behaviour for locating large tubers which are randomly distributed (Brett, 1991). Burrow systems in arid regions have been noticeably longer and more linear than those of mesic regions (Spinks, 1998) due to the lower geophyte distribution and the random foraging technique used to locate food resources.

Burrow systems can range from temporary to semi-permanent and the length of usage by the animal is often depicted by the burrow’s complexity. Simple burrows often consist of little more than a single tunnel with a blind ended chamber often used for nesting purposes (Lacey, 2000). Complex burrow systems comprise of numerous temporary foraging tunnels that are used to locate food resources and are generally multi-layered and shallow with several more permanent deeper tunnels that are used for nesting. There are often numerous chambers within a burrow system used for different purposes such as latrines, food storage areas and nesting areas. Burrows provide effective protection against many predators (Lacey, 2000).

Avian predators and most terrestrial carnivores cannot chase prey down small burrows (Reichman & Smith, 1990). Burrows offer effective protection against climatic conditions and at a depth of approximately 30cm a significant amount of the daily temperature fluctuations disappear, although long term seasonal changes in temperature do still occur (Reichman & Smith., 1985). Although burrows do offer many advantages to their occupants, they has one main disadvantage, this being it is energetically more expensive to create an underground burrow system and foraging for food and searching for potential mates. Several factors may increase the foraging costs for mole-rats inhabiting arid environments with low and unpredictable rainfall patterns (Vleck, 1979), sporadic distribution of food resources and “blind” foraging methods (Lovegrove & Wissel, 1988; Lovegrove, 1991; Jarvis *et al.*, 1998).

Mole-rats provide an ideal model group with which to test theories regarding foraging behaviour and habitat exploration as foraging literally takes place “blind”. The idea that foraging takes place blind has been challenged (Heth *et al.*, 2002) as it contradicts the optimality theory (Lange *et al.*, 2005). They inhabit an environment that is thermally buffered and protected from most predators but is energetically expensive to create and maintain (Nevo, 1979; Bennett *et al.*, 1988). Travelling underground has been estimated to be as much as 3400 times more energetically expensive than travelling the same distance on the surface (Vleck, 1979); therefore, selection should favour a foraging strategy that it is efficient during the summer when the ground is hard and the excavation of burrows is more difficult.

The seasonality of burrow system geometry in subterranean mammals remains a poorly studied topic. Seasonal data with respect to burrow system characteristics are available for three solitary species of mole-rat: *Bathyergus suillus* (Thomas *et al.*, 2009; 2012), *Heliophobius argenteocinereus* (Sumbera *et al.*, 2008), and *Georychus capensis* (Thomas *et*

al., 2012) and for one social species, *Fukomys mechowii* (Sichilima *et al.*, 2008; Sumbera *et al.*, 2003). The few existing studies investigating burrow architecture and geometry in *C. h. hottentotus* have not made a direct comparison between seasons (Davies & Jarvis, 1986; Spinks *et al.*, 1998). Davies & Jarvis (1986) excavated one system of *C.h.hottentotus* in February (summer) just North of Cape Town, western Cape and noted that the burrow system of three animals comprised of 93% foraging tunnels (< 35cm), nest chambers, food stores and bolt holes. In total the burrow length of the entire system was 500m. Burrow systems of *C. h. hottentotus* have been compared in two separate regions (arid and mesic) (Spinks *et al.*, 1998) and no difference in colony size was found between mesic and arid regions (range 2-8 in mesic, 2-9 in arid). The burrow systems were excavated between the months of September and November (Autumn). Burrow length ranged from 50 – 200m in the mesic region with a mean burrow depth ranging from 18 – 21cm. Whereas burrow length ranged from 150-510m in the arid region with a mean burrow depth ranging from 13 – 19cm. Food stores were found in three of the burrow systems. Overall burrows were longer and less reticulate in arid region (Spinks *et al.*, 1998).

