Seasonal effects on digging activity and burrow architecture in the Cape dune mole-rat, *Bathyergus suillus* (Rodentia: Bathyergidae)

H.G. Thomas[1]*, P.W. Bateman[1,2], M. Scantlebury[1,3] & N.C. Bennett[1]

[1]*Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa*

[2]*School of Veterinary and Biomedical Sciences, Murdoch University, Murdoch WA 6150, Australia*

[3]*School of Biological Sciences, Queen's University Belfast, BT9 7BL, Northern Ireland, U.K.*

Most polygynous male mammals exhibit little or no parental care or involvement raising young. Instead, they invest indirectly in their own morphological and physiological attributes which enhance their chance of reproduction. Such secondary morphological sex traits may contribute to differences in the burrow architecture of fossorial mammals, such as the Cape dune mole-rat, *Bathyergus suillus*. Indeed, little is known about the seasonal changes in burrow architecture or differences in burrow configuration may differ between the sexes of subterranean African mole-rats (Bathyergidae). We excavated burrow systems of male and female *B. suillus* during the summer and the winter to investigate whether male burrow architecture reflected putative mate-seeking behaviour. We consider burrow geometry in response to mating strategies. Male burrow systems explored the environment more efficiently than females. This is presumably because of the increase in associated energetic costs of being a large male. Males produce more mounds indicating territorial behaviour even when it is energetically costly to dispose of soil onto the surface when the soil is less friable during the summer. Overall tunnel dimensions did not differ between the sexes. It appears that a change in season does not affect the geometry of the burrow system or tunnel dimensions in a climatically buffered environment.

Key words: burrow structure, seasonality, sexual selection, mate choice, energetics.

INTRODUCTION

Fossorial and subterranean species such as golden moles (Chrysochloridae), marsupial moles (Notoryctidae), true moles (Talpidae), gophers (Geomyidae), tuco tucos (Ctenomyidae), and mole-rats (Spalacinae and Bathyergidae) offer ideal taxa in which to investigate reproductive investment (Nevo 2000). They inhabit a niche environment that although climatically stable and primarily isolated from predators is energetically more expensive to travel below ground than above (Vleck 1979). Furthermore, they leave behind a semi-permanent record of their past movements in the form of underground burrows.

The expansion of an established burrow system should be associated with factors that reduce energetic output or enhance the benefits derived from the extension of the burrow. Most burrowing activity of subterranean species occurs when there is increased soil moisture levels making the soil friable (Miller 1957). Other factors influence burrowing patterns seasonally such as the acquisi-

tion of mates and patterns of foraging (Miller & Bond 1960; Hickman & Brown 1973). For example, habitat exploration in the social mole-rat (*Fukomys mechowii*) increases in efficiency during the rainy season compared to that of the dry season (Sichilima *et al*. 2008). Yet, in the solitary species (*Heliophobius argenteocinereus*) burrows become more reticulated as aridity increases, suggesting an increased efficiency in exploring the surrounding environment with a reduction in rainfall (Sumbera *et al*. 2003). One theory expounded for the seasonal expansion of burrow systems draws on the Aridity Food Distribution Hypothesis (AFDH) which has been originally put forward to explain how social species manage to survive in arid regions (Jarvis 1978; Jarvis *et al*. 1994). It posits that sociality evolved in mole-rats due to the clumped distribution of food resources and the greater energetic costs of acquiring these resources in areas where rainfall is sporadic.

The Cape dune mole-rat (*Bathyergus suillus*) is the largest truly subterranean rodent (up to 2.5 kg) (Jarvis & Bennett 1991; Kotze *et al*. 2006), with

*Author for correspondence. E-mail: hgthomas@zoology.up.ac.za

males being significantly larger (Davies & Jarvis 1986; Kinahan *et al.* 2007). *Bathyergus suillus* is limited in its distribution to the sandy loams of the southern and western Cape Provinces, South Africa, possibly due to the high energetic costs of excavation using its enlarged mole-like forepaws (Bennett & Faulkes 2000). The Cape dune mole-rat exhibits a polygynous mating system with minimal courtship and advertisement of sex by seismic drumming (Bennett & Faulkes 2000; Kinahan *et al.* 2008). Breeding is seasonal and the onset of the rains in winter stimulates males to extend their burrow systems in search of mates (Hart *et al.* 2006).

