Seasonal patterns of burrow architecture and morphological adaptations to digging in three sympatric species of South African mole-rat, *Bathyergus suillus* (Shreber, 1782), *Georychus capensis* (Pallas, 1778) and *Cryptomys hottentotus hottentotus* (Lesson, 1826)

by

H.G. Thomas

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Declaration:

I, …**Hannah Grace Thomas…….** declare that the thesis / dissertation, which I hereby submit for the degree………. **PhD Zoology**……….. at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

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Student: Hannah Grace Thomas

Supervisors: Prof. Nigel C. Bennett

Dr. Philip W. Bateman

Dr. Michael Scantlebury

Department: Zoology and Entomology, University of Pretoria

Degree: Doctor of Philosophy (Zoology/Mammalogy)

Summary

Mammals use burrows for numerous functions. As these functions become more complex so does the burrow system. Although this underground environment is buffered from many climatic factors, it does pose an energetically expensive way of life. Due to the increased energy expenditure that is needed to forage and live underground, most subterranean mammals have evolved morphological adaptations to living in such a specialised environment. To this end, the burrow systems of three different African mole rats were considered, which range in body size, sociality and apparent foraging behaviour.

Bathyergus suillus excavate their burrow systems using their enlarged forelimbs. Their burrow systems generally have one or two main, deeper, central tunnels that connect to a varying number of shallow 'foraging' tunnels in both sexes. In this study, winter burrow geometry did not differ from summer burrow geometry. The fractal dimension and thus

habitat exploration differed with sex; males exploring the environment more efficiently than females.

The burrows of *G. capensis* did not differ with the sex of the occupant but rather with season. The burrows in winter were generally longer and covered a greater area, but they did not necessarily explore the surrounding environment any more efficiently than burrows in summer. The lack of difference in burrow geometry coupled with the sexual dimorphism of the skull (reverse sexual size dimorphism) indicates that an alternative mating strategy may be employed by *G. capensis* compared to other species of mole-rats.

Finally, *Cryptomys hottentotus hottentotus* create elaborate multi-layered burrow systems with numerous foraging tunnels and a few central deep tunnels. The burrow systems in this case differed between the winter and summer. Burrows in the winter were generally longer, covered a greater area and had more branching of the tunnels than those burrows in the summer, i.e. were more efficient. Burrow size appears to be dependent upon colony size; the larger the colony, the larger and the more branching the burrow system.

At a glance the mole-rats face suggests that their incisors may play a special role in mole-rat behaviour. Mole-rats move objects, excavate burrows, carry young, eat and display in social interactions using external procumbent incisors. Mole-rats also use their incisors as a somatosensory organ and *Cryptomys h. hottentotus* has been suggested to use its incisors to sense vibrations (Poduschka, 1978). This study revealed no evidence of sexual dimorphism in bite force even within solitary species that have marked sexual size dimorphism. Bite force does not appear to be allometric to body size as previously reported in other studies.

Macro-anatomical osteological descriptions are non-existent for South African mole-rats. Within the forelimb, the skeletal system has presumably adapted to withstand the greater pressures exerted due to the excavation methods employed by the mole-rats. To this end, the forelimb bones are generally more robust and have larger areas than terrestrial rodents with more tuberosities for extra muscle attachment to enable them to dig proficiently.

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Chapter 1

General introduction

Introduction

African mole-rats spend their entire lives underground and very rarely come to the surface. This section of the thesis aims to introduce the niche environment in which the African mole-rats inhabit; furthermore the function and form of burrows are introduced. Mole-rats are introduced including the foraging strategies used to locate mates and food. Finally the morphological adaptations to living in such a specialised environemt are discussed.

Shelters

Most animals use shelter in some form or other, either daily or seasonally or both. These shelters may range from simple and temporary structures (for example the shade of a tree or lee of a rock) to complex permanent structures (dens, nests or burrows) (Reichman & Smith, 1990). These permanent complex shelters offer many benefits to the animal. Many mammalian species construct shelters that do not involve burrowing into soil, for example squirrels and other rodents often use the hollow of a tree or leaf nests above ground (Allen, 1942). Some large primates construct temporary nests among trees on a daily basis (e.g. Goodall, 1986). Other mammals use existing structures such as fallen logs or rock crevices (woodrats, *Neotoma floridana*) or in water (beavers, *Castor fiber*) (Reichman & Smith, 1990).

Burrows

Burrowing has probably been used by mammals very early on in mammalian evolution. Fossil evidence from the Pliocene period points to morphological adaptations for a fossorial existence in rodents (*Mylagaulus*) (Webb, 1966; Rose & Emry, 1983) and fossil burrows have been identified (Voorhies, 1974).

The soil is obviously the main substrate used when constructing burrows in most terrestrial habitats. It serves to provide effective physical protection from predators and from inclement weather conditions. For many mammals the soil also supports the plants and animals (primarily insects) that many fossorial or subterranean mammals feed upon (Reichman & Smith, 1990).

Function of burrows

The majority of fossorial mammals use burrows simply as a resting place when they are not foraging, searching for mates or defending their territory (Lacey, 2000). Even so, a large proportion of their time is spent underground, up to as much as three quarters of the day e.g. the Great basin kangaroo rat, (*Dipodomys microps*) (Kenagy, 1976). The advantage of using a burrow is that at a depth of approximately 30cm a significant amount of the daily temperature fluctuations disappear although long term seasonal changes in temperature do occur (Reichman *et al*., 1985).

Burrows provide effective protection against many predators (Lacey, 2000). Avian predators and most terrestrial carnivores cannot chase prey down small burrows (Reichman & Smith, 1990). The exceptions to this are weasels (*Mustela nivalis:* Mustelidae), ferrets (*Mustela putorius furo*: Mustelidae) (Smith, 1967; Halpin, 1983) and badgers (*Taxidea taxus:* Mustelidae), the latter of which can dig their prey out of burrows (Knopf & Balph, 1969). Plugging the burrow may inhibit some snakes from entering (Hickman, 1973), but predatory mammals will dig through the soil plug to get to the animal (Hickman, 1973) and may actually be drawn to fresh soil as a sign of recent excavations by potential prey (Brett, 1990).

Burrows that provide basic protection can be quite simple, comprising of little more than an entrance, a short tunnel and an expanded chamber as a nest (Reichman & Smith, 1990). The vast majority of mammals that construct burrows use such simple designs (Reichman & Smith, 1990). An example of one of the simplest types of excavation is shown by the Namib golden mole (*Eremitalpa granti namibensis*: Chrysochloridae) and the marsupial mole (*Notorytctes typhlops*: Notoryctidae) both of which species tunnel through loose sandy soil that is too fluid in form to support a permanent structure (Mason & Narins, 2001).

Many large mammals construct simple linear burrows, for example, platypuses (*Ornithorhynchus anatinus* : Ornithorhynchidae) construct tunnels into the banks of rivers or ponds (Grant, 1983). Armadillos (*Dasypus novemcinctatus*: Dasypodidae) excavate burrows that are slightly angled into the ground and are up to 1.25m in length and terminate with a simple nest chamber (Taber, 1945; Clark, 1951). Pangolins (*Manis culionensis*: Manidae) excavate very similar structures to armadillos except they may extend up to 3m in length (Walker, 1983). Carnivores such as honeybadgers (*Mellivora capensis*: Mustelidae), weasels (*Mustela nivalis*: Mustelidae), and genets (*Genetta genetta*: Viverridae) utilise similar tunnel systems, although suricates (*Suricata suricatta*: Herpestidae) and mongooses (*Cynictis penicillata*: Herpestidae) that live in communal groups may excavate longer and more complex structures (Smithers, 1983) (See illustrations in Bronner, 1992). Most burrows contain nests which are usually expanded chambers, which may be lined with vegetation or fur, which keeps the inhabitant dry and warm (Reichman & Smith, 1990). The beneficial feature of a nest for an individual is realised when females give birth to young that are relatively helpless with poor thermoregulatory capabilities, and remain in the nest for days or even weeks (Bronson, 1989). Among mammals, rodents excavate some of the most complex burrow systems that are (assumed to be) used for protection (Reichman & Smith, 1990). These burrows frequently have numerous entrances that interconnect below ground and have more than one nest site (Butynski & Mattingly, 1979).

Mole-rats

The order Rodentia is divided into three sub-orders, the Myomorpha, the Scuiromorpha and the Hystricognathi. The placement of taxa into these three groups is determined by morphometric parameters including the placement of the jaw muscles and the skull structure. The Hystricognathi sub-order of rodents has been divided further into four old world phiomorph families (Hystricidae, Thryonomyidae, Petromuridae and Bathyergidae) and one new world caviomorpha family (Nedbal *et al.*, 1994). The Bathyergidae is a family of subterranean rodents that are endemic to sub -Saharan Africa. They occur in a wide range of geographic localities ranging from mesic to arid habitats (Bennett & Faulkes, 2000). They are found in a variety of soil types ranging from consolidated clays to fine sand (Bennett & Faulkes, 2000) and can be found in a range of altitudes, rainfall patterns and vegetation types (Bennett & faulkes, 2000). Within the Bathyergidae, there are six genera which Roberts (1951) and De Graaf (1981) categorised into two sub-families (Bathyerginae and Georychinae) based on their dental characterisics. The Bathyerginae contains one genus with two species (*Bathyergus suillus* and *B. janetta*). The Georychinae contain five genera (*Fukomys*, *Heterocephalus*, *Heliophobius*, *Georychus* and *Cryptomys*). The Bathyerginae are socially solitary claw-diggers characterised by a large body mass (up to 2.5kg, M. Scantlebury unpublished data), enlarged forelimbs, mole-like forepaws and grooved upper incisors; whereas the Georychinae are either solitary, social or eusocial and are chisel-tooth diggers characterised by a small body mass (less than 400g) and rodent-like forelimbs and forepaws.

The Cape dune mole-rat, *Bathyergus suillus*, is the largest truly subterranean (i.e. dwelling mostly in a burrow system) rodent in the world (Jarvis & Bennett, 1991; Kotze *et al*., 2006). They are sexually dimorphic with males being significantly heavier than females (Davies & Jarvis, 1986; Kinahan *et al*., 2007); some individuals may reach 2.5 kg in body mass (M. Scantlebury unpublished data). Indeed, the large size and the associated energy costs of digging appear to be factors restricting this species to the sandy soil areas of the South and Southwestern regions of South Africa (Bennett & Faulkes, 2000; Kotze *et al*., 2006).

The Cape mole-rat, *Georychus capensis* appears to exhibit no physical signs of sexual dimorphism with a mean body mass of 180g for both sexes (Jarvis & Bennett, 1991). The Cape mole-rat inhabits areas that have on average over 500mm of rainfall per annum (the Western Cape) (Bennett & Faulkes, 2000). This solitary mole-rat inhabits sandy loams and alluvial soils, but unlike *B. suillus* they are also found in heavy clay soils (Bennett & Faulkes, 2000). Both *B. suillus* and *G. capensis* appear to have a polygynous mating system involving very little courtship compared to some social species of bathyergid (Bennett & Faulkes, 2000; Kinahan *et al*., 2007).

The common mole-rat, *Cryptomys hottentotus hottentotus* is a social species occurring in colonies of up to nine individuals in arid regions (Spinks, Bennett & Jarvis, 2000) and up to 16 animals in mesic regions (Davies & Jarvis, 1986). In the southern Western Cape the common mole-rat has a mean body mass of 83g and 58g for males and females respectively (Davies & Jarvis, 1986). C*ryptomys h. hottentotus* occur sympatrically with the solitary *G. capensis* and *B. suillus* in the Western Cape Province of South Africa. These three species have been used in this study as they not only occur sympatrically in the Western Cape Province, but they occupy the same fields eliminating multiple confounding variables.

Mole-rat burrow systems

From the limited data available regarding burrow systems and burrow structure it appears that African mole-rats seem to have a similar burrow architecture to other rodents: they comprise numerous long superficial foraging burrows (15 – 35 cm deep), connected to a deeper, central, permanent system of chambers used for nesting, food storage, sanitisation and retreat (Thomas *et al*, 2009). These shallower foraging burrows are reported to form 80 – 95% of a burrow system (Miller, 1957; Jarvis & Bennett, 1991). Burrow dimensions vary with species, individuals, sex, age, and local habitat conditions (Nevo, 1979).

