

Season but not sex influences burrow length and complexity in the non-sexually dimorphic solitary Cape mole-rat (Rodentia: bathyergidae)

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Abstract

Little is known about how environmental factors such as season influence burrowing activity, burrow structure or reproductive behaviour in subterranean mammals. We excavated burrow systems of male and female *Georychus capensis*, a solitary, subterranean rodent, in winter (wet season) and summer (dry season) to investigate whether any seasonal differences due to putative mate-seeking behaviour of males were apparent. Burrow structure did not differ between sexes, but did differ between seasons. For both sexes, summer burrows were shorter in length and covered a smaller area but explored the surrounding environment more efficiently than did winter burrows. Summer burrows had fewer mounds present indicating less expansion of the burrow systems in this season. We discuss these differences in exploration and use of the environment between seasons but not between sexes in terms of mating strategies

of *G. capensis* and observed levels of sexual dimorphism in our populations. This study supports recent concepts regarding female competition and selection that may favour the expression of female exaggerated traits, which affect a female's ability to acquire reproductive resources that often appear similar to that selected for by males.

Keywords

Burrow systems, seasonality, sexual selection, *Georychus*, mate choice

Introduction

Burrows offer shelter to fossorial and subterranean mammals (Reichman & Smith, 1990), but burrows that are only used for shelter are often simple in structure, i.e. little more than an entrance, a short tunnel and an expanded chamber as a nest (Kenagy, 1973). As more functions are incorporated into the role of a burrow, such as rearing offspring and storage of food, burrows tend to become more elaborate, with numerous side branches, latrines, nest chambers and food stores.

African mole-rats (Bathyergidae) vary in their degree of sociality, from solitary species (*Bathyergus*, *Georychus*, *Heliophobus*) through to social (*Cryptomys*, *Fukomys*) and eusocial representatives (*Fukomys*, *Heterocephalus*) (Jarvis & Bennett, 1990). This variation in sociality may be linked to both the aridity of the environment and the distribution of food resources contained within the home range (Bennett, 1988; Faulkes *et al.*, 1997; Lovegrove, 1991). All bathyergids are completely subterranean, living, feeding and mating in burrows of their own construction (Bennett & Faulkes, 2000). Like other subterranean mammals (e.g. Notoryctidae, Talpidae, Chrysochloridae, Geomyidae and Ctenomyidae) home ranges are generally

exclusive and defended except for brief periods during the breeding season (Nevo, 1979; Lacey, 2000). In general, the territories of males or females do not overlap, but partial overlap occurs between the sexes probably as a response to spatio-temporal changes of exploitable resources (Nevo 1979).

From limited data on burrow systems and burrow structure in subterranean rodents, the burrow architecture of African mole-rat shares many similarities with other fossorial species filling this specialised niche. The burrows comprise numerous long superficial foraging tunnels (15 – 35 cm deep), connected to a deeper, central, permanent system of chambers used for nesting, food storage, sanitation and retreat (Bennett & Faulkes, 2000; Thomas *et al.*, 2009). The shallower foraging tunnels make up 80 – 95% of a burrow system (Miller, 1957; Jarvis & Bennett, 1991).

Burrow dimensions vary across individuals, sex, age, and local habitat conditions (Lacey, 2000). Differences in burrow length may correlate with the availability of food and/or to the number of animals occupying a single burrow system (Jarvis & Sale, 1971; Hickman, 1979; Jarvis, 1985).

Bathyergid burrow length may be influenced by a number of factors including food supply (Jarvis & Sale, 1971; Reichman *et al.*, 1982; Heth, 1989; Rosi *et al.*, 2000; Spinks *et al.*, 2000), mate acquisition, (Thomas *et al.*, 2009), soil hardness (Heth, 1989), duration of occupancy (Brown & Hickman, 1973), energetic requirements (Heth, 1989), population density (Sumbera *et al.*, 2003; Sichilima *et al.*, 2008), food resource characteristics (Bennett & Faulkes, 2000) and body mass (Sumbera *et al.*, 2003). Extensive tunnelling by colonies of bathyergid mole-rats results in burrows

that, although hundreds of metres in length, structurally they generally retain a basic design and biomass ratio similar to those of solitary species living in more productive environments (Jarvis & Bennett, 1991). Thus, burrows constructed in unproductive habitats will tend to be longer to encompass larger foraging territories.