In this study we investigate how intra-colony size and foraging behaviour (as determined by burrow structure and geometry) in a mesic environment may vary during two seasons, winter (wet) and summer (dry) as part of on-going research into foraging behaviour in bathyergids (Thomas *et al.*, 2009; Sichilima *et al.*, 2008; Thomas, *et al.*, 2012; Le Comber *et al.*, 2002; Romañach & Le Comber, 2004). We predicted that the winter burrow systems of colonies would: (1) be longer and cover a greater area as the soil is more friable and less energetically costly to excavate than during summer; (2) have a higher fractal dimension (an indicator of efficiency of habitat exploration)(Le Comber *et al.*, 2002) as burrowing is tougher and more energetically costly during summer thus it is necessary to forage more efficiently than in

winter; (3) have proportionally more mounds than summer burrows (indicating more active burrowing) and (4) contain proportionally more shallow tunnels that are used for foraging than the summer burrow systems. We also predicted that (5) larger colonies would have larger burrow systems covering a greater area than that of smaller colonies.

Methods

Study animals

The common mole-rat, *Cryptomys hottentotus hottentotus* is social and occurs sympatrically with two species of solitary mole-rat species, the Cape mole-rat, *Georychus capensis* and the Cape dune mole-rat, *Bathyergus suillus* in the western Cape Province of South Africa. It is characterised by a small mean body mass, in the southern western Cape, mean body mass has been reported as 83g and 58g for males and females respectively (Davies & Jarvis, 1986).

Study site

The study was carried out during the winter (July 2011) and summer (February 2011 and 2012) seasons in the coastal fynbos biome near the town of Darling in the south-western Cape Province, South Africa (33°38'33" S, 18°38'33" E). The study site comprised of one large agricultural field used for grazing livestock. It consisted of evenly-distributed vegetation, mostly *Lolium perennae* and *Trifolium repens*. The bulbs of the geophytes, *T. repens* and *L. perennae* were present within and in close proximity to the foraging tunnels in both seasons and did not significantly differ. The soil consisted of a mixture of clay and sandy loam which remained consistent throughout the field (Thomas *et al.*, 2009; 2012). The study site was

chosen as *C.h.hottentotus* occurs in a wide range of environments including grasslands. In Darling they are classed as pests by the farming community as their burrow systems often result in livestock injury. Active burrow systems were identified by location of fresh mounds on the surface in winter. In summer, possible active burrow systems were identified by small, round flattened areas of soil often with vegetation growing from the soil. Active summer burrow systems were confirmed upon the location of the burrow run and capture of an animal from the system. Animals were captured using modified Hickman live traps (Hickman, 1979) baited with sweet potato. Traps were checked every 2 hours in winter during daylight and left open overnight. Traps were checked every hour during summer between the morning hours of 04.00 and 11.00 and the evening hours of 16.00 and 21.00 to prevent the animals suffering from heat stress. Traps were left open overnight and closed during the heat of the day. A total of 77 animals were caught from 15 different colonies: 6 colonies in winter and 9 colonies in summer. Colony size ranged from one to twelve animals. On capture, mole-rats were sexed, weighed (± 0.1 g Sartorius balance, Epsom, Surrey, UK), and housed in a ventilated plastic container. Animals were defined as either being adult or young. Young animals were defined as being less than 40g (Bennett & Faulkes, 2000). Animals were kept on a natural substrate and were given paper towelling as bedding and supplied with sweet potato ad-lib. Once entire colonies were caught, the animals were then euthanized with chloroform and taken to the University of Pretoria (University of Pretoria ethics number AUCC 040702/015) for use in another further study. Animals were cared for in accordance with the regulations stipulated by the ethical committee of the University of Pretoria.