The costs of reproducing may be divided into ecological and physiological costs (Kunz & Orrell 2004). The ecological costs centre around reproductive turnover within a population (Randolph 1977). Physiological costs, on the other hand, can be either 'direct' or 'indirect'. Direct costs include the energetic and nutrient requirements of reproducing and the morphological changes that are necessary for acquiring such demands. Indirect costs of reproduction result from minimizing aspects of the animal's physiology to enable greater investment into reproduction. Energetic investment into reproduction tends to show considerable inter-sexual difference with males investing less energy into reproduction than females (Thomas *et al.* 2009). Instead, their energetic investment is often territorial and hierarchical and is utilized in searching for and the acquisition of mates (Gittleman & Thompson 1988). Male reproductive effort may be 'indirect' because they invest in secondary sex traits to enhance the likelihood of mate acquisition such as larger body size, greater bite force or more elaborate ornaments rather than in offspring production *per se* (Clutton-Brock & Vincent 1991; Clutton-Brock & Parker 1995). In solitary species, due to their behavioural and reproductive differences, males generally attempt to occupy territories with a high female density whereas females appear to be resource based and locate themselves in areas of high food productivity (Macdonald 1983).

Despite the valuable insight into the evolution of sexual differences in energetic investment and its relationship between seasons in subterranean mammals the burrow structure of *B. suillus* remains poorly recorded, with only a few studies focused on this species. Only one study examining the burrow systems of *B. suillus* has investigated the burrow geometry between the sexes (Thomas *et al.*

2009) but, this was only recorded during the winter season. The remaining studies on the burrow systems of *B. suillus* have not investigated differences with regard to the sex of the occupant, were limited in sample size and made no comparisons between seasons (Schultz 1978; Davies & Jarvis 1986). The objective of this study was, therefore, to describe the burrow systems of both male and female *B. suillus* during the winter (wet) and summer (dry) seasons. Sexual selection predicts that architectural differences in burrow structure should exist due to the behaviour of males seeking mates during the breeding season (winter). We therefore hypothesized that the burrow systems of males and females would show differences in geometry that will reflect male mate seeking behaviour during winter but not during the summer. We further expected males to show increased habitat exploration and greater efficiency in burrowing activity. We predicted that male burrow systems in winter would: (1) be longer and cover a greater area; (2) have a higher fractal dimension (a measure of habitat exploration efficiency); (3) have more mounds than females indicating increased burrowing activity; (4) contain proportionally more shallow foraging tunnels to fuel mate seeking behaviour compared to that of summer burrow systems. In contrast, we predicted that female burrows in winter would: (1) be longer and cover a greater area and (2) have a lower fractal dimension (a measure of habitat exploration efficiency).

METHODS

Study animals

The genus *Bathyergus* is closely related to two other solitary mole-rat genera, *Heliophobius* and *Georychus* (Honeycutt *et al.* 1991). *Bathyergus suillus* is the largest of the bathyergids and is endemic to the fynbos region of South Africa (Davies & Jarvis 1986) and occurs sympatrically with two other species of mole-rat (*Georychus capensis* and *Cryptomys hottentotus hottentotus*). It is found predominantly in sandy soils and exhibits an overall more catholic diet when compared to other bathyergids, supplementing its diet with above-ground grass and forbes as well as underground storage organs or geophytes (Bennett & Jarvis 1995).

Study site

The study was carried out in the winter (July 2008, 2009 and 2010) and summer (February 2009