For species living in areas with marked wet and dry seasons, such as many of the African bathyergids, burrow architecture, within the same burrow system, may alter seasonally depending on a number of biotic and abiotic factors e.g. soil conditions, temperature and food distribution. In the solitary silvery mole-rat, *Heliophobius argenteocinereus* burrow architecture did not change between two periods within the dry season but the burrows had a higher fractal dimension (indicating increased burrow complexity) during the peak of the dry season probably indicating increased foraging (Sumbera *et al.*, 2003). In contrast, in the social giant Zambian mole-rat, *Fukomys mechowii*, burrow length did not differ between seasons but fractal dimension was greater in the rainy season than in the dry season indicating greater foraging efficiency (Sichilima *et al.*, 2008).

The Cape mole-rat (*Georychus capensis*) occurs sympatrically with two other species of mole-rat, the common mole-rat (*Cryptomys hottentotus hottentotus*) and the Cape dune mole-rat (*Bathyergus suillus*), in geophyte-rich areas of fynbos in the Western Cape Province of South Africa. *Georychus capensis* consumes a variety of vegetation which includes bulbs, corms and the aerial parts of plants (Du Toit *et al.*, 1985). *Georychus capensis* is a solitary mole-rat that digs extensive burrows systems using its incisors. *Georychus capensis* exhibit no signs of sexual size dimorphism with males and females having a mean body mass of 181g (max. of 360g) (Smithers,

1983). Although the Cape mole-rat does not exhibit sexual size dimorphism it does exhibit sexual differences in its method of communication via foot-drumming: males have a faster rate than females during breeding season (Bennett & Jarvis, 1988; Narins *et al.*, 1992).

The objective of this study was to examine the seasonal aspects of the spatio-temporal pattern of the burrow system in *G. capensis* in the Western Cape Province of South Africa during two seasons (a wet winter and dry summer). As seasonal change affects environmental factors, particularly the availability of food, soil characteristics and climate, which in turn is likely to affect burrowing ability, we predicted that summer burrow systems (i.e. when the ground would be drier and harder to excavate) would: (1) be shorter in length and cover a smaller area; (2) have a lower fractal dimension indicating poor environmental exploration; (3) have proportionally fewer mounds indicating a decrease in activity and (4) contain more deep semi-permanent tunnels to reduce energetic costs.

We also predicted that burrow structure would reflect mate-seeking behaviour (as shown in *Bathyergus suillus*; Thomas *et al.*, 2009) as sexual selection theory predicts there would be sex-differences in burrow structure and morphology due to the greater need of males to search for females during the wet winter (mating season) when burrowing conditions are optimal. We predicted that winter burrow systems of the male (i.e. when the soil is wetter and easier to excavate) would therefore: (1) be greater in length and cover a wider area; (2) have a higher fractal dimension; (3) have proportionally more mounds; (4) contain relatively more shallow foraging tunnels to fuel the extra burrowing activities. We predicted that morphology would differ

between males and females, with males exhibiting sexually dimorphic secondary sex traits to enable competition over mates.

Materials and methods

Study animals

Georchus capensis is a monotypic genus that appears to be most closely related to two other solitary mole-rat genera, *Heliophobius* and *Bathyergus* (Honeycutt *et al.*, 1991). *Georchus capensis* generally occurs in mesic areas that receive an average of over 500mm of rainfall per year. They are often found in sandy loams but are not commonly found in sandy areas inhabited by *B. suillus*. The Cape mole-rat has a russet pelage with characteristic black and white markings around the head and distinct white eye rings. There appears to be no sexual size dimorphism in this species, and they have an average body mass of 181g (Bennett, Jarvis & Davies, 1988).