Excavation of burrow systems

Upon removal of the occupant, burrow systems were excavated manually with hoes to expose the tunnels along their entire length. A total of 15 burrows were excavated (six for winter and nine for summer). The lengths of the burrows and their dimensions and shape were recorded *sensu* Thomas *et al.*, (2009; 2012; 2012) for *B. suillus* and *G. capensis*. 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 (> 20 cm deep) or shallow, foraging (< 20 cm deep) tunnels. The distinction between tunnel usages was determined by the depth of the bulbs and roots of the plants in the localities. Tunnels were defined as arched if the ratio of the tunnel height divided by the tunnel width exceeded 1.4 or circular if not. Arched tunnels tend to be used in areas where the substrate is instable (Thomas *et al.*, 2009). 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, food stores, bolt holes and latrines were recorded. Nests were defined as chambers with single or multiple entrances filled with nesting material (Thomas *et al.*, 2009). Food stores were blind-ended tunnels filled with bulbs or roots. Bolt holes were steep-angled tunnels (almost vertical) that were greater than 30 cm in length and were assumed to have an anti-predatory or thermoregulation function, or were drainage sumps (Hickman, 1990; Nevo, 1999). Latrines were defined as being blind-ended tunnels packed with soil and faeces. The position and ages of the mounds were recorded as in Thomas *et al.*, (2009). Once digitised the area of the burrow was determined by creating a convex polygon around the system and the branch angles and turn angles were measured following Romañach *et al.*, (2004).

Analysis of burrow structure

Fractal dimension is an independent measure of burrow complexity (Le Comber *et al.* 2002; Le Comber, Seabloom & Romañach, 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 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 15 burrow systems in this study were calculated using the Fractal Dimension Calculator V 1.2 2010 program as used in Thomas *et al.* 2009; 2012, 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

Colony size ranged from one – twelve animals and each colony was treated individually rather than being categorised into groups. The burrow data collected in this study were assessed for normality using the Anderson-Darling test. The data were normally distributed therefore a General Linear Model (GLM) was used to conduct a two-way ANOVA to compare burrow characteristics between different seasons and different colony sizes. The Tukey’s method was used to specify a 95.0% confidence level. Previous analysed fractal dimension data used in Le Comber *et al.* (2002) were compared to the fractal dimension results of this study using a non-parametric Mann Whitney *U* test. All statistical analyses were conducted in Minitab 16 (Minitab 16 Statistical Software, 2010).

Results

Animals

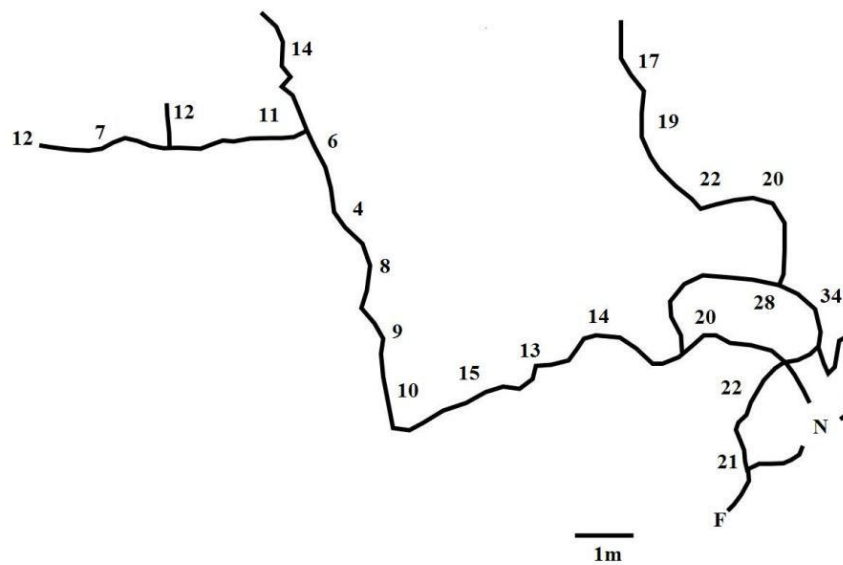
A total of 77 animals were caught from 15 burrow systems. The number of animals caught per burrow system varied both in winter and summer (Table 1). Colony size ranged from one (presumed) 'dispersing' animal to 12 animals (\bar{x} 5.13 \pm 2.97 SD). The ratio of males to females varied ranging from a 1:1 ratio to a 9:3 ratio (female: male). In summer juveniles and young were present in 22% of colonies. One female was pregnant and gave birth whilst in captivity to two young during the colony capture period. There were two lactating females each with two young from two separate colonies.