and 2010) seasons in the coastal fynbos biome near the town of Darling in the southwest of the western Cape Province, South Africa (33°3833'S, 18°3833'E). The study site comprised four large agricultural fields used for grazing livestock. Site A (*c.* 1500 ha) was the largest of the sites and consisted of a level field with even distribution of vegetation (*Lolium perennae* and *Trifolium repens*). Site B (*c.* 900 ha) ran parallel to a railway track and consisted of evenly distributed vegetation (*L. perennae* and *T. repens)* with scattered bushes and trees (*Eucalyptus globulus*). Site C (*c.* 750 ha) consisted of a large hill with an adjacent small marsh with reed beds, and was used during winter as Site D was prone to flooding during this season. Site D the smallest of the four fields (*c.* 500 ha) consisted of a level field with an even distribution of vegetation (mostly *L. perennae,* rye grass and *T. repens*). The soil in sites A and B comprised a mixture of clay and sandy loam and sites C and D consisted of sandy loam (Thomas *et al*. 2009). Active burrow systems were identified by the location of fresh mounds on the surface. Animals were captured using modified Hickman live traps (Hickman 1979) baited with sweet potato. Traps were checked every two hours in winter during daylight and left overnight. Traps were checked every hour during the summer daylight hours to prevent the animals suffering from heat stress. A total of 23 animals were caught: six animals at site A (summer; three females), (winter; one female, two males), six animals from site B (summer; one male, one female), (winter; two females, two males), six animals from site C (summer; one female, two males), (winter; two females, one male) and five animals from site D (summer; two males), (winter; two females, one male). On capture, mole-rats were sexed, weighed (±0.1g Sartorius balance, Epsom, Surrey, UK), euthanized with diethyl ether and taken to the University of Pretoria (University of Pretoria ethics number AUCC 040702/015).

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 23 burrows were excavated (10 for summer and 13 for winter). The lengths of the tunnels and their dimensions and shape were recorded *sensu* Thomas *et al*. (2009, 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) or shallow, foraging (<20 cm) tunnels. The distinction between tunnel usages were determined by the depth of the bulbs and roots of the plants in the localities reached. Tunnels were defined as arched if the ratio of the tunnel height divided by the tunnel width exceeded 1.4 or circular if not (Thomas *et al.* 2009). A map of each burrow system was recorded relative to magnetic north and later digitized. Tunnel depths were recorded approximately every 2 m and the location and dimensions of any nests, food stores, bolt holes and latrines were recorded. Nests were defined as chambers with only a single entrance and 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 potentially used as anti-predatory escape sites, thermoregulation or as drainage sumps (Hickman 1990; Nevo 1999). Latrines were blind-ended tunnels packed with soil and faeces. The position and ages of the mounds were recorded as in Thomas *et al*. (2009).

Once digitized using a scalable vector graphics (SVG) imaging package, 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 (LeComber *et al*. 2002; LeComber, Seabloom & Romañach 2006). An increasingly complex burrow system is characterized 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 23 burrow systems in this study were calculated using the Fractal Dimension Calculator V 1.2 2010 program as used in Thomas *et al*. (2012), which is designed to assist with the application of the 'box counting' method as in LeComber *et al*. (2002) for determining the fractal dimension of a structure.

Statistics

General linear models (GLM) were used to analyse differences in burrow characteristics in summer and winter, between sexes and to investigate any interactions between season and sex. A principal components analysis (PCA) was used to

Table 1. External morphometric measurements taken of *Bathyergus suillus* in Darling, Western Cape, South Africa.

Ref.	Season (0=winter, 1=summer)	Site	Sex (0=female, 1=male)	Body mass (g)	Body length (cm)	Zygomatic arch width (mm)	Head Length (mm)	Tail length (mm)	Hind foot length (mm)
Suillus 2	1	A	0	664	23.5	34	45.3	39	43
Suillus 1	1	A	0	1963.8	34.7	33	46.2	36	45
S31	1	C	0	766.6	25.9	32	43.3	32	44
S32	1	B	0	542.4	22.6	30	38.9	33	47
S42	1	B	1	497.9	21.7	30	37.7	34	48
Suillus 5	1	C	1	892	30.87	45	59.9	40	44
Suillus 4	1	C	1	1147	36.54	48	60.8	37	43
Suillus 3	1	D	1	936.6	32.74	44	60.1	35	49
S33	1	D	1	1113.9	34.4	49	64.3	36	44
S41	1	A	0	752.9	24.3	30	32.4	37	43
S21	0	B	0	725	23.5	30	33.8	33	46
S22	0	C	0	735	24	31	35.9	34	44
S6	0	D	0	477	21	28	34.2	35	47
S3	0	A	0	774.1	25.7	30	36.5	37	45
S4	0	B	0	983.9	28	31	39.2	39	44
S5	0	C	0	1055.5	29	31	38.6	41	45
S7	0	D	0	444	21	28	32.4	34	46
S23	0	A	1	895.1	25.6	36	42.1	38	48
S24	0	B	1	694.7	22.3	34	40.6	37	42
S25	0	C	1	899.6	26.1	37	43.2	36	40
S1	0	A	1	662.2	25.5	33	44.9	35	42
S2	0	B	1	561.4	25.5	33	47.6	33	41
S8	0	D	1	507.7	26.8	32	46.5	32	46

examine differences between the sexes in external morphology. All statistical analysis was conducted in Minitab 16 (Minitab 16 Statistical Software, 2010).