Study site

The study was carried out in the winter (July 2009, July 2010) and summer (February 2010) seasons in the coastal fynbos biome near the town of Darling in the south-west of the Western Cape Province, South Africa (33°22 S, 15°25 E).

The study site comprised two large agricultural fields used for grazing livestock. Site A was the larger (c. 750 ha) and consisted of a large hill with an adjacent small marsh with reed beds, and was used during winter as Site B was prone to flooding during this season. Site B, the smaller of the two fields (c. 500 ha), consisted of a level field with an even distribution of vegetation (mostly *Lolium perennae*, rye grass and

Trifolium repens, white clover). The soil in both sites consisted of a sandy loam. 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 2 hours at site A and every 30 minutes at site B during daylight and left overnight. Traps were checked more frequently at site B due to high temperatures to prevent the animals suffering from heat stress. A total of 40 animals were caught: 18 animals at site A (winter) (2 males, 16 females) and 20 animals from site B (summer) (8 males, 12 females) and 2 animals from site B (winter) (1 male, 1 female). On capture, mole-rats were sexed, weighed (± 0.1 g Sartorius balance, Epsom, Surrey, UK), euthanized with chloroform 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 40 burrows were excavated (20 for winter and 20 for summer). The lengths of the tunnels and their dimensions and shape were recorded *sensu* Thomas *et al.*, (2009) for *B. suillus*. 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. A map of each burrow system was recorded relative to magnetic north and later digitised. Due to the shorter length of *G. capensis* burrow systems compared to *B. suillus* (Thomas *et*

al., 2009), tunnel depths were recorded approximately every 1m instead of every 2m 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 30cm in length used as anti-predatory function, thermo-regulation 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).

The locations of the burrow systems within the field were recorded to calculate inter-burrow system distances. Intra-burrow distance (distance between side branches of the same system) and inter-fork distance (distance between branching points) were also calculated (as in Reichman *et al.*, 1982). 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 (LeComber *et al.* 2002; LeComber, Seabloom & Romañach, 2006). 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 40 burrow systems in this study were calculated using the Fractal Dimension Calculator V 1.2 2010 program, 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. All 40 burrow diagrams were converted into Scalable Vector Graphics (SVG) representation by using Inkscape v 0.47 (2009), an open-source vector graphics editor to trace the outline of a burrow map scanned into a bitmap-based format (JPG). After loading the SVG file into the calculator, a minimum and maximum box size, the number of intervening box sizes to use in the calculation, the algorithm for choosing the intervening sizes (either evenly spaced, or logarithmically spaced such that the data points on the resulting graph are evenly spaced), the number of different grid orientations (angles) to try and the number of different positions of the grid to try for each combination of album and size (specified as the square root of the number of positions, so if the user specifies 3, then 9 different positions will be tested) were chosen based upon the complexity of the burrow diagram. This then calculates the fractal dimension of the diagram based on the options chosen.

Statistics

T-tests and a Principle Components Analysis (PCA) were used to examine differences between the sexes in morphology. Burrow data were log transformed and a general linear model was used to analyse the interactions between sex and season.

Results

Animals

A PCA of logs of morphological data revealed a size axis accounting for 50.8% and a shape axis accounting for 16.9% of variation (Fig 1). It is evident in the bivariate plot that size and shape differ in females but not significantly in males. The PCA revealed that factor one describes a variation gradient based primarily on body mass and hind