Burrow systems

In both seasons, burrow systems generally had one or two main deep central tunnels that connected to the nest area and a varying number of shallow foraging tunnels (winter Figure 1a and 1b; summer Figure 2a and 2b). Burrow systems had a varying number of chambers (nest, latrines and food stores) and bolt holes (Table 1). 78% of summer burrows contained nests compared to 83% of winter burrows. Nests were often located in the centre of the burrow system with more than one tunnel connecting the nest chamber to the rest of the system the largest nest found was 60cm x 45cm x 30cm in dimension and had 13 connecting tunnels on four different levels. Only 22% of burrow systems in summer contained food stores compared to 83% of winter burrows. The food within the store appeared to be all white clover bulbs with husks intact. The bulbs were packed into old foraging tunnels with soil.

Figure 1

Burrow systems of (a) a colony of 4 (burrow length 21.9m, fractal dimension 1.107) and (b) a colony of 10 *C. h. hottentotus* (burrow length 510.7m, fractal dimension 1.293) during the winter in Darling, Western Cape, South Africa. Numbers indicate the burrow depths (cm)

(a)

(b)



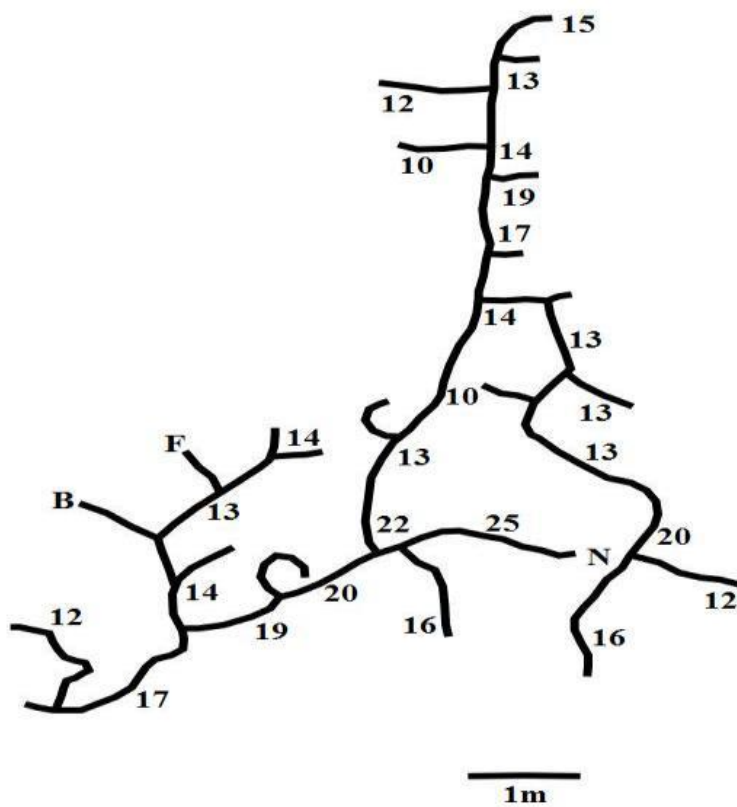
Table 1
Burrow characteristics of *C. h. hottentotus* colonies in winter and summer