Burrow length has previously been suggested to 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), soil hardness (Heth, 1989), duration of occupancy (Brown & Hickman, 1973), energetic requirements (Heth, 1989), population density (Sumbera *et al.,* 2003; Sichilima *et al.,* 2008) and body mass (Sumbera *et al.,* 2003).

Extensive tunnelling by colonies of bathyergid mole-rats can result in burrows which are hundreds of metres in length (Lacey, 2000). These burrows retain a basic design and biomass ratio similar to those of solitary species living in more productive environments (Jarvis & Bennett, 1991). Specifically, burrows constructed in unproductive habitats tend to be longer suggesting that they encompass larger foraging territories (Reichman & Smith, 1990). Food resource characteristics have also been implicated in the construction of extremely large communal burrows occupied by social bathyergids. Sociality is adaptive as cooperative foraging shares the energetic costs of burrowing and increases the likelihood of locating food resources as predicted by the Aridity Food Distribution Hypothesis (AFDH) (Jarvis, 1978). In arid regions, opportunities for burrow expansion are limited because of the energetic costs of excavation and are possible only immediately following infrequent and unpredictable periods of rainfall. The AFDH argues that individuals are better able to take advantage of limited burrowing opportunities for burrow expansion if they live in groups. This reasoning suggests that lone individuals may not be able to dig fast enough or far enough to reach new food resources while conditions for excavation in the soil are optimal (Jarvis *et al*. 1994). By living in groups however, mole-rats are able to complete extensive excavations very quickly thus allowing the animals to locate new food resources before the soil conditions make excavation energetically and physically impossible (Lovegrove, 1987).

Foraging habits

As herbivores, subterranean rodents feed extensively on vegetation and appropriate plant species must be available to support the animals. In addition to providing critical food resources, the type of vegetation present may determine the distribution of subterranean rodents through effects on patterns of ventilation (Busch *et al.,* 1989). In particular, the structure and density of vegetation may influence patterns of heat flux within subterranean burrows which may, in turn, determine whether a given habitat is suitable for underground existence; for example Comparatore *et al*. (1991) found that in warmer months, favourable zones for *Ctenomys talarum* were those with greater density and height of the vegetation. Subterranean plant tissues may represent a more variable resource, in terms of nutritional value, than above-ground plant tissues (Andersen 1987), This difference in nutritional quality may influence food selectivity. In addition to the availability of suitable roots and tubers, the cost of foraging for these items may prevent some species from specializing on subterranean plant parts. Heth *et al*. (1989) argued that subterranean herbivores cannot afford to be selective feeders because the costs of searching for food items would exceed the benefits of this selectivity; as a result, subterranean rodents should utilise all food that they encounter. Generally, most species of mole-rats feed on corms, bulbs and geophytes of plants (Bennett & Jarvis, 1995). Exceptions to this are *B. suillus* and *G. capensis* which also consume the aerial portions of vegetation (Beviss Challinor, Broll and Jarvis unpublished data).

Exploring the environment

The complexity of a burrow system and the exploration efficiency of the surrounding environment can be examined though fractal dimensions. A fractal is defined as a set for which the Hausdorff Besicovitch dimension strictly exceeds the topological dimension and every set with a non-integer D is a fractal (Mandelbrot, 1983). When investigating complex shapes such as coastlines it was proposed that the exponent D is not an integer, it can and then should be interpreted as a fractal dimension (Mandelbrot, 1983).

The key property of a fractal is self-similarity on different length scales - that is, if you take a section and zoom in, what you see looks similar to the original version. A good example of this is a coastline, which looks crinkly when viewed from a distance, and when zoomed in new bits of detail emerge so that it maintains roughly the same complexity.

For real-world objects like coastlines, this process inevitably stops after a while - as you can only zoom in so many times. However, one can imagine mathematical creations where you can repeat this magnification process infinitely and the results of magnifying it a few times would result in an image the was recognizably the same as the first and it would not be possible to tell what scale it was.

The fractal dimension is a more complex concept, the general idea is that an image such as the Koch curve is more than just a line - if you take the Koch curve between any two points on it, the length of the line between them is infinite. So an infinite amount of one-dimensional lines are placed into a two-dimensional plane, and the line is somehow more than one-dimensional, but less than two-dimensional. It can be calculated precisely for fractals which are defined mathematically (such as the Koch curve ($D = \log 4/\log 3 \sim 1.2618 > 1$, while $D_T = 1$), Cantor set ($D = \log 2/\log 3 \sim 0.6309 > 0$, While $D_T = 0$) and Brownian motion ($D = 2$, while $D_T = 1$). For real-world fractals, methods such as block counting (Le Comber *et al.*, 2002) can be shown to do the same thing. Obviously, it is pointless counting blocks infinitely as previously mentioned as for real-world fractals detail breaks down after a while.

Seasonality

It follows from the paucity of data relating to burrow architecture generally that very little information is available about temporal changes in burrow architecture in subterranean African mole-rats between the rainy and dry seasons. Two exceptions to this are manuscripts from Sumbera *et al.* (2003) and Sichilima *et al.* (2008). In solitary species (*Heliophobius argenteocinereus*) burrow architecture differed between seasons and had a higher fractal dimension during the rainy season indicating increased foraging. In the social species (*Fukomys mechowii*), burrow length did not differ between seasons but, interestingly, the fractal dimension was greater during the rainy season than in the dry season, indicating greater foraging efficiency (Sichilima *et al.,* 2008). Although there was no difference in the number of food stores between seasons the food mass within the stores was greater during the rainy season and the mass of food was generally greater in burrows with higher fractal dimensions. Sichilima *et al.* (2008) also found that foraging was more efficient in larger colonies and that such colonies had a higher fractal dimension and stored a greater mass of food. The results of Sichilima *et al.* (2008) agree with the foraging models of Lovegrove & Wissel (1998) and Spinks & Plaganyi (1999), which suggest that colony size is important with regards to foraging risk and success. Generally it is assumed that the larger the colony the more likely the colony is to find food resources especially in arid regions.

Morphology

Morphology has previously been used to elucidate phylogenetic relationships and evolutionary patterns in organisms (Sasaki *et al.*, 2006). However, with the development of molecular techniques, morphological studies have become secondary lines of evidence for patterns of evolutionary changes for some phylogeneticists (Barraclough & Nee, 2001). It is generally accepted that an organism's design is a compromise between adaptation to its environment and phylogenetic constraints (Wainwright, 1996). The evolutionary history of a few highly specialised subterranean fossorial eutherian mammals is well known, particularly in more modern species that represent different stages of adaptation to burrowing. Subterranean and fossorial species spend most of their lives underground and display classical morphological adaptations to such a lifestyle. These adaptations include small cylindrical bodies with reduced ears, tails and eyesight (Bennett & Faulkes, 2000). Limbs are also reduced in length but are more robust allowing for increased excavation of burrows (Lessa & Thaeler, 1989).

Excavation methods

Most mammals that dig using feet and forelimbs are adapted to enable them to manipulate substrates to create burrows. However, only a few mammals excavate burrow systems using their teeth. Within Bathyergidae, in contrast, only two species (*Bathyergus suillus* and *Bathyergus janetta*) excavate intricate burrow systems using their forefeet, whereas all the other species excavate their burrows using modified, evergrowing extrabuccal incisors.

Chisel-tooth digging

The shape of the incisors in subterranean rodents enables the animal to apply a great deal of force to a restricted area. The incisors are intimately involved in the construction of burrow systems, even if they are not the primary method of excavation. In general the upper incisors of subterranean rodents are more chisel-shaped (with a sharp, tapered tip) than those of surface-dwelling taxa, thus enhancing the animals' ability to loosen soil and cut through underground vegetation. The longer the incisor with a tapered tip, the more functionally efficient the incisors are because soil resistance is decreased with increased applied force from the incisors (Lessa 1990). Characteristically, the elongated roots of the upper incisors of subterranean rodents extend to, or beyond the first cheek molar. The roots extend above or posterior to the upper molar tooth row. This condition is unique within rodents (Ellerman, 1940). Roots of the lower incisor are also shifted posteriorly and insert into or close to the mandibular condyles (Gromov & Polyakov, 1992).

The procumbency of the incisor is influenced by both the degree of curvature of the teeth and their position in the rostrum (Landry, 1957; Akersten, 1973). Incisor curvature is a function of both the radius of curvature of the teeth and tooth length. Curvature is produced by the difference in growth rate between the dorsal and ventral surfaces – that is between the deposition of the rates of enamel and dentine (Lacey, 2000). Hard enamel only exists on the anterior surface and ensures that the dentine portion of the tooth will wear away more quickly producing and maintaining a self-sharpening edge that is critical to the survival of these mammals (Lacey, 2000). Incisor growth rate for subterranean taxa is almost double those recorded for terrestrial taxa (Howard & Smith, 1952). *Cryptomys* and *Heliophobius* have the most procumbent upper incisors of any rodent with tips that project far from the rostrum

(Landry, 1957). *Heterocephalus* and *Georychus* also have procumbent incisors. However, in *Bathyergus*, the scratch-digging member of the clade, the incisors are not procumbent. In these species, lower incisors are generally less procumbent than upper incisors as their primary function is to manipulate dirt rather than to break it up, but in bathyergid chisel- tooth diggers this is not the case (Hildebrand, 1985).

Bite force

Bite force capacities may be tightly linked to both the type and magnitude of the ecological challenges of food acquisition, mate acquisition, and anti-predation in vertebrates (Anderson *et al.* 2008). Van Daele *et al.* (2008) demonstrated that mole-rats have evolved a very powerful bite which is associated with a subterranean lifestyle. Amongst mammals they have a bite force that is not allometric for their body mass, such that the bite force does not increase as the size of the animal increases, but it seems to be independent of mass. Although they have a powerful bite they still follow the same basic mammalian morphological design, with gape angles and bite points influencing the generation of a large bite force. It has been suggested that mole-rats have evolved a large powerful bite force to enable them to consume a wide range of geophytes which have a hard outer husk (van Daele *et al.*, 2008). There is considerable intra-specific variation in the masticatory physiology contributing to a powerful bite force in mole-rats (van Daele *et al.*, 2008). Intra-specific variation in skull morphology has been linked to variation in sociality (Van Daele *et al.*, 2008). The biting capacity of subterranean taxa is likely to have been shaped within severe evolutionary constraints as the animal's dentition is often used for consuming hard geophytes and in most species of African mole-rat is also for excavating extensive tunnel systems which can reach hundreds of metres in length (Davies & Jarvis, 1986).

In addition, a mole-rat's primary defence mechanism is its teeth which are often used for aggressive encounters either with predators or conspecifics. In solitary species, males use their teeth to spar with and out-compete other males for access to females, especially during the breeding season by interlocking their incisors (Bennett & Faulkes, 2000). Within social species of African mole-rat, teeth are used for social interaction with conspecifics (Bennett & Faulkes, 2000). For example, defensive positions are held with gaping incisors and aggressive encounters are often seen with two animals incisors interlocked during sparring.

Forelimb digging

Comparative anatomy has long served as evidence for evolution; it indicates the fact that various organisms share a common ancestor. Comparing various aspects of morphology also assists scientists in classifying organisms based on similar characteristics of their anatomical structures (Campbell & Reece, 2002).

Rodents show a great diversity in their locomotor habits including semi-aquatic, arboreal, ricochetal, gliding and fossorial species from multiple families (Samuels & Valkenburgh, 2008). Subterranean rodents spend the majority of their life underground and therefore all their movements are influenced by their ability to excavate the environment.

Forelimb structure

In addition to the teeth, head and neck, the forelimbs constitute the third primary component of the digging apparatus in subterranean rodents. Digging activity has caused diverse adaptations in subterranean rodents (Reig *et al*., 1990; Casinos *et al*., 1993).