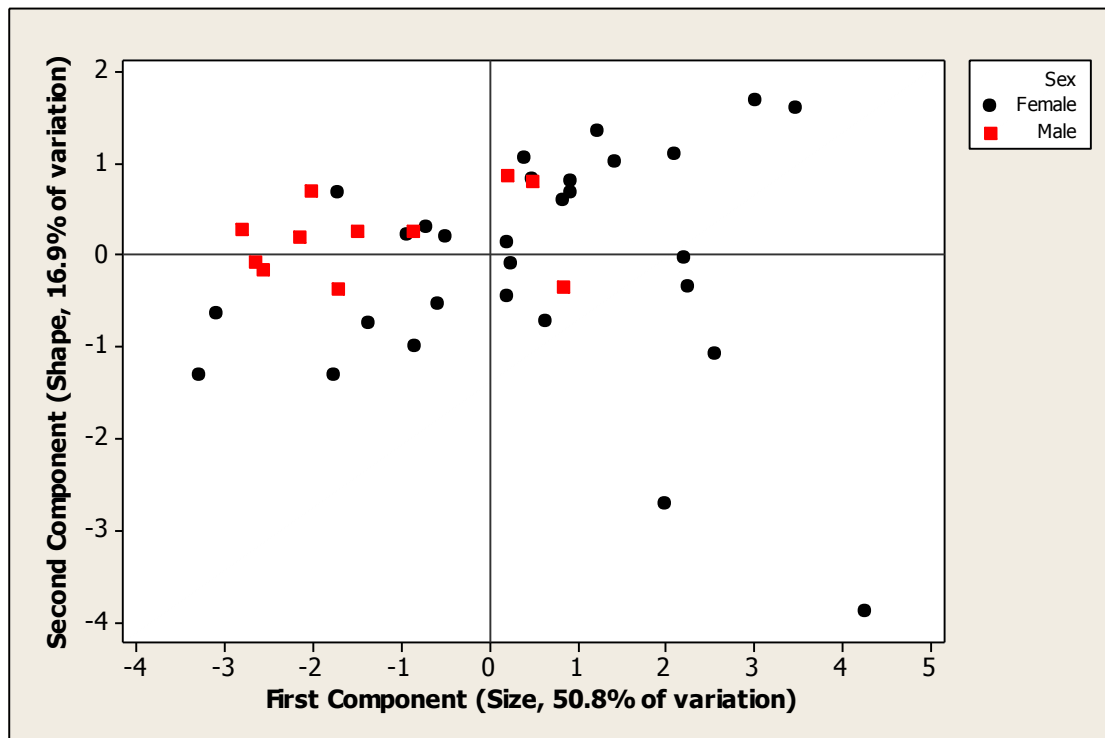


Figure 1 Bivariate plot of PCA on morphological characteristics of male and female *G. capensis* showing the first two principle components (PC) of log-transformed morphological data.

foot length and factor two describes a variation gradient based primarily on tail length (Table 1). Females have a larger mean body mass than males [182.5 ± 54.5 standard deviation (SD)] versus (149.5 ± 38.4) for females and males, respectively. Females have a significantly larger zygomatic arch width ($F = 8.139$, $P = 0.007$), with a mean width of 33.3 ± 5.4 SD for females and 31 ± 1.7 SD for males (Table 2).

Table 1 Factor scores (unrotated) for PCA on log-transformed morphological variables

Variable	PC1	PC2
Sex	-0.234	0.119
Body mass	0.46	0.248
Body length	0.453	-0.13
Head length	0.337	-0.383
ZAW	0.442	0.17
Hind foot	0.465	0.172
Tail length	-0.064	0.838
Eigen values	3.5543	1.1823
% of variance	50.8	16.9

Table 2 External morphometrics (mean and standard deviations) of *Georychus capensis*. *U* and *P* values denote the results of a Mann–Whitney *U*-test examining differences between males and females ($n_1 = 29, n_2 = 11$)

	Female		Male		<i>F</i>	<i>P</i>
	Mean	S.D	Mean	S.D.		
Body mass (g)	182.5	54.5	149.5	38.4	1.243	0.272
Body length (mm)	185	18.6	173.4	14.3	1.434	0.239
Head mass (g)	27.7	8.4	21.5	6.4	1.466	0.233
Head length (mm)	52.5	30.7	44.5	2.8	1.166	0.287
Zygomatic arch width (mm)	33.3	5.4	31	1.7	8.139	0.007
Tail length (mm)	14	5.4	13.2	3	5.237	0.028
Hind foot length (mm)	26.3	2	25.6	2.2	0.145	0.705