RESULTS

Animals

A total of 23 animals were caught from the four different trapping areas. Eleven male and 12 female burrow systems were excavated. All animals caught were adult (presence of all four cheek teeth, van Rensburg *et al*. 2004). No females were obviously pregnant or lactating. Body mass ranged from 444 g to1963.8 g for females and from 497.9 g to 1147 g for males. Females had the smallest body length, ZAW, head length and tail length, but males had the smallest HFL (Table 1). Males had significantly longer heads than females ($U = 181$, $P = 0.0028$) with significantly larger zygomatic arch widths than females ($U = 184$, $P = 0.0015$) (Table 2).

A PCA of logs of morphological data revealed a size axis accounting for 61% and a shape axis accounting for 18.3% of variation (Fig. 1). The bivariate plot indicates size and shape vary the most in males but not significantly in females. The PCA revealed that factor one describes a variation gradient based primarily on body length and factor two describes a variation gradient based primarily on hind foot length.

Burrow systems

Burrow systems generally had one or two main deeper central tunnels that connected to a varying number of shallow foraging tunnels for females (Fig. 2a) and males (Fig. 2b) in winter and in summer (Fig. 3a and Fig. 3b for females and males, respectively). Burrow systems had a varying number of chambers (nests, latrines and food stores) and bolt holes (Table 3). Nests were fairly limited but present in both sexes. Latrines were only present in female burrow systems. Food stores and bolt holes were not present in any of the burrow systems excavated. Burrow systems did not overlap with each other even when in the same field site. Nests were located in small oval chambers that were 10–20 cm deeper than the connecting tunnel. Nests were all blind-ended with a single entrance. Nesting material comprised

Table 2. External morphometrics (mean and standard deviation) for *Bathyergus suillus*. *U*- and *P*-values denote results of a Mann Whitney test examining differences between males and females ($n1 = 11$, $n2 = 12$).

	Male		Female		*U*	*P*
	Mean	S.D.	Mean	S.D.		
Body mass	800.7	229.9	824	402	138	0.735
Body length	28	4.9	25.27	3.85	154	0.1858
Head length	49.79	9.56	38.06	4.79	181	0.0028
Zygomatic arch width	38.27	6.9	30.667	1.775	184	0.0015
Tail length	35.727	2.284	35.833	2.823	132.5	1
Hind foot length	44.273	0.925	44.917	1.379	119	0.4417

mainly of dried grasses and other dried foliage from forbes. Latrines were located in disused foraging tunnels >25 cm deep and faecal matter was packed with soil.

Seasonality and sex differences

Winter burrow characteristics did not significantly differ from summer burrows (Table 4). Although the burrow length and burrow area of males and females were not significantly different, the reticulation of the burrow systems and thus, the fractal dimension of the burrow systems differed significantly between sexes ($F = 9.41$, $P = 0.015$). Males produced significantly more mounds than females ($F = 7.63$, $P = 0.025$) and of the mounds produced males significantly had more old mounds present along their burrow systems than the females ($F = 16.49$, $P = 0.004$). There were no other sex differences in burrow geometry (Table 4). There were

also no interactions between season and sex with respect to burrow geometry (Table 4).