Season	Number of occupants	Burrow length (m)	Burrow area (m ²)	Fractal dimension	Mound number	Old mounds	Fresh mounds	Branch number	Depth (cm)	Tunnel height	Tunnel width	Foraging tunnel (%)	Nest	Food store	Bolt hole
Summer	6	32.6	84	1.087	1	0	1	16	14.1	5.9	5.8	89	1	0	1
Summer	1	13.2	7	1.049	1	0	0	4	15.4	7	7	90	0	0	0
Summer	2	14.3	9	1.073	2	2	0	10	12.7	6.8	6.5	100	1	0	1
Summer	5	29.8	216	1.27	3	3	0	13	14.1	7.1	7.7	78	1	0	1
Summer	12	41.6	35	1.24	1	1	0	24	23.1	7.2	7.2	60	1	1	1
Winter	8	278.1	1911	1.261	79	56	23	64	12	7.1	6.5	91	1	1	0
Winter	2	10	8	1.174	2	0	2	3	12.1	5.1	4.3	95	0	0	0
Winter	4	21.9	38	1.107	16	6	10	9	11.9	6.5	5.4	79	1	1	0
Winter	10	510.7	35020	1.293	798	465	333	165	12.6	6.3	5.8	82	1	2	1
Winter	5	37.5	113	1.086	63	54	9	6	14.9	7.4	5.8	90	1	1	1
Winter	4	31.7	80	1.106	52	41	11	4	9.5	5.3	4.9	100	1	1	0
Summer	4	24.8	35	1.209	4	4	0	17	11.8	5.8	5.6	86	1	0	0
Summer	4	11.9	9	1.151	1	1	0	11	12.2	5.8	4.9	100	0	0	1
Summer	6	41.4	88	1.218	1	1	0	20	14.8	5.8	5.3	91	1	1	2
Summer	4	18.3	36	1.138	3	0	3	19	8.9	6.1	5.6	100	1	0	0