Compared to non-digging mammals, the humerus of subterranean rodents has a well-developed humeral head with a pronounced deltoid tuberosity. Subterranean mammals that use their forelimbs for burrowing display a variety of distinct morphological modifications of the pectoral girdle as burrowing results in greater forces being generated by and placed on the limbs. Most digging mammals have relatively short, but dense limb bones that are able to resist both torsion and bending (Casinos *et al*., 1993). Even chisel-tooth diggers benefit from such adaptations, as these taxa use their forefeet to counterbalance the upward pressure that the lower incisors exert against the soil. Those rodents that remove excavated soil using their hind feet often stand on their fore feet while the posterior portion of the body is dorsally inclined (Genelly, 1965). Functionally this change in shape is the equivalent to increasing the out force by decreasing the out lever of the forelimb. The limb bones also have pronounced processes and tuberosities for muscle attachment that may reflect the mode of burrow excavation. Biknevicius (1992, 1993) has shown that differences in the burrowing styles in at least some subterranean genera are reflected in specific differences in the humerus, where increased buttressing by cortical bone is observed.

The limbs of mammals are capable of extensive rotation, flexion and extension owing to the spherical shape of the head of the humerus and the femur which is closely adapted to the articular cavity of the corresponding girdle (Goldstein, 1972). Ligaments in the elbow prevent it from dislocation; where the olecranon process engages in the posterior fossa of the humerus which functions as a stop. The rotation of the radius about the ulna brings about pronation and supination, affecting in particular the turning of the paw.

Fossorial mammals typically show muscular and osteological modifications that produce large forces for digging. Considering the physics of levers, improved mechanical advantage may be acomplished in three ways: by improving the in-force, by increasing the length of the in-lever or by decreasing the length of the out lever. Considering the morphological adaptations a subterranean rodent has evolved to cope with the challenges an underground lifestyle imposes, it is suprising that there are very few macro-anatomical investigations on wild subterranean mammals.Only one species of subterranean rodent (*Spalax leucodon*: Spalacidae) has had observations made on its forelimb structure (Özkan, 2002).

Sex differences in forelimb structure

There are no reported differences in muscle mass of sexes or between juveniles and adults in pocket gophers (Lessa & Thaeler, 1989). In subterranean rodents claw diggers are characterised by large forelimb muscles, enlarged insertion sites on forelimb bones and enlarged claws, whereas chisel tooth diggers typically have procumbent incisors and enlarged jaw muscles (Dubost, 1968; Hildebrand, 1985; Nevo, 1979). Other characteristics in the forelimbs of pocket gophers suggest that differences are related to excavation modes (Lessa & Thaeler, 1989).

Summary

This study is split into two distinct themes: ecology and morphology. The objective of the ecological aspect of this study was to investigate the intergration of mole-rats into a subterranean environment by excavating and describing the burrow architecture for the solitary Cape dune mole-rat *B. suillus* (Chapter Two), the Cape mole-rat *G. capensis* (Chapter Three) and the social common mole-rat, C. *h. hottentotus* (Chapter Four). Within each chapter I examine the seasonal aspects of the spatio-temporal patterns of the burrow systems in the Western Cape Province of South Africa during two seasons (a wet winter and a dry summer). The aim of this section was to examine the effects of seasonal change on environmental factors, particularly climate, the availability of food and soil characteristics, how they are likely to affect burrowing ability and hence how differences in burrow architecture reflect this.

Second, I explore the evolutionary morphology of selected bathyergids and investigate natural and sexual selection on phenotypic traits associated with digging and mate acquisition. By doing this I examine the relationship between an animal's ecology and its morphology. I describe the forelimb structure of the bones of *B. suillus*, *G. capensis* and *C .h. hottentotus* to elucidate adaptations that reflect the excavation mode used for creating their subterranean habitat (chapter five). I also investigate the incisors and their bite force capacity as an adaptation to "life underground" as an effective method for excavation in a range of mole-rats with varying degrees of sociality (chapter five).In Chapters two to four there may be some overlap in methodology as these three chapters have been submitted as stand-alone publications.

Chapter 2

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

(accepted in African Zoology)

Abstract

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 how differences in burrow configuration may differ between the sexes of subterranean African mole-rats (Bathyergidae). I 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. I 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 that territorial behaviour may be operative even though it is energetically costly to dispose of soil onto the surface when the soil is less friable during the summer. Overall the burrow system dimensions did not differ with sex of the occupant. It appears that a change in season does not affect the geometry of the burrow system or tunnel dimensions in a climatically buffered environment.

Keywords

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 is climatically stable and primarily isolated from predators is energetically more expensive to produce than above ground dwelling (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 an increased soil moisture level making the soil friable (Miller, 1957). Other factors influence burrowing patterns seasonally such as the acquisition 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 with aridity, 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 was originally postulated 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 2.5kg) (Jarvis & Bennett, 1991; Kotze *et al*., 2006), with 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, 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 on reproductive turnover within a population (Randolph, 1977). Physiological costs, on the other hand, can be either ‘direct’ or ‘indirect’ (Speakman, 2007). 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 minimising 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 utilised 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), however, 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 of the western Cape. Sexual selection predicts that architectural differences in burrow structure should exist due to the behaviour of males seeking mates during the breeding season (winter). I 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. I further expected males to show increased habitat exploration and greater efficiency in burrowing activity. I 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 and (4) contain proportionally more shallow foraging tunnels to fuel mate seeking behaviour compared to that of summer burrow systems. In contrast, I predicted that female burrows in winter would: (1) be longer and cover a greater area and (2) have a lower fractal dimension.

Materials and 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 forbs 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 south-west of the western Cape Province, South Africa (33°22 S, 15°25 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 2 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: 6 animals at site A (summer:3 females), (winter:1 female, 2 males), 6 animals from site B (summer:1 male, 1 female), (winter: 2 females, 2 males), 6 animals from site C (summer:1 female, 2 males), (winter: 2 females, 1 male) and 5 animals from site D (summer: 2 males), (winter: 2 females, 1 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 for analysis (University of Pretoria ethics number AUCC 040702/015).

Morphometrics

Once caught and euthanized the animals were sexed and weighed. All standard morphometric measurements were then taken using digital calipers ± 0.01mm. Measurements taken were body length (length from the tip of the nose to the tip of the tail), head length (tip of the nose to the base of the skull), tail length (from the base of the trunk to the tip of the tail), hind foot length (from the heel to the tip of the longest toe) and zygomatic arch width (ZAW (cheek to cheek).

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*, 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 (± 0.1cm). Tunnels were defined as either being deep, semi-permanent (> 20cm) or shallow, foraging (< 20cm) 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 digitised. Tunnel depths were recorded approximately 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 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 digitised 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 (Le Comber *et al*. 2002; Le Comber, 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 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 Le Comber *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 examine differences between the sexes in external morphology. All statistical analyses were 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 4 cheek teeth, van Rensburg *et al*., 2004). No females were obviously pregnant or lactating. Body mass ranged from 444.0g to 1963.8g for females and from 497.9 to 1147.0g for males. Females had the smallest body length, ZAW, head length and tail length, but males had the smallest HFL (Table 2.1). 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 2.2).

Table 2.2

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

	Male		Female			
	Mean	SD	Mean	SD	*U*	*P*
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	1.000
Hind foot length	44.273	0.925	44.917	1.379	119	0.4417

A PCA of logs of morphological data revealed a size axis accounting for 61% and a shape axis accounting for 18.3% of variation (Figure 2.1). The bivariate plot indicates size and shape vary the most in males but not significantly in females. The PCA revealed that factor one effectively describes a variation gradient based primarily on body length and factor two describes a variation gradient based primarily on hind foot length.

Figure 2.1

Bivariate plot of PCA on morphological characteristics of male and female *B. suillus* showing the first two principal components of log transformed morphological data.

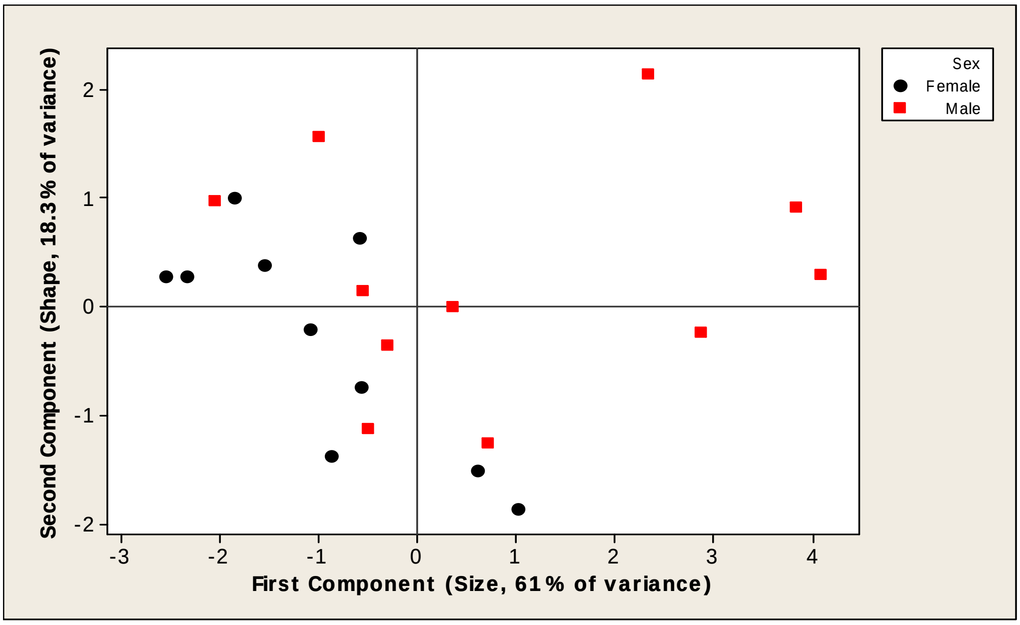

Table 2.1

External morphometric measurements taken of *B. 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	664.0	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	892.0	30.9	45	59.9	40	44
Suillus 4	1	C	1	1147.0	36.5	48	60.8	37	43
Suillus 3	1	D	1	936.6	32.7	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	725.0	23.5	30	33.8	33	46
S22	0	C	0	735.0	24.0	31	35.9	34	44
S6	0	D	0	477.0	21.0	28	34.2	35	47
S3	0	A	0	774.1	25.7	30	36.5	37	45
S4	0	B	0	983.9	28.0	31	39.2	39	44
S5	0	C	0	1055.5	29.0	31	38.6	41	45
S7	0	D	0	444.0	20.1	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

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 (Figure 2.2a) and males (Figure 2.2b) in winter and in summer (Figure 2.3a and 2.3b for females and males respectively). Burrow systems had a varying number of chambers (nest, latrines and food stores) and bolt holes (Table 2.3). 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 – 20cm deeper than the connecting tunnel. Nests were all blind ended with a single entrance. Nesting material comprised mainly of dried grasses and other dried foliage from forbs. Latrines were located in disused foraging tunnels >25cm deep and faecal matter was packed with soil (Burrow data located in appendix 1).

Figure 2.2a

Burrow system of a single female *B. suillus* at the study site in Darling, Western Cape, South Africa in winter with a total burrow length of 56.83m and a fractal dimension value of 1.094. 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.