DISCUSSION

Mole-rats provide an ideal model group to investigate theories of sexual selection and energetics of mate choice. They have a truly subterranean lifestyle and rarely, if ever, come to the surface (Bennett & Faulkes 2000). They also inhabit an environment that is largely protected from predators and is thermally stable but is energetically expensive to create and maintain (Nevo 1979; Bennett *et al.* 1988). They excavate their burrow systems by moving substrate using enlarged forelimbs which they then push up to the surface to create mole-mounds when energetically possible. This method of burrow extension and excavation can be up to 3400 times as energetically expensive to travel a set distance as it is to travel the same
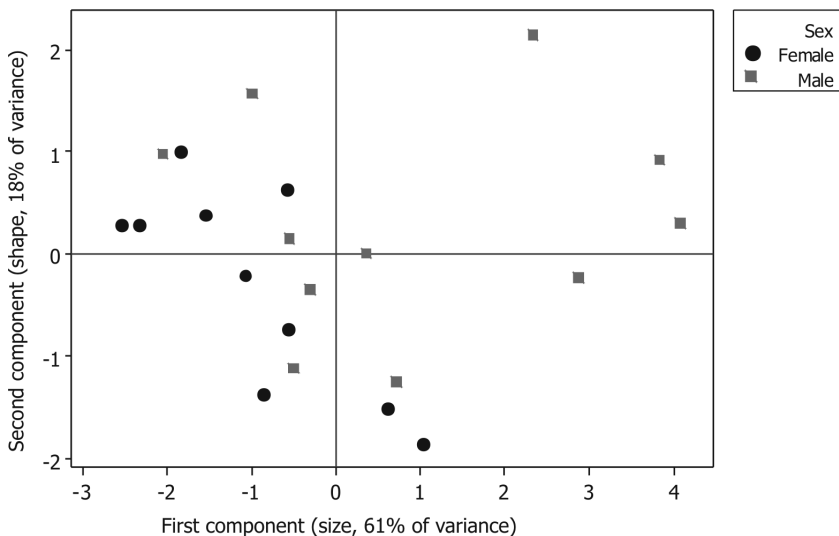

Fig. 1. Bivariate plot of PCA on morphological characteristics of male and female *Bathyergus suillus* showing the first two principal components of log transformed morphological data.
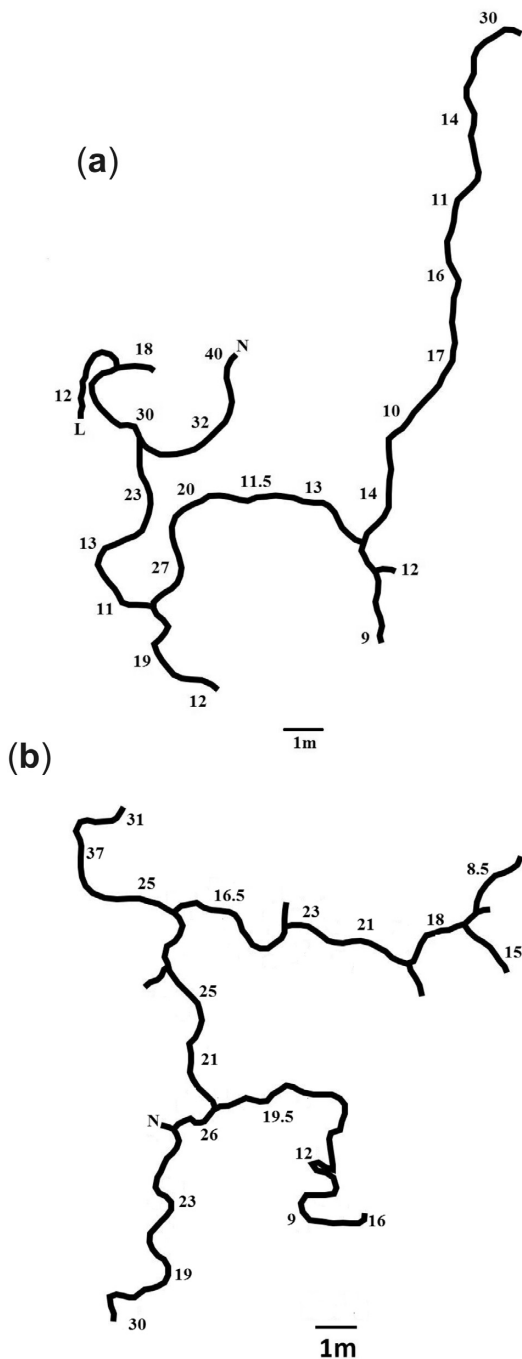
Fig. 2. **a**, Burrow system of a single female *Bathyergus suillus* at the study site in Darling, Western Cape, South Africa in winter. **b**, Burrow system of a single male *Bathyergus suillus* at the study site in Darling, Western Cape, South Africa in winter. Numbers indicate burrow depths (cm) measured from the top of the burrow to the soil surface. Nests and latrines are indicated by N and L.
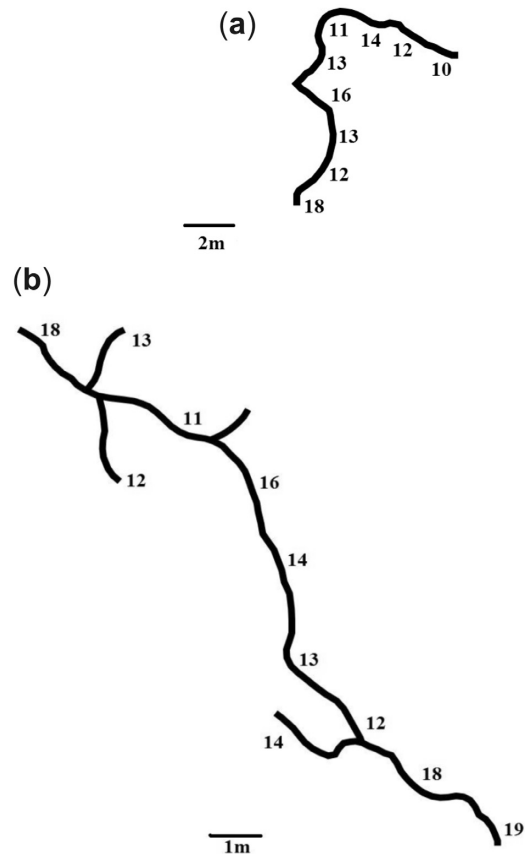