Burrow systems

A total of forty burrow systems were excavated (11 males, 29 females): three male and 17 female burrow systems for winter and eight male and 12 female burrow systems for summer. There were no significant differences between male and female burrows in either season. Burrow systems of both sexes in winter had significantly longer, larger burrows and had more mounds than in summer. The winter burrow systems covered a greater area but did not explore the surrounding environment any less efficiently than burrow systems in summer (Table 3).

Burrow systems ranged from being extremely short; consisting of only a few metres of shallow tunnels with no or few branches, to extensive burrow systems with numerous branches (Table 3). The burrow systems also varied in the number of chambers, latrines and bolt holes (Figs. 2 and 3). Nest chambers occurred in both males and females burrow systems in both seasons. Food stores were found in burrow systems of both sexes in summer but were only present in one female burrow system during winter. Bolt holes occurred in burrow systems of both sexes in winter, but

were only present in one male burrow system during summer. Only one latrine was present in all of the burrow systems that were excavated, in a female burrow system

Table 3 Winter and summer burrow characteristics (Mean and standard deviations SD) of *Georchus capensis*. *WS* and *P* values denote results of a General Linear Model examining the effects of season.

	Winter		Summer		<i>F</i>	<i>P</i>
	Mean	S.D	Mean	S.D		
Burrow area (m ²)	182.79	212.97	21.72	38.43	27.661	<0.00
Burrow length (m)	25.42	11.38	10.34	8.15	28.6	<0.00
Fractal dimension	1.0509	0.02	1.0684	0.04	1.252	0.271
Mounds	12.55	8.8	4.3	2.3	20.962	<0.00
Old mounds	5.15	4.3	2.75	1.5	3.237	0.081
Fresh mounds	7.4	5.4	1.55	2.1	29.287	<0.00
Branch number	2.3	2.57	3.15	2.06	0.012	0.912
Depth (cm)	14.52	5.4	11.629	5.04	6.029	0.02
Tunnel height (cm)	8.894	1.62	7.5285	0.66	14.792	0.001
Tunnel width (cm)	8.263	1.04	7.36925	0.66	15.3	<0.00
Arched tunnels	12.535	14.41	4.41	11.57	4.408	0.044
Round tunnels	87.465	14.41	95.59	11.57	1.622	0.212
Shallow tunnels	78.9	20.85	86.675	19.08	6.268	0.018
Deep tunnels	21.1	20.85	12.255	16.81	4.137	0.5
Turning angles (°)	145.9	25.09	152.3	19.13	2.091	0.158
Branch angles (°)	5.41	3.53	2.17	1.33	0.001	0.959
Intra branch distance (m)	5.4	3.53	2.2	0.35	1.908	0.19

during summer. Nests occurred at the centre and the periphery of the burrow systems.

Nests were small oval chambers and packed with dried husks from clover bulbs. Food stores, when present, occurred in small chambers located close to the centre of most burrow systems. Bulbs were stored in a small chamber that contained from 20 – 160 bulbs. The latrine occurred in what appeared to be a disused tunnel which was packed with faeces and soil and was close to a nest chamber.

Distribution of burrow systems

Male systems at site A were located approximately 110m apart from each other in winter and had a mean distance of 185.9 ± 207.7 m in summer. The mean distance between females in winter and in summer was 149.7 ± 136.5 m and 261.5 ± 296.8 m

respectively. The distance between male and female systems in winter ranged from 17.5 to 550m (11 ± 283 m) and in summer ranged from 41 to 983m (56 ± 88 m) Figs.2 and 3.