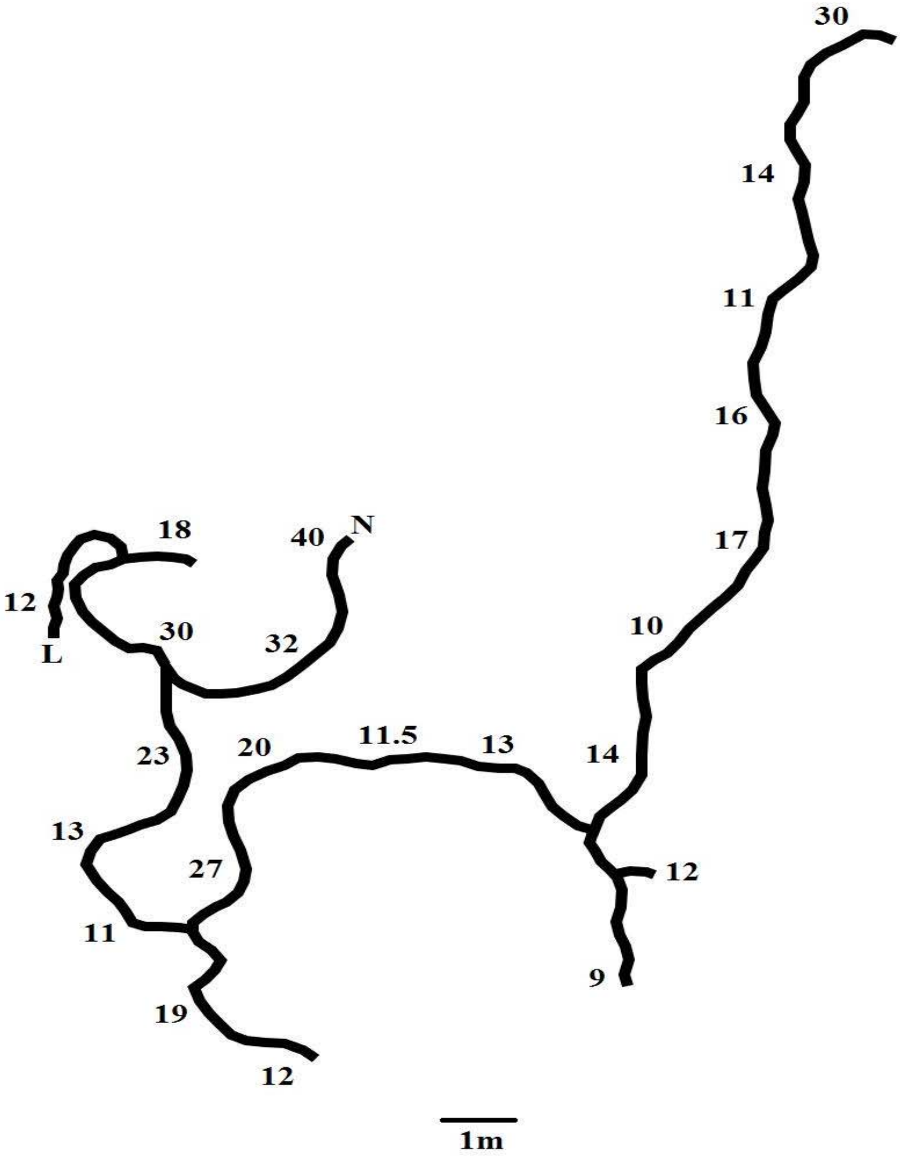

Figure 2.2b

Burrow system of a single male *B. suillus* at the study site in Darling, Western Cape, South Africa in winter. The length of the burrow was 62.2m with a fractal dimension value of 1.181. 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.

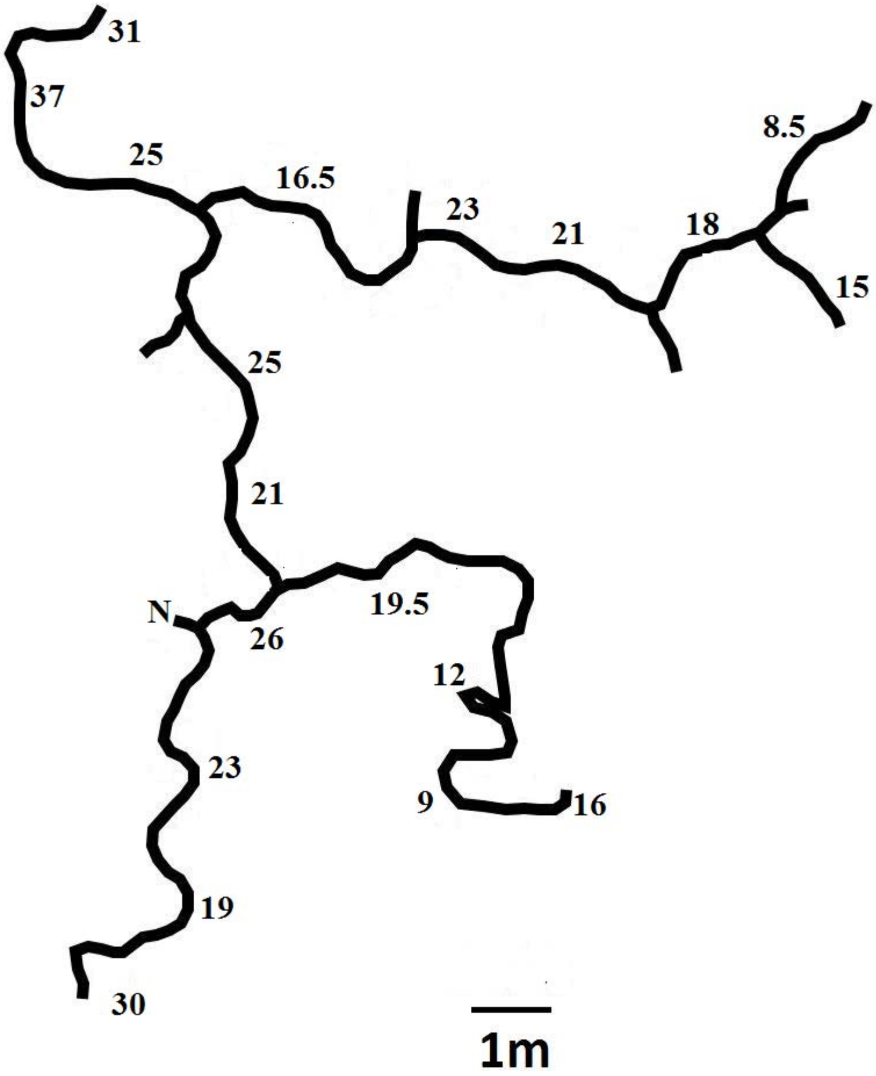

Figure 2.3a

Burrow system of a single female *B. suillus* at the study site in Darling, Western Cape, South Africa in summer. Burrow length was 26.2m with a fractal dimension value of 1.036. Numbers indicate burrow depths (cm) measured from the top of the burrow to the soil surface.

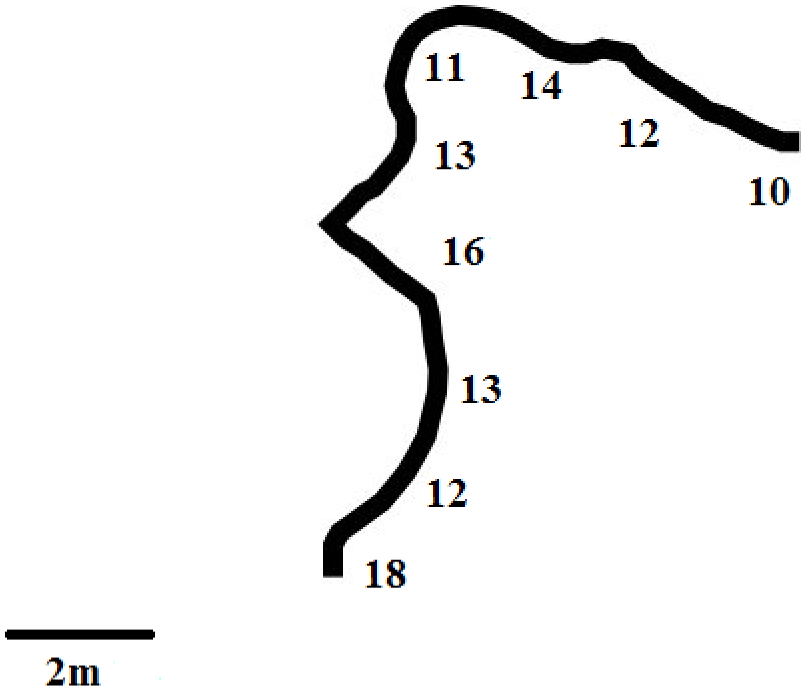

Figure 2.3b

Burrow system of a single male *B. suillus* at the study site in Darling, Western Cape, South Africa in summer. Burrow length was 21.5m with a fractal dimension value of 1.105. Burrow depths (cm) are indicated by numbers and were measured from the top of the burrow to the soil surface.

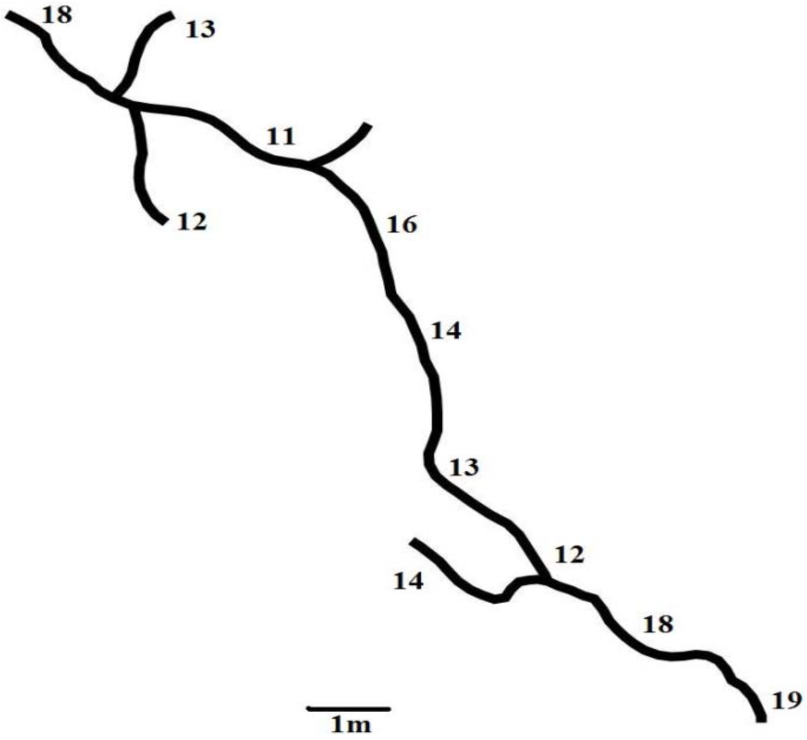

Table 2.3.

Burrow characteristics of *B. suillus*. Mean and standard deviation (SD) of male and female burrow systems in winter and in summer.

	Males (winter)		Females (winter)		Males (summer)		Females (summer)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
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	13.17	4.05	12.95	2.08	13.29	3.21	16.68	1.39

(cm)								
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

Seasonality and sex differences

Winter burrow characteristics did not significantly differ from summer burrows (Table 2.4). 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 ($F = 7.63$, $P = 0.025$). Males had significantly more old mounds present along their burrow systems than females (F = 16.49, $P = 0.004$). There were no other sex differences in burrow geometry (Table 2.4). There were also no interactions between season and sex with respect to burrow geometry (Table 2.4).

Discussion

Mole-rats provide an ideal model group to investigate theories of sexual selection and to investigate the 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, Jarvis & Davies, 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

Table 2.4

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

		Sex			Season			Sex * season	
	DF	*F*	*P*	*DF*	*F*	*P*	*DF*	*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
DF error	8			8			8		

distance on the surface (Vleck, 1979). In this 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, Jarvis & Bennett, 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, Whitham & Ruffner, 1982; Gastal, 1994). It has been proposed that this may be due to active mate-seeking behaviour of males (Thomas *et al.*, 2009). In the closely related species *Bathyergus janetta,* burrow lengths were greater in males than those of females, supporting the notion that males seek out females (Herbst & Bennett, 2006). The only study to previously investigate the difference in burrow length between the sexes in *B. suillus* also reported putative mate seeking behaviour in males (Thomas *et al.*, 2009). However, results from the current study fail to support this suggestion. Thomas *et al.* (2009) showed increased habitat exploration efficiency by males as indicated by an increase in male fractal burrow dimension (Le Comber *et al.*, 2006) during the breeding season, which our study supports, but also in our study male burrows had a greater fractal dimension in the summer as well as in the 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 fractal dimensions were not significantly different between seasons. Fractal dimensions were investigated in the solitary *Heliophobius argenteocinereus* 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 suggests 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*., In review) and the solitary *Georychus capensis* (Thomas *et al*., 2012).