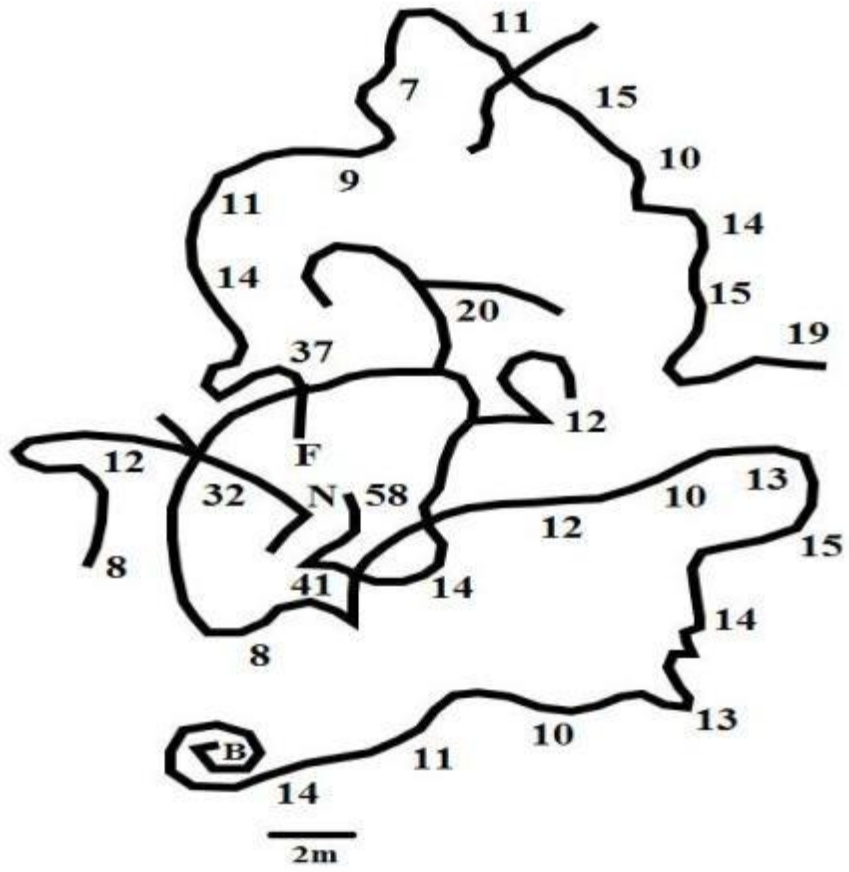
Figure 2

2 Burrow systems of (a) a colony of 4 (burrow length 24.8m, fractal dimension 1.209) and (b) a colony of 12 *C. h. hottentotus* (burrow length 41.6m, fractal dimension 1.24) during the summer in Darling, Western Cape, South Africa. Numbers indicate burrow depths (cm) measured from the roof of the burrow to the soil surface. N, F and B indicate nests, food stores and bolt holes respectively.

(a)



(b)



There were 22% more bolt holes present in summer burrows than in winter burrows. The longest bolt hole was 45cm in length. There were no latrines present in summer or in winter burrows. Burrow systems did not overlap with one another although they were located in the same field. Summer burrows had a mean distance of 273m between each other compared to 83m in winter. Back filled burrows were present in all burrows in both seasons but these were not excavated and measured as this study was investigating active working burrow geometry.

Seasonality

The length of the burrow systems differed significantly between the seasons with winter burrows being longer than summer burrows and almost significantly in the area encompassed ($F_{(1, 14)} = 19.96$ $P = 0.001$, $F_{(1, 14)} = 4.48$ $P = 0.058$, for length and area respectively). The burrow systems also differed significantly between seasons in the number of branches with summer burrow containing significantly more branches than winter burrows ($F_{(1, 14)} = 13.26$, $P = 0.004$), but did not differ in fractal dimension, burrow depth or in tunnel dimensions (Table 1). Overall the number of mounds produced did not differ between seasons. The mounds were split into old mounds and fresh mounds. The number of old mounds did not significantly differ between seasons ($F=2.38$, $P=0.183$) but the number of fresh mounds significantly differed ($F_{(1, 14)} = 18.05$, $P=0.008$) with burrows during winter having more fresh mounds (Table 1).

Occupancy

Burrow systems which were occupied by a larger number of animals differed significantly from burrows that were occupied by fewer individuals, being longer, ($F_{(1, 14)} = 67.53$ $P =$

<0.001) and covering a greater area ($F_{(1, 14)} = 10.85$, $P = 0.007$). Burrows which belonged to larger colonies also explored the surrounding environment more efficiently, as indicated by a higher fractal dimension value ($F_{(1, 14)} = 9.9$, $P = 0.009$), and had a greater number of branches within the burrow system ($F_{(1, 14)} = 39.1$, $P = <0.001$). Tunnel dimensions and tunnel depth did not differ significantly with the numbers of occupants within a burrow system. The number of animals within the burrow system had a significant effect on the amount of mounds present ($F_{(1, 14)} = 73.45$, $P = <0.001$). The number of individuals had an effect on the amount of old ($F_{(1, 14)} = 26.67$, $P = 0.001$) and fresh mounds produced ($F_{(1, 14)} = 586.79$, $P = <0.001$) with larger colonies producing larger amounts of mounds (Table 1).

Interactions

There were significant interactions between season and the number of animals occupying a burrow system for burrow length, burrow area and number of branches ($F_{(1, 14)} = 56.12$, $P = <0.001$; $F_{(1, 14)} = 10.8$, $P = 0.007$ and $F_{(1, 14)} = 28.39$, $P = <0.001$). There were no interactions for any of the other burrow characteristics.