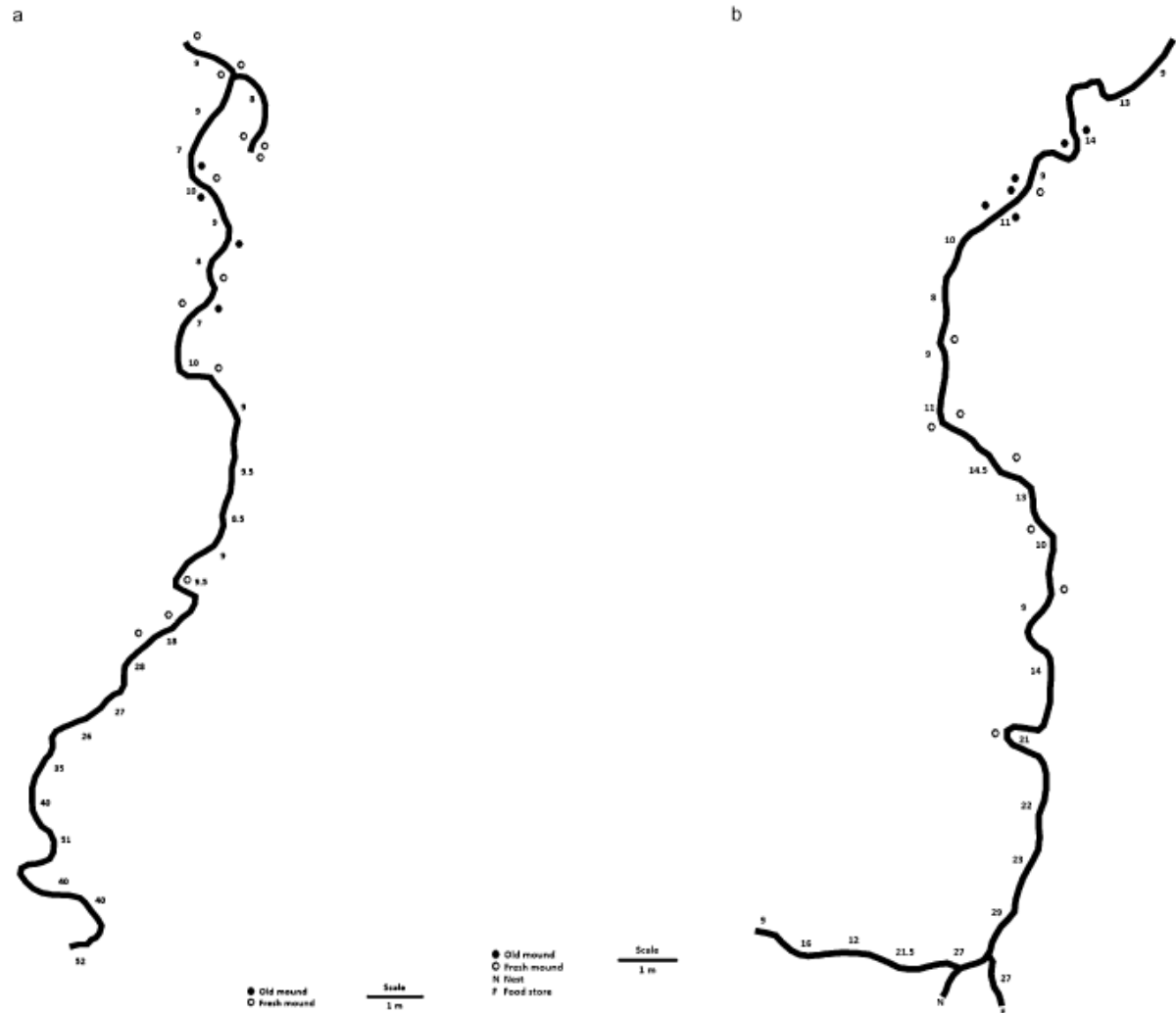


Figure 2 Burrow systems of a single male (a) and a single female (b) *Georychus capensis* at site B during summer. Numbers indicate burrow depths (cm) measured from the top of the burrow to the soil surface. Open and solid circles represent positions of old and fresh mounds, respectively.