This study indicates that males produce more mounds than females suggesting that males are constantly reworking their burrow systems and perhaps patrolling their territory. Despite this species being relatively large compared to other mole-rats, our study suggests that it is not too energetically expensive to produce mounds. 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 this 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 the harsh summer weather conditions after a previous unproductive winter.

My prediction that there are differences in the burrow geometry between males and females of *B.suillus* was only partially supported. Males tended to explore the surrounding environment more efficiently than females. Possibilities may include that males were actively seeking females despite the season or indeed 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. My 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.

Chapter 3

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 season influences burrowing activity, burrow structure or reproductive behaviour in subterranean mammals. I excavated burrow systems of male and female *Georychus capensis*, a solitary, subterranean rodent, in winter (wet season) and summer (dry season) to investigate whether, if any, seasonal differences were due to putative mate-seeking behaviour of males. Burrow structure differed between seasons but not between sexes. For both sexes, summer burrows were shorter and covered a smaller area, but explored the surrounding environment more efficiently than winter burrows. Summer burrows had fewer mounds, which indicated that less expansion of the burrow systems occurred during this season. I discuss these differences in exploration and the use of the environment between seasons in terms of mating strategies of *G. capensis* and observed levels of sexual dimorphism in our populations. This study supports recent ideas regarding sexual selection relating to exaggerated traits in females, 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

There is a general paucity of information pertaining to the burrow architecture and pattern of mating in subterranean rodents, due to the difficulty of investigating animals that inhabit an underground environment. The aim of this study was to investigate seasonal changes in the architecture of the burrow systems of a solitary species of mole-rat.

Burrow systems provide shelter for fossorial and subterranean mammals (Reichman & Smith, 1990). Burrows that are only used for shelter are often simple in structure, with 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, latrine areas, nest chambers and food stores (Bennett & Faulkes, 2000). The burrow systems may also vary in complexity with the number of occupants (Le Comber et al. 2002).

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 and hence rainfall pattern of the environment as well as 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).

Burrow architecture of African mole-rat shares many similarities with other fossorial species. The burrows comprise numerous long superficial (15 – 35 cm deep) foraging tunnels, connected to a deeper, central, permanent system of chambers that are used for nesting, food storage, sanitisation 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 with the size of 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 the social bathyergid mole-rats results in excavations amounting to hundreds of metres in length, although structurally they retain a basic design and biomass ratio similar to those of solitary species which inhabit more productive environments (Jarvis & Bennett, 1991). Thus, burrows constructed in unproductive habitats will tend to be longer in order to encompass larger foraging territories.

For species occurring in areas with marked wet and dry seasons, as many of the African bathyergids do, the architecture of a single burrow system may alter seasonally depending on a number of biotic and abiotic factors such as soil conditions, temperature and food distribution. In the solitary silvery mole-rat, *Heliophobius argenteocinereus*, burrow architecture did not differ 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 Zambian mole-rat, *Fukomys mechowii*, burrow length did not change between seasons, but fractal dimension was greater in the rainy season than in the dry season indicating greater foraging efficiency (Sichilima *et al.*, 2008).

In geophyte-rich areas of fynbos in the western Cape Province of South Africa, 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*). *Georychus capensis* consumes a variety of vegetation which includes bulbs, corms and the aerial parts of plants (Du Toit *et al*., 1985). *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 of drumming 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 part of on-going research into sexual behaviour and mate choice in bathyergids. As seasonal change affects environmental factors, particularly climate, the availability of food and soil characteristics in turn are likely to affect burrowing ability, hence I 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.

I also predicted that burrow structure would reflect mate-seeking behaviour (as in *Bathyergus suillus*; Thomas *et al*., 2009). Sexual selection theory predicts sex-differences in burrow structure and morphology due to the apparent greater need of males to search for females during the wet winter (mating season) when burrowing conditions are preferable. I predicted that winter burrow systems (when the soil is wetter and easier to excavate) of male animals would: (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. Finally, I predicted that morphology would differ between males and females (as in *B. suillus*), with males exhibiting sexually dimorphic secondary sex traits to enable competition over mates.

Materials and methods

Study animals

The Cape mole-rat, *Georychus capensis* is a monotypic genus closely related to two other solitary mole-rat genera, *Heliophobius* and *Bathyergus* (Honeycutt *et al*., 1991). *Georychus capensis* generally occurs in mesic areas with an average of over 500mm of rainfall per year**.** *Georychus capensis* is often found in sandy loams but is not common in sandy areas inhabited by *B. suillus*. No sexual size dimorphism occurs 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. Site A 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 comprised 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 because of high ground 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).

External morphometrics

Mole-rats were sexed, weighed (±0.1g Sartorius balance, Epsom, Surrey, UK) and external morphometric measurements were taken once the animals were euthanized with chloroform (University of Pretoria ethics number AUCC 040702/015). All external morphometric measurements were taken using digital callipers (±0.1mm Draper digital callipers, UK). Body length was measured from the tip of the nose to the tip of the tail. Head length was measured from the tip of the nose to the base of the skull and head mass was taken (±0.1g Sartorius balance, Epsom, Surrey, UK). The zygomatic arch width (ZAW) was measured as the maximum width across the zygomatic arches. Tail length was measured from the base of the tail to the tip. Hind foot length was measured from the base of the heel to tip of the longest toe (excluding nail).

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 during winter and 20 during 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 (± 0.1cm). Tunnels were defined as either being deep, semi-permanent (> 20cm) or shallow, foraging (< 20cm) tunnels. The distinction between tunnel usages were determined by the depth of the bulbs and roots of the plants reached 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. 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.

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, 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).

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 (Le Comber *et al*. 2002; Le Comber, 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 Le Comber *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). Once the SVG file has been loaded into the calculator, options for minimum and maximum box size, the number of intervening box sizes to use in the calculation and 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) can be selected. Additional options for the calculation included 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). Option values were chosen based upon the complexity of the burrow diagram. The programme then calculated the fractal dimension of the diagram based on the options chosen.

Statistics

Mann Whitney U tests and a Principal Components Analysis (PCA) were used to examine differences between the sexes in morphology. Significant *P* values were less than 0.025. 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 3.1). The bivariate plot indicates size and shape vary in females but not significantly so in males. The PCA revealed that factor one describes a variation gradient based primarily on body mass (eigenvalue 3.46) and hind foot length (eigenvalue 1.857) and factor two describes a variation gradient based primarily on tail length (eigenvalue 0.918). Females had a larger mean body mass than males (182.5 ± 54.5 SD) vs (149.5 ± 38.4) for females and males respectively. Females had 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 3.1).

Figure 3.1

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

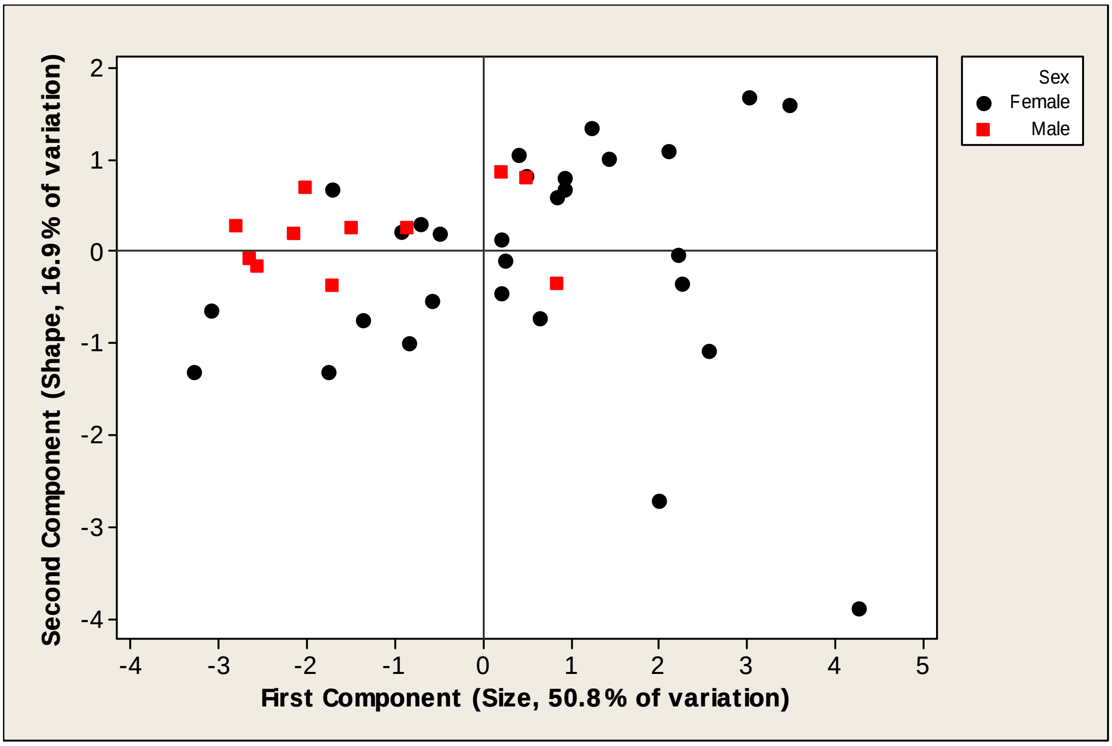


Table 3.1.

External morphometrics (Mean and standard deviations) of *G. capensis*. *U* and *P* values denote results of a Mann Whitney U test examining differences between males and females (n1=29, n2=11).

	Female Mean	SD	Male Mean	SD	*U*	*P*
Body mass (g)	182.5	54.5	149.5	38.4	1.243	0.272
Body length (mm)	18.5	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. Male and female burrows did not differ 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 3.2).

Table 3.2

Winter and summer burrow characteristics (mean and standard deviations SD) of *G. capensis*. *F* and *P* values denote the results of a General Linear Model examining the effects of season. Results for sex and sex* season are excluded as they are all insignificant

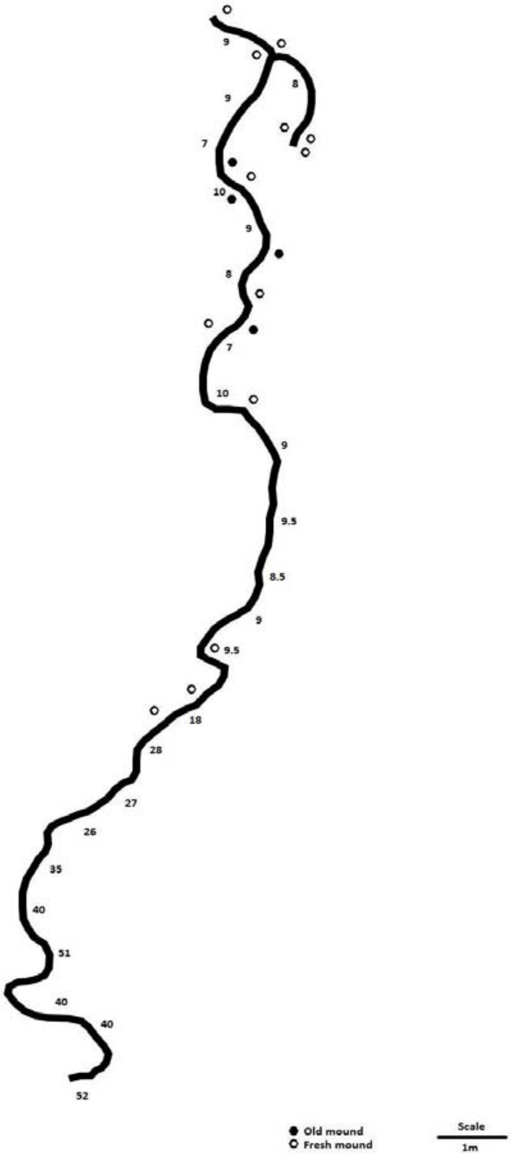
	Winter		Summer			
	Mean	S.D	Mean	S.D	*F*	*P*
Burrow area (m^2)	182.8	213	21.7	38.4	27.6	<0.00
Burrow length (m)	25.4	11.4	10.3	8.2	28.6	<0.00
Fractal dimension	1.0509	0.02	1.0684	0.04	1.3	0.271
Mounds	12.6	8.8	4.3	2.3	21	<0.00
Old mounds	5.2	4.3	2.8	1.5	3.2	0.081
Fresh mounds	7.4	5.4	1.6	2.1	29.3	<0.00
Branch number	2.3	2.6	3.2	2.1	0.1	0.912
Depth (cm)	14.5	5.4	11.6	5	6	0.02
Tunnel height (cm)	8.9	1.6	7.5	0.7	14.8	0.001
Tunnel width (cm)	8.3	1.04	7.4	0.7	15.3	<0.00
Arched tunnels	12.5	14.4	4.4	11.6	4.4	0.044
Round tunnels	87.5	14.4	95.6	11.6	1.6	0.212
Shallow tunnels	78.9	20.9	86.7	19.1	6.3	0.018
Deep tunnels	21.1	20.9	12.3	16.8	4.1	0.5
Turning angles (°)	145.9	25.1	152.3	19.1	2.1	0.158
Branch angles (°)	5.4	3.5	2.2	1.3	0.001	0.959
Intra branch distance (m	5.4	3.5	2.2	0.4	1.9	0.19

Burrow systems ranged from being extremely short; only a few metres of shallow tunnels with no or few branches, to extensive with numerous branches (Table 3.2). Burrow systems varied in the number of chambers, latrines and bolt holes (Figs.3.2 and 3.3). Nest chambers occurred in both male and female 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; this was in a female burrow system 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.