Discussion

As predicted, the burrow characteristics in this study differed significantly between seasons. The greatest amount of habitat exploration and excavation took place in winter with burrow systems being longer and covering a greater area as has been found in, *F. mechowii* (Sichilima *et al.*, 2008), *B. suillus* (Thomas *et al.*, 2009) and *G. capensis* (Thomas *et al.*, 2012). This is most likely because during winter the soil is moist and friable and can be

worked easily in comparison to summer and burrows can be extended by the extrusion of mounds . Unfortunately in this study the seasonal data interacted with the colony size data therefore burrow length and burrow area cannot be attributed to either seasonal differences or colony size differences. In the previous study on *F. mechowii* interactions were not performed in the statistical analysis of the burrow data. Habitat exploration (as defined by the fractal dimension value) did not differ between seasons, but did differ with the numbers of occupants within a burrow system. Burrow systems with larger number of occupants explored the surrounding underground environment more efficiently than burrows occupied by a few individuals.

Previous studies investigating fractal dimensions of mole-rat burrow systems have primarily focused on associations between environmental characteristics (namely seasonal differences) and burrow structure (Spinks & Plaganyi, 1999; Sumbera *et al.*, 2003, 2012; Sichilima *et al.*, 2008; Thomas *et al.*, 2009; 2012). The current study indicates that relatively low fractal dimensions were found both in winter and summer in a mesic region. The only other study analysing fractal dimensions of *C. h hottentotus* burrows (Le Comber *et al.*, 2002) showed four burrow systems of *C.h. hottentotus* from an arid region having similar fractal values (1.29 - 1.42) as the burrows in our study. Three burrows from the same area (Darling) as our study had significantly higher fractal values ($U = 51$ $P = 0.0092$) (1.4, 1.51 and 1.62) (Le Comber *et al.*, 2002) than our study, suggesting that intra specific variation in burrow characteristics may depend upon other environmental factors which are not associated with seasonal variation. High fractal dimensions in *Heliophobius argenteocinereus* have been correlated with body mass (Sumbera *et al.*, 2008) but this is not the case in this study as *C. h. hottentotus* is a social mole-rat with a division of labour.

We found that more mounds were produced in winter than in summer. This does not necessarily equate to the fact that burrowing does not occur during summer, because disused tunnels are back-filled rather than the spoil being expelled as a mound (Skliba *et al.*, 2009; 2010). Mounds are produced less frequently during summer as the transport of soil from the burrow to the surface involves manipulating the soil vertically which is more energetically expensive than back filling disused tunnels. It appears that adverse winter weather conditions (ground frost and heavy precipitation) do not inhibit mound production (H. Thomas, pers. obs). A possible factor that may affect mound production in summer is the environmental temperature the mole-rats would be exposed to pushing soil to the ground surface as there is very little temperature fluctuation below 30cm Thomas *et al.* (2009) . The common mole-rats in Darling appear to be able to withstand cold conditions over hot conditions (H. Thomas, pers. obs). We also found no difference in the proportion of foraging tunnels produced in winter compared to summer, which suggests that mole-rats forage during all seasons (Skliba *et al.*, 2009) and may not need to rely on food stores or caches, although there were a greater number of food stores present in the winter burrow systems. In agreement with this observation, Sichilima *et al.* (2008) found fewer food stores in summer than in winter which suggests that mole-rats may use the food stores in spring during the breeding season. The food storage method could be dependent upon food availability as *C. h. hottentotus* have been found to farm geophytes (Spinks *et al.*, 2000) yet there was no evidence of geophyte farming but rather they tended to create typical food storage areas as in Thomas *et al.* (2009; 2012).

In conclusion, our hypothesis that differences in burrow structure occur between seasons was generally supported, but the seasonal data for burrow length, area and branch number were

influenced by the interaction of colony size. In summer it is presumed that mole-rats were unable to produce mounds and extend burrow systems, presumably because it was too costly to transport the soil to the surface. Therefore the mole-rats resorted to back-filling, resulting in a change in location but the system remains the same size. Further research on the burrow structure of other social species of mole-rat for both winter and summer seasons would help elucidate the factors that affect burrow dynamics, colony size, foraging behaviour and their interactions in a mesic environment.

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