Fig. 3. **a**, Burrow system of a single female *Bathyergus suillus* at the study site in Darling, Western Cape, South Africa in summer. **b**, Burrow system of a single male *Bathyergus suillus* at the study site in Darling, Western Cape, South Africa in summer. Numbers indicate burrow depths (cm) measured from the top of the burrow to the soil surface.

distance on the surface (Vleck 1979). In this current study we showed a range of differences in the burrow architecture of the Cape dune mole-rat between the sexes and across seasons (winter and summer).

It is presumed that male mole-rats increase their burrowing activity during winter breeding season when they seek mates (Herbst et al. 2004; Hart *et al.* 2006). Burrow lengths in pocket gophers and tuco tucos differ between sexes, with the burrow lengths of males being longer than females (Reichman *et al.* 1982; Gastal 1994). It has been proposed that this may be due to active mate seeking behaviour. In the closely related *Bathyergus janetta*, burrow length was greater in males than those of females supporting the notion that males seek out females (Herbst & Bennett 2006). The only study to

Table 3. Burrow characteristics of *Bathyergus suillus*. Mean and standard deviation (S.D.) of male and female burrow systems in winter and summer.

	Males (winter)		Females (winter)		Males (summer)		Females (summer)	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Burrow length (m)	71.37	51.28	43.15	11.97	16.89	12.44	28.62	15.4
Burrow area (m²)	1292.99	1339.82	382.24	350.78	37.97	48.32	158.63	96.48
Fractal dimension	1.14	51.07	1.09	0.05	1.05	0.02	1.13	0.04
Mound number	72.17	27.36	34.43	12.39	59.25	65.37	34.5	39.2
Old mounds	42.17	29.41	19	10.28	6.5	4.44	32	38.48
Fresh mounds	30	8.78	15.43	16.9	1.5	4.09	2.5	0.89
Branch number	9.33	6.38	4.57	3.1	25.55	6.01	6.5	2.7
Depth (cm)	26.83	2.56	24.86	7.23	14.39	3.1	31.59	5.83
Tunnel height (cm)	13.17	4.05	12.95	2.08	13.29	3.21	16.68	1.39
Tunnel width (cm)	15.48	23.32	16.76	3.74	18.75	32.86	15.95	1.62
% of arched tunnels	23.75	10.98	23.74	20.63	81.25	32.86	42.5	20.22
% of round tunnels	76.25	10.98	76.26	20.63	30.5	41.28	57.5	20.22
% of shallow tunnels	33.38	0.41	41.01	22.7	69.5	14.72	19.9	14.93
% of deep tunnels	66.62	0.45	58.99	22.7	69.5	14.72	80.1	14.93
Nests	0.17	0.41	0.29	0.49	0.25	0.45	0.25	0.5
Food stores	0	0	0	0	0	0	0	0
Latrines	0	0	0.43	0.53	0.25	0.45	0	0
Bolt holes	0	0	0	0	0	0	0	0