Figure 3.2.

Burrow systems of a single male (Burrow length 46.1m, fractal dimension 1.045) (a) and a single female (burrow length 62.9m, fractal dimension 1.218) (b) *G. 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.

(a)



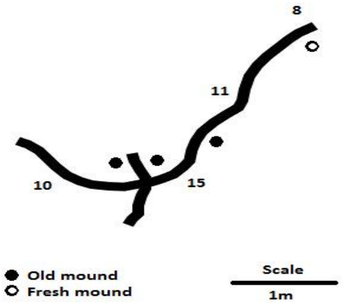
(b)


9
13
14
9
11
10
8
9
11
14.5
13
10
9
14
21
22
23
29
9
16
12
21.5
27
27
N
F
● Old mound
○ Fresh mound
N Nest
F Food store
Scale
1m

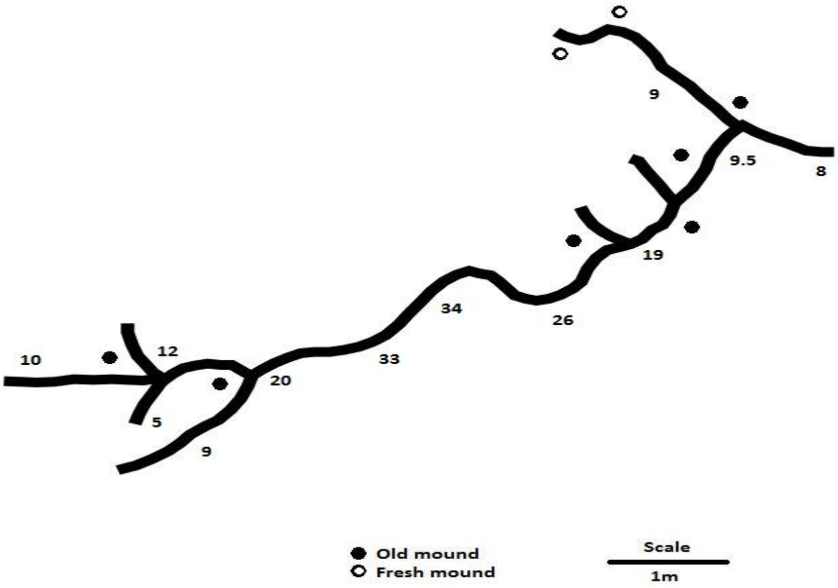
Figure 3.3

Burrow systems of a single male (Burrow length 12.4m, fractal dimension1.134) (a) and a single female (burrow length21.2m, fractal dimension 1.142) (b) *G. 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.

(a)



(b)



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 ± 207.7m in summer. The mean distance between females in winter and in summer was 149.7 ± 136.5m and 261.5 ± 296.8m respectively. The distance between male and female systems in winter ranged from 17.5 to 550m (11 ± 283m) and in summer ranged from 41 to 983m (56 ± 88m).

Discussion

My prediction that burrow length and associated burrow architecture of both sexes would differ between seasons was supported, but I 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 my 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* is 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 enable *G. capensis* to reduce digging effort in summer as 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 shorter length of the burrow systems and the few food stores coupled with the higher 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, and was deeper in winter than in summer, perhaps this might have acted as a buffer against lower 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), males increase burrowing activity in winter and excavate longer burrows than females, perhaps as mate-searching activity. Interestingly, *G. capensis* shows no sex-difference in burrow length, area or environmental exploration, even during winter when males would 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 being significantly larger, possessing wider zygomatic arch widths than females (Thomas *et al*., 2009, Kinahan *et al*., 2008) and have burrow systems that 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 some reverse sexual dimorphism as indicated by a wider zygomatic arch width in females, suggests a different mating strategy. *Georychus capensis* may be an opportunistic breeder (Oosthuizen & Bennett, 2007), is an induced ovulator (Van Sandwyk & Bennett, 2006) and communicates via foot drumming (Bennett & Jarvis, 1988). This seismic signalling is more frequent in males, who show sex-specific foot drumming patterns, at the onset of the mating season (Bennett & Jarvis, 1988).

The data indicate greater size and shape variation in females rather than that in males. Sexual dimorphism was present, with females exhibiting a greater tail length and a wider zygomatic arch width than males. A larger head size has been considered as a secondary sexual 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; Holland et al., 2004). Female competition for resources may be associated with overtly aggressive behaviour (Stockley & Bro-Jorgensen, 2011). It has long been known 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 involved in the mating procedure (Bennett & Jarvis, 1988). The sex ratio may be biased in favour of females, and if so, males might be resources that determine where females are located.

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

Chapter 4

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

Submitted to Naturwissenschäften

Abstract

It has been proposed that sociality in mole-rats has evolved as a response to widely dispersed food resources and the limited burrowing opportunities that result from sporadic rainfall events. The "Aridity Food Distribution Hypothesis" (AFDH) posits that as food resources become more widely dispersed and rainfall becomes more sporadic, cooperatively digging and foraging animals will be more likely to survive than solitary ones. In the most arid regions, individual foraging efficiency is reduced and energetic constraints increase. In this study I describe the burrow architecture for both the winter (wet) and summer (dry) seasons. Burrow systems in winter were significantly longer, covered a greater area and had more side branches than those in summer. As the number of animals within a burrow system increased so did the burrow length and the burrow area investigated. Thus, the size of the area of habitat explored differed between seasons and the complexity of the burrow and efficiency of foraging is dependent upon the number of individuals present in the social group.

Keywords

Burrow systems, seasonality, *hottentotus*, AFDH, 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: *Georychus, 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 *Georychus capensis*.

The aridity food distribution hypothesis (AFDH) attempts to explain the degree of sociality within Bathyergidae: it proposes that in climatically constrained environments, social groups have evolved to ensure energetically efficient foraging (Jarvis *et al*., 1994; Lacey & Shermen, 1997). 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). The AFDH is broadly supported by investigations that indicate that aridity may limit dispersal, colony formation and foraging efficiency in mole-rats (Spinks et al., 2000); therefore, the opportunity for dispersal by *C. h. hottentotus* colonies in xeric regions is lower than populations inhabiting mesic regions (Spinks *et al*., 2000).

Seasonal data are available for three solitary species of mole-rat: *Bathyergus suillus* (Thomas *et al*., 2009), *Heliophobius argenteocinereus* (Sumbera *et al*., 2008), and *Georychus capensis* (Thomas *et al*., 2012) and for one social species, *Fukomys mechowii* (Sichilima *et al*., 2008). In the current study I have shown that differences in the burrow systems of common mole-rats occur with season and colony size. To date, this study is the most extensive investigating the burrow systems of *C. h.*

hottentotus and is the only study to compare seasonal burrow data. Previously, burrow systems of *C. h. hottentotus* have been compared in two separate regions (arid and mesic) to test the theory of the AFDH intra-specifically (Spinks *et al*., 2000) and no difference in colony size was found between mesic and arid regions, nor did the burrow characteristics differ.

In this study I investigate how intra-colony size and foraging behaviour (as determined by burrow structure and geometry) in a mesic environment differ between seasons, winter (wet) and summer (dry). Despite being a source of potentially important ecological information, the seasonality of burrow system geometry in subterranean mammals remains a poorly studied area of research. Furthermore, the few existing studies investigating burrow architecture and geometry in *C. h. hottentotus* have not made comparisons between seasons (Davies & Jarvis, 1986; Spinks *et al*., 1998). The objective of this study was to describe the burrow geometry of *C. h. hottentotus* over two seasons (summer and winter).

I predict 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) 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.

Materials and methods

Study animals

The common mole-rat, *Cryptomys hottentotus hottentotus* is a social species occurring in colonies of up to nine individuals in arid regions of southern Africa (Spinks, Bennett & Jarvis, 2000) and up to 16 animals in mesic regions (Davies & Jarvis, 1986). C*ryptomys hottentotus hottentotus* occur sympatrically with two other species of solitary mole-rat, the Cape mole-rat Georychus *capensis* and the Cape dune mole-rat, *Bathyergus suillus* in the Western Cape Province of South Africa. *Cryptomys hottentotus hottentotus* is characterised by a small mean body mass 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-west of the Western Cape Province, South Africa (33°22 S, 15°25 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 soil consisted of a mixture of clay and sandy loam (Thomas *et al*., 2009, unpublished data). Active burrow systems were identified by location of fresh mounds on the surface in winter. In summer, active burrow systems were identified by small, round flattened areas of soil often with vegetation growing from the soil. 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 4am and 11 am and the evening hours of 4pm and 9pm 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. On capture, mole-rats were sexed, weighed (±0.01g 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 15 burrows were excavated (6 for winter and 9 for summer).The lengths of the burrows 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 (± 0.1cm). Tunnels were defined as either being deep, semi-permanent (> 20cm deep) or shallow, foraging (< 20cm deep) tunnels. The distinction between tunnel usages was 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. 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 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 and were assumed to have an anti-predatory or thermoregulation function, or were 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 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). An increasingly complex burrow system is characterised by more 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, 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.

Statistics

Pearson product moment correlations and a General Linear Model (GLM) were used to examine differences between the seasons and colony size. A Mann Whitney U test was used to investigate differences in fractal dimensions of previous analysed *C. h. hottentotus* burrows. All statistical analysis was 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 4.1). Colony size ranged from one (presumed) ‘dispersing’ animal to 12 animals ($\bar{x}$ 5.13 ± 2.97 SD). The ratio of males to females varied. In summer, juveniles and young were present in 22% of colonies. One female was pregnant and gave birth whilst in captivity to two young. There were two lactating females each with two young from two separate colonies. Young animals were defined as being less than 6 months old and less than 40g.Juveniles were defined as being over 40g but less than 50g.

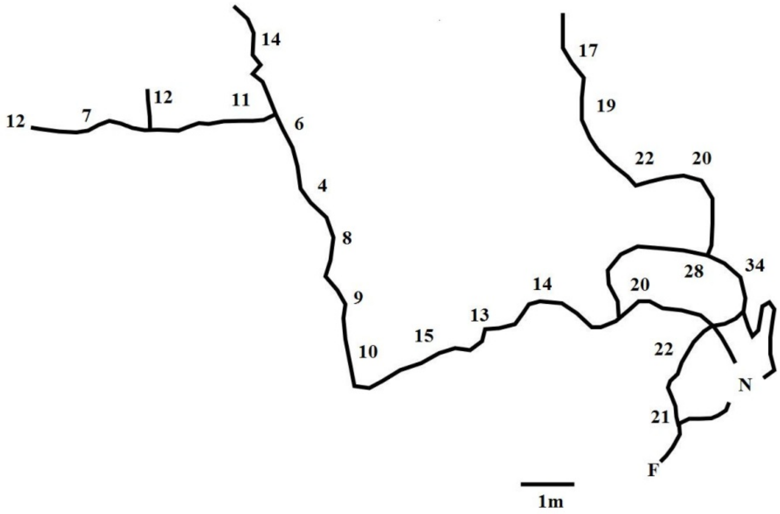
Burrow systems

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 4.1a and 4.1b; summer Figure 4.2a and 4.2b). Burrow systems had a varying number of chambers (nest, latrines and food stores) and bolt holes (Table 4.1). Burrow systems did not overlap with one another although they were located in the same field.

Figure 4.1

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)



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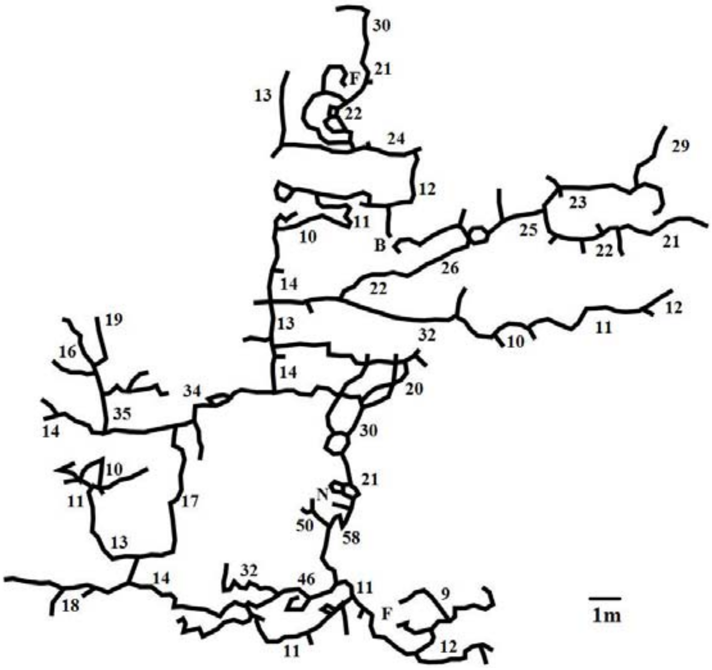
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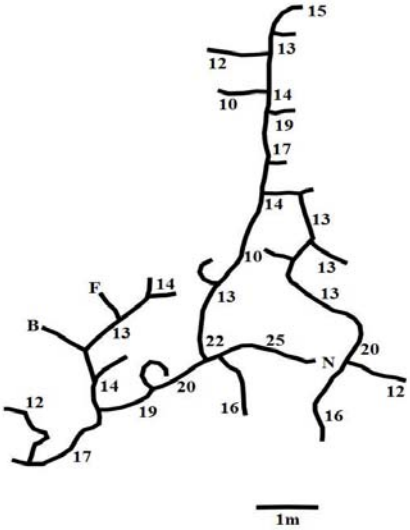
Figure 4.2

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)

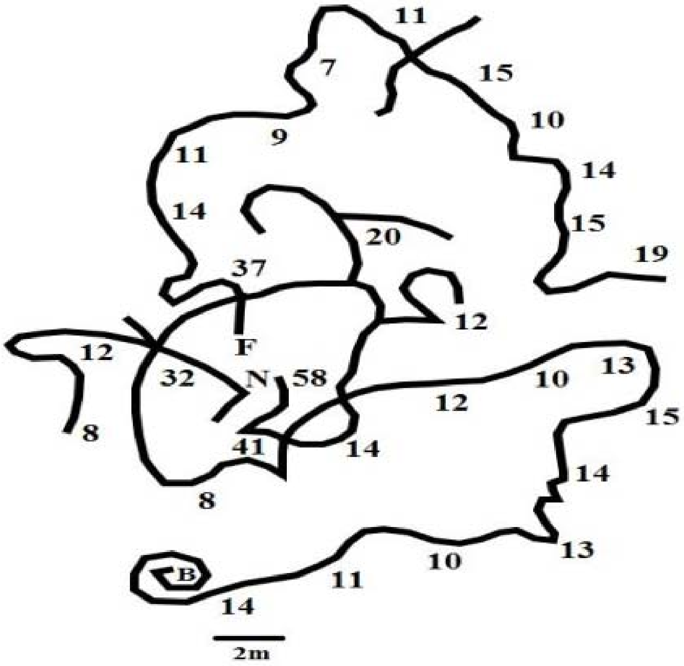

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Table 4.1

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

Season	Number of occupants	Burrow length (m)	Burrow area (m²)	Fractal dimension	Mound number	Old mounds	Fresh mounds	Branch number	Depth (cm)	Nest	Food store	Bolt hole
Summer	6	32.6	84	1.087	1	0	1	16	14.1	1	0	1
Summer	1	13.2	7	1.049	1	0	0	4	15.4	0	0	0
Summer	2	14.3	9	1.073	2	2	0	10	12.7	1	0	1
Summer	5	29.8	216	1.27	3	3	0	13	14.1	1	0	1
Summer	12	41.6	35	1.24	1	1	0	24	23.1	1	1	1
Winter	8	278.1	1911	1.261	79	56	23	64	12.0	1	1	0
Winter	2	10	8	1.174	2	0	2	3	12.1	0	0	0
Winter	4	21.9	38	1.107	16	6	10	9	11.9	1	1	0
Winter	10	510.7	35020	1.293	798	465	333	165	12.6	1	2	1
Winter	5	37.5	113	1.086	63	54	9	6	14.9	1	1	1
Winter	4	31.7	80	1.106	52	41	11	4	9.5	1	1	0
Summer	4	24.8	35	1.209	4	4	0	17	11.8	1	0	0
Summer	4	11.9	9	1.151	1	1	0	11	12.2	0	0	1
Summer	6	41.4	88	1.218	1	1	0	20	14.8	1	1	2
Summer	4	18.3	36	1.138	3	0	3	19	8.9	1	0	0

Seasonality

The length of the burrow systems differed significantly between the seasons with winter burrows being longer than summer burrows but not in the area encompassed (*F* = 19.96 *P* = 0.001, *F* = 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* = 13.26, *P* = 0.004), but did not differ in fractal dimension, burrow depth or in tunnel dimensions (Table 4.2).

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* = 67.53 *P* = <0.001) and covering a greater area (*F* =10.85 *P*= 0.007) and explored the surrounding environment more efficiently, as indicated by a higher fractal dimension value (*F* = 9.9, *P* = 0.009), and had a greater number of branches within the burrow system (*F* = 39.1, *P* = <0.001). Tunnel dimensions and tunnel depth did not differ significantly with the numbers of occupants within a burrow system (Table 4.2).

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* = 56.12, *P*= <0.001; *F* = 10.8, *P* = 0.007 and *F* = 28.39, *P* = <0.001). None of the other burrow characteristics were significantly different (Table 4.2).

Table 4.2

General Linear Model (GLM) results for seasonal differences (winter: summer), differences in the number of occupants in the burrow systems and their interactions in relation to *C. h. hottentotus* burrow characteristics.

		Season			Number of occupants			Season* number of occupants	
	DF	*F*	*P*	DF	*F*	*P*	DF	*F*	*P*
Burrow length (m)	1	19.96	<0.001	1	67.53	<0.001	1	56.12	<0.001
Burrow area (m^2)	1	4.48	0.058	1	10.85	0.007	1	10.8	0.007
Fractal dimension	1	0.27	0.612	1	9.9	0.009	1	0.36	0.56
Branch number	1	13.26	0.004	1	39.1	<0.001	1	28.39	<0.001
Depth (cm)	1	0.44	0.522	1	4.67	0.054	1	2.82	0.121
Tunnel height (cm)	1	0.95	0.351	1	1.77	0.211	1	0.81	0.389
Tunnel width (cm)	1	2.77	0.124	1	2.5	0.142	1	0.92	0.359
Total error	8			8			8		

Discussion

Mole-rats provide an ideal model group with which to test theories regarding foraging behaviour and habitat exploration as foraging literally takes place "blind". They inhabit an environment that is thermally buffered and protected from most predators but is energetically expensive to create and maintain (Nevo, 1979; Bennett, Jarvis and Davies, 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, it is especially important that any foraging is efficient during the summer when the ground is hard and the excavation of burrows is difficult.

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. This is most likely because during the winter the soil is moist and friable and can be worked easily in comparison to during summer. Despite the differences in the size of the burrow systems between the seasons, habitat exploration (as defined by the fractal dimension value) did not differ between seasons, but did differ with 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 focused on associations between environmental characteristics (namely climate) and burrow structure (Spinks & Plaganyi, 1999; Sichilima *et al*., 2008). 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, 1.27, 1.33 and 1.42) as the burrows in our study. Three burrows from the same area (Darling) as our study had significantly higher fractal values (W = 130.5 P = 0.0005) (1.4, 1.51 and 1.62) (Le Comber *et al*., 2002) than our study indicating that intra specific variation in burrow characteristics may depend upon habitat rather than the climatic environment.

I 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, but because disused tunnels are back-filled rather than the spoil being expelled as a mound. I 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 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 (ie winter).

In conclusion, the hypothesis that differences in burrow structure occur between seasons was generally supported. Burrows in winter tended to be longer in length and cover a greater area with more side branches. The main reason for this may be that mole-rats were unable to produce mounds and extend burrow systems during the summer season, presumably because it was too costly to transport the soil to the surface and therefore resort to back-filling, resulting in the burrow systems remaining small.

Chapter 5

Bite force and sociality in African mole-rats (Rodentia: Bathyergidae)

Abstract

African mole-rats inhabit a subterranean environment in which they have to excavate extensive tunnel systems to enable them to locate food and find mates. Members of the Bathyerginae (*Bathyergus*) excavate burrow systems using enlarged forelimbs, unlike the Georychinae species (*Heterocephalus*, *Heliophobius*, *Georychus*, *Cryptomys* and *Fukomys)* which dig using chisel-like extrabuccal incisors. African mole-rats vary in their degree of sociality from strictly solitary (e.g. *Bathyergus janetta*) through to social (e.g. *Cryptomys hottentotus hottentotus*) and eusocial (e.g. *Fukomys damarensis*) species. This study set out to examine whether bite force in is affected by sociality, digging behaviour and sex. I found no evidence of sexual dimorphism with bite force even in solitary species, nor did bite force appear to be allometric to body size as has been previously suggested. Of all species, the solitary Cape mole-rat, *G. capensis* has the greatest bite force.

Keywords: Bite force; sociality; sexual dimorphism; sexual selection; mole-rats

Introduction

African mole rats (Bathyergidae) vary in degree of sociality, from solitary species (*Bathyergus*, *Georychus*, *Heliophobus*) through to social (*Cryptomys*, *Fukomys*) and eusocial (*Fukomys*, *Heterocephalus*) (Bennett & Faulkes, 2000). This variation in sociality appears to be linked to aridity and the distribution of the food resources (Jarvis et al. 1994; Faulkes *et al*., 1997). For example, *Bathyergus suillus*, the Cape dune mole rat, is solitary and occurs in a mesic habitat with loose sandy soils in the Cape region of South Africa and feeds primarily upon grasses and some forbs and corms (Bennett & Faulkes, 2000). The eusocial

Damaraland mole-rat occurs in colonies of up to 41 individuals (Bennett & Jarvis, 1988; Jarvis & Bennett, 1993) and inhabits arid regions with compacted sandy soils in south western Africa where they feed on corms and tubers that are distributed in widely-spaced clumps. These differences in the resource distribution and the period of time that the substrate is favourable for excavation may be considered the major driving forces in the evolution of the different levels of sociality within this taxon (Burland *et al*., 2002).

African mole-rats demonstrate a range of body masses and different degrees of sexual dimorphism. Solitary *B. suillus* are large (up to 2.5kg, M. Scantlebury unpublished data) and both *B. suillus* and *B. janetta* show a higher degree of male sexual dimorphism (mean body masses for *B. suillus* are 933g and 635g and *B. janetta* are 451g and 332g for males and females respectively, Jarvis & Bennett, 1991). Solitary *Georychus capensis* show little size dimorphism (mean body mass 137g and 127g for males and females respectively, Scantlebury *et al.*, 2006). The social *Cryptomys hottentotus hottentotus* and eusocial *F. damarensis* are small and exhibit male sexual dimorphism. *Cryptomys h. hottentotus* has a mean body mass of 83g and 58g for males and females respectively (Davies & Jarvis, 1986) whereas *F. damarensis* has a mean of 165g and 142g for males and females respectively sexes (Bennett & Jarvis, 2004).

In mammals male sexual dimorphism, with the male being larger than the female indicates inter and/or intrasexual conflict, where the larger sex uses its larger size to fight rivals or to coerce females in order to gain copulations (Clutton-Brock & Harvey, 1978). For bathyergids, the normal method of fighting is through incisor fencing, using the greatly enlarged extrabuccal incisors: *B. suillus* males have a large pad of thickened skin on their necks that appears to be adapted to protect them in such fights (Davies & Jarvis, 1986). Greater bite force might then be an adaptive, sexually-selected trait. While the two species of *Bathyergus* are primarily 'scratch' diggers which excavate with their forepaws, *Georychus, Cryptomys* and *Fukomys* are primarily 'chisel–tooth' diggers which excavate with their teeth, using them to chisel away sand and soil, before kicking it back with their hind quarters. The 'scratch' digging species are limited to sandy loose soils and use their forepaws as this the most energetically efficient method of excavation for these larger species. Mole-rats range in sociality. Solitary species (where males are larger than females) often have to fight to gain access to and copulations with females. It would be expected that males of solitary species would have a larger bite force than females to give them an advantage for fighting. Although an increased bite force in social and eusocial animals is not expected for fighting it may be an adaptive mechanism as these animals are chisel-tooth diggers and construct large elaborate burrow systems using their incisors. In the light of the variation in sociality, sexual dimorphism and feeding/digging behaviour, I examined bite force in five species of bathyergid and made the following predictions:

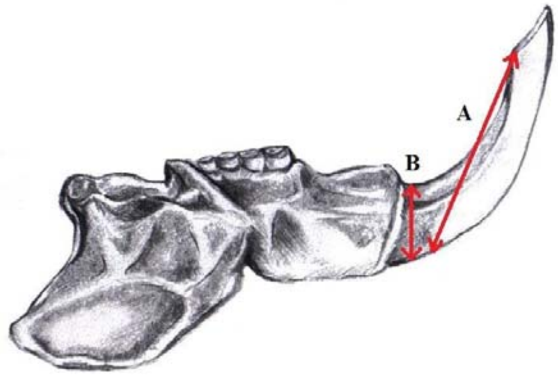
1) Larger individuals will have a greater bite force,
2) Males of solitary species will have a greater bite force than females,
3) Solitary species will have a greater bite force than social or eusocial species.

Materials and methods

I measured bite force in five species of African mole-rat namely *G. capensis*, *B. janetta, F. damarensis,* and *C. h. hottentotus* from skull collections held at the Department of Zoology & Entomology, (*B. janetta, F. damarensis, G. capensis and C. h. hottentotus*) and from the Transvaal Museum of Natural History (Ditsong National Museum of Natural History), Pretoria (*B. janetta, F. damarensis, G. capensis, C. h. pretoriae* and *C. h. hottentotus*). I used body length as a measure of individual size as this was available for all specimens. All specimens used were of adult age as indicated by the presence of all 4 cheek teeth fully erupted on either side (age class 4-9 as defined by Janse van Rensburg *et al*., 2004). To calculate bite force I used a highly predictive single index of strength based on two measurements of the lower incisors at the level of the alveolus identified by Freeman & Lemen (2008a). The bite force method has been accurately correlated with results from peizo force tranducers (Freeman and Lemen, 2008a). The incisor was measured for length (anterior – posterior length) and width (medial – lateral width) (Figure 5.1 a and b for length and width respectively), both taken at the level of the dorsal-most rim of the alveolus using digital callipers (±0.01mm). The index of strength was calculated using the equation Zi = (anterior – posterior length) ^{2} × (medial – lateral width)/6 (Freeman & Lemen, 2008b).

Figure 5.1

Image showing incisor measurements taken on the lower mandible to calculate bite force A: anterior - posterior length, B: medial - lateral width.



Statistics

A general linear model was used to examine bite force, with body length as a covariate. Factors entered into the analyses were “social type”, with species nested within social type, and sex. Species were categorised as being solitary, social or eusocial. The analyses also tested for interactions between sex and species, and between sex and social type. We examined interactions between sex and species, and social type and sex. Finally we used a Tukey post hoc comparisons test to compare differences between species. The results were analysed using a General Linear Model (GLM) in Minitab 16 (Minitab 16 Statistical Software, 2010).

Results

Bite force varied significantly amongst species ($F_{(2,268)} = 8.81$, p = <0.001), but body length of individuals had no significant effect on bite force ($F_{(1,268)} = 0.10$, p = 0.754), nor was there an effect of sex in any species ($F_{(1,268)} = 1.66$, p = 0.198) (Table 5.1). Level of sociality significantly affected bite force ($F_{(2,268)} = 3.66$, p = 0.027) with solitary species having the largest bite force, (Table 5.1). The Tukey post hoc test comparisons between species revealed that *G. capensis* differed from *F. damarensis* and *C. h. hottentotus* in bite force and the data showed that *G.capensis* has the greatest bite force (Table 5.2).

Table 5.1

General linear model results with body length entered as a covariate of bite force and factors which include social type (categorised as solitary, social and eusocial), with species nested within social type, and sex. Interactions between sex and species and between sex and social type are included.

Source	*DF*	*F*	*P*
Body length	1	0.1	0.754
Social type	2	3.66	0.027
Species (Social type)	2	8.81	<0.001
Sex	1	1.66	0.198
Sex*Species (Social type)	2	0.95	0.39
Social type*sex	2	0.88	0.416
Error	268		
Total	278		

Table 5.2

Tukey post hoc test comparison results showing *G. capensis* differing from *F. damarensis* and *C.h. hottentotus* in respect to bite force.

Social type	Species	*N*	Mean bite force
Solitary	*G. capensis*	90	31.8
Social	*C.h. pretoriae*	25	23.8
Solitary	*B. janetta*	8	22.3
Eusocial	*F. damarensis*	73	13.6
Social	*C.h. hottentotus*	83	8.9

Discussion

It is generally accepted that an organism's design is a compromise between adaptation to its environment and phylogenetic constraints (Wainwright, 1996). For many taxa there are likely to be evolutionary trade-offs in the relationship between morphology, diet and feeding ecology that may ultimately constrain phenotypic variation (Freeman, 1984). More specifically, bite force capacities may be closely related to both the type and magnitude of the ecological challenges of food acquisition, mate acquisition, and anti-predation in vertebrates (Anderson *et al.,* 2008). Among mammals, subterranean rodents have the greatest bite force in relation to their body size (Van Daele *et al*., 2008).

An *in vivo* study of bite force using force transducers by van Daele et al. (2008) in *F. damarensis* revealed that bite force in mole-rats is positively related to head length. Scaling of bite force has been shown to positively related to a range of morphological characteristics, such as body mass, body length and jaw length in other animals (mammals; Meers 2002, sharks; Huber 2006, alligators; Erickson *et al.* 2003, finches; Herrel *et al.* 2005, turtles and lizards; Herrel & O'Reilly 2005). It has been suggested that patterns of positively scaling allometry may be attributable to unique growth scales of individual skeletal elements (Erickson et al., 2003). In the current study, body length had no effect on bite force in any of the species and therefore the scaling of bite force may be related to other features such as jaw muscle size.

My results revealed that bite force varied significantly among species and appeared not to be influenced by the level of sociality. In addition, *Bathyergus janetta* did not differ significantly in bite force from any of the other species analysed, even though they are part of a different subfamily (Bathyerginae as opposed to Georychinae) and are larger and are sexually dimorphic for body mass.This suggests that the differences in bite force may not be phylogenetically constrained nor sexually-selected but, more likely are been influenced by the external environment eg. range of soil hardness or range of food types available. The bite force data suggest that social animals generally have a smaller bite force than those of solitary species, even though it was not significantly smaller. Smaller bite forces appears to be regardless of body size and is probably as a consequence of reproductive suppression in their natal colonies , which obviates the need for most individuals to compete sexually. Division of labour in social and eusocial species reduces the need for individuals to invest in chisel-digging as excavation is shared amongst colony members.

In previous studies, bite force has been linked to male dominance and is correlated with social-display structures in several taxa (Anderson, McBrayer & Herrel, 2008). Therefore, bite force performance measure can be viewed as a sexually selected trait as a larger bite force enables males to be more dominant and gainaccess to females. However, *Bathyergus janetta* which is strictly solitary, and exhibits sexual size dimorphism, did not differ significantly from any of the other species in terms of bite force variation between the sexes. Therefore these data do not support our prediction. This was unexpected as the jaws and teeth of *B. janetta* are reported to be used in sexual interactions including male – male combat and coercion of copulation of females by males (Herbst, Bennett & Jarvis, 2004).

The species with the highest bite force was *Georychus capensis*, which, despite being solitary exhibits was not sexually dimorphic in body size (Thomas *et al*., 2012). There are conflicting views regarding male – male aggression; it has been suggested that it is high as with other solitary species of mole-rat (Bennett & Faulkes, 2000). Recent work, however, indicates an alternative mating strategy where males are the limiting resource and female's exhibit heightened aggressive behaviour towards other females (Thomas *et al*., 2012). In our study *G. capensis* differed in bite force from *F. damarensis* and *C.h. hottentotus.* This is likely to be due to both sexes potentially competing intra-sexually for access to mates and, as solitary chisel-diggers, investing in digging ability. Further research into bite force in other species of mole-rat could highlight morphological adaptations to a subterranean existence in which bite force plays an important role in mole-rat ecology enabling them to locate food and mates.

Chapter 6

Skeletal structure and function in the forelimb bones of three species of southern African mole-rat (Bathyergidae)

Abstract

Burrowing is an integral part of life in a subterranean mammal. A life underground that requires consistent burrowing will mould the osteology and morphology of an organism to optimise efficient burrowing. In subterranean rodents of the family Bathyergidae, the excavation of burrow systems is carried out using either strong claws on the forelimb or procumbent extrabuccal incisors. Within the forelimb, skeletal system adaptations have occurred to withstand greater pressure such as increased bone robustness allowing for attachment of larger muscles resulting in efficient digging. This study describes the principle bone structure for the major forelimb cones involved in digging. The bones described are the scapula, humerus, ulna and radius. It highlights slight variations in the structure of the scapula, humerus and ulna between claw digging and chisel tooth digging mole-rats, which allows for greater stride distance rather than increased dexterity in the forelimb. This study increases our knowledge of basic macro-anatomical descriptions that are lacking for mole-rats and suggests areas for further research.

Keywords

Functional morphology, mole-rats, forelimbs, ulna, radius scapula, humerus

Introduction

The forelimbs are the primary component of the digging apparatus in subterranean rodents along with the teeth, head and neck (Lacey, 2000). Subterranean mammals that use their forelimbs for burrowing display a variety of distinct morphological modifications of the pectoral girdle as burrowing results in greater forces being generated by, and placed on, the limbs; therefore most digging mammals have relatively short but, robust limb bones (Casinos et al., 1993) that are able to resist both torsion and bending. The limb bones also have pronounced processes and tuberosities for muscle attachment that may reflect the mode of burrow excavation. Biknevicius (1992, 1993) for example has shown that differences in the burrowing styles in at least some subterranean genera are reflected in specific differences in the humerus, where increased widening of cortical bone is observed. Fossorial mammals typically show muscular modifications to allow the production of large forces for digging. Considering the physics of levers, improved mechanical advantage may be accomplished in three ways: by changing the point of muscle attachment, by increasing the length of the in-lever or by decreasing the length of the out lever. No proportional differences in muscle mass have been reported between the sexes or between juveniles and adults in the pocket gophers implying the same method of excavation in different ages and sexes (Lessa & Thaeler, 1989).

In subterranean rodent mole-rats, claw diggers (e.g. *B. suillus* and *B. janetta*) are characterised by the possession of large forelimb muscles, enlarged insertion sites on forelimb bones and enlarged claws, whereas chisel-tooth diggers (*C. h. hottentotus* and