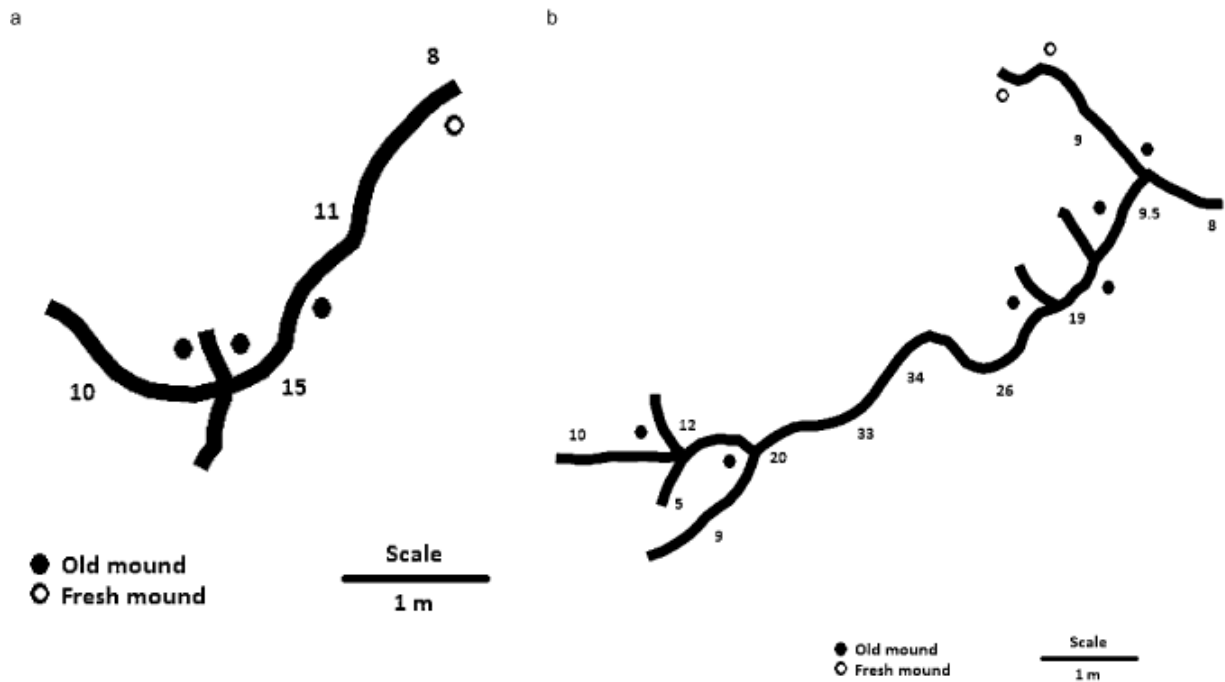


Figure 3 Burrow systems of a single male (a) and a single female (b) *Georychus capensis* at site A during winter. Numbers indicate burrow depths (cm) measured from the top of the burrow to the soil surface. Open and solid circles represent positions of old and fresh mounds, respectively. N and F represent the position of nests and food stores, respectively.

Discussion

Our prediction that burrow length and associated burrow architecture of both sexes would differ between seasons was supported, but we found no differences between burrow systems of males and females. In other solitary subterranean mammals, burrow length, reticulation and complexity of burrow systems have been attributed to sex and population density (Reichman *et al.*, 1982; Davies and Jarvis, 1986; Rosi *et al.*, 1996; Thomas *et al.*, 2009) but the major differences observed in our study appear to be due to season. Burrow length was shorter in summer, probably due to the associated difficulty in excavating new tunnels during this dry season (Skliba *et al.*, 2009). Burrowing rate by *Heterocephalus glaber* has previously been reported to be affected by soil conditions and moisture content and that burrowing activity tends to