previously investigate the difference in burrow length between the sexes in *B. suillus* (Thomas *et al.* 2009) also reported putative mate seeking behaviour in males. However, results from the current study fail to support this suggestion. Thomas *et al.* (2009) also showed increased habitat exploration efficiency by males as indicated by an increase in male fractal burrow dimension (LeComber *et al.* 2006) during the breeding season, which our study supports, but also in our study males have a greater fractal dimension in summer as well as in winter. In the social giant mole-rat, *Fukomys mechowii,* burrow length was not found to differ with season, but fractal dimensions differed between seasons (Sichilima *et al.* 2008). This finding was not supported in our study, since the

Table 4. Burrow characteristics of *Bathyergus suillus*. *F*- and *P*-values denote results of a General Linear Model examining the effects of season.

	Sex			Season			Sex × season		
	d.f.	F	P	d.f.	F	P	d.f.	F	P
Burrow length	1	4.04	0.079	1	3.11	0.116	1	0.11	0.745
Burrow area	1	4.29	0.072	1	3.12	0.115	1	0.89	0.373
Fractal dimension	1	9.41	0.015	1	0.24	0.635	1	0.04	0.838
Mounds	1	7.63	0.025	1	0.15	0.709	1	0.38	0.554
Old mounds	1	16.49	0.004	1	1.01	0.345	1	3.85	0.085
Fresh mounds	1	1	0.346	1	2.07	0.188	1	0.42	0.537
Depth	1	0.27	0.617	1	0.31	0.596	1	0	0.965
Branch number	1	3.4	0.102	1	0.23	0.641	1	0.09	0.775
Tunnel height	1	3.44	0.101	1	0.08	0.782	1	0.42	0.535
Tunnel width	1	4.12	0.077	1	1.48	0.259	1	0.93	0.362
Arched tunnels	1	1.11	0.323	1	0.78	0.404	1	0.11	0.745
Round tunnels	1	1.11	0.323	1	0.78	0.404	1	0.11	0.745
Shallow tunnels	1	0.46	0.516	1	0.98	0.351	1	0	0.977
Deep tunnels	1	0.46	0.516	1	0.98	0.351	1	0	0.977
d.f. error	8			8			8		

fractal dimensions were not significantly different between seasons. Fractal dimensions were also investigated in the solitary *Heliophobius argenteo-cinereus* between seasons (Sumbera *et al.* 2003) and showed the more arid the environmental conditions were, the more reticulated the burrow architecture and therefore the higher the fractal dimension. In our study the fractal dimensions did not differ in the burrows between seasons suggesting that the search for mates by males is on-going rather than seasonal. Our study shows that there is no seasonal effect of burrow length and therefore burrow area. This contradicts the investigations conducted in two other species of mole-rat, the social *Cryptomys hottentotus hottentotus* (Thomas *et al.*, unpubl. data) and the solitary *Georychus capensis* (Thomas *et al.* 2012).

Our study indicates that males produce more mounds than females suggesting that males are constantly reworking their burrow systems and patrolling their territory. Despite being large our study suggests that it is not too energetically expensive to produce mounds, although back-filling disused tunnels may reduce energetic costs, during the summer months when the ground is hard. The only previous study that examined tunnel dimensions (Thomas *et al.* 2009) in relationship to the sex of the occupant of the burrow did not reveal any correlation between tunnel height and the sex of the mole-rat; this was further supported by our study.

Bathyergus suillus has been reported as sexually size dimorphic with males being significantly larger than females (Davies & Jarvis 1986; Kinahan *et al.* 2007). This notion is supported in this study only by head length and zygomatic arch width. However, in the case of body mass the animals may have not have been up to maximum body mass due to harsh summer weather conditions after a previous unproductive winter.

Our hypothesis that there are differences in burrow geometry between males and females in *B.suillus* was only partially supported. Males tended to explore the surrounding environment more efficiently than females. One possibility may be that males are actively seeking females despite the season or that males are more efficiently exploring the environment for food resources due to greater energetic costs of burrowing as a result of being larger than females. Our hypothesis that differences in burrow structure are seasonal was also partially upheld, this is believed to be in accordance with the predictions of the AFDH.

More research on the energetic costs of being a large, sexually dimorphic subterranean species would be useful in identifying the constraints of living in an underground habitat.

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