decline as summer (the dry season) approaches (Miller, 1957). Although the burrow systems of *G. capensis* covered a smaller area during the summer (the dry season) than during the winter, the fractal dimension did not differ between seasons. This complements the findings reported in two other species of mole-rat, the solitary *Heliophobius argenteocinereus* and the social *Fukomys mechowii* (Sumbera *et al.*, 2003; Sichilima *et al.*, 2008). The higher productivity of the Cape mole-rat's mesic habitat compared to the arid habitats of some social species e.g. the Damaraland mole-rat (*Fukomys damarensis*), might allow them to reduce digging effort in summer reflected by the few new mounds observed in summer - fresh mound production appears to be related to new excavation rather than maintenance of an existing system (Thomas *et al.*, 2009). The short length of the systems and the few food stores found within the burrow systems coupled with the high energetic costs of excavation during the summer periods (Romañach *et al.*, 2004, Vleck, 1979, Miller, 1957) suggests that the environment meets the animal's energetic costs without food storing or the excavation of extensive burrow systems. The depth of the burrow systems alter with the change in seasons being deeper in winter than in summer which may indicate buffering against low temperatures.

In other solitary mole-rat species such as *B. suillus* (Hart *et al.*, 2006; Thomas *et al.*, 2009) and *B. janetta* (Herbst, Jarvis & Bennett, 2004) the males increase burrowing activity in winter when males appear to go in search of mates by excavating longer burrows than females. Interestingly the *G. capensis* shows no sex difference in burrow length, area or environmental exploration, even during the winter when males are thought to search for females. This lack of sexual difference in burrow characteristics may reflect the low level of morphological dimorphism in this species. The solitary

B. suillus, shows marked sexual dimorphism, with males significantly larger than females (Thomas *et al.*, 2009, Kinahan *et al.*, 2008) and have burrow systems that appear to reflect a loose polygynous mating strategy (Thomas *et al.*, 2009, Bennett & Faulkes, 2000). In contrast, the burrow systems of *G. capensis*, a species which exhibits no sexual dimorphism, suggests a different mating strategy. *Georychus capensis* has the potential to be an opportunistic breeder (Oosthuizen & Bennett, 2005), is an induced ovulator (Van Sandwyk & Bennett, 2006) and communicates via foot drumming (Bennett & Jarvis, 1988). This seismic signalling increases in males, who show sex-specific foot drumming patterns, at the onset of the mating season (Bennett & Jarvis, 1988). Our data indicates greater size and shape variation in females rather than in males. Sexual dimorphism was present with females having a greater tail length than males. A larger head size has been considered as a secondary sex trait attributed previously to competition over mates in *B. suillus* (Thomas *et al.*, 2009). Variation in body size has been attributed to dominance in other mammalian species, with higher ranking animals having access to better quality food resources thus resulting in greater body mass (Espmark, 1964; Holand *et al.*, 2004). The longer tail length in *G. capensis* is also coupled with heightened aggression towards both male and female conspecifics and other potential threats (H.G. Thomas pers. obs.). Female competition for resources has been previously associated with overtly aggressive behaviour (Stockley & Bro-Jorgensen, 2011). It has long been clear that the expression of secondary sex traits is dependant upon the type of mating system and the parental roles in the raising of offspring (Andersson, 1994). In *G. capensis* the male has little or no involvement with the rearing of offspring and little courtship is often involved in the mating procedure (Bennett & Jarvis, 1988). From figs. 2 and 3 it

is clear that the sex ratio is biased in favour of females and as such males might be a resource that determines where females are located.

Our hypothesis that differences in burrow architecture occur between seasons in this species was, therefore, generally upheld. Our hypothesis that differences in burrow architecture would reflect differences in male and female behaviour was not supported suggesting that the Cape mole-rat have a different mating strategy to that recorded for other solitary subterranean rodents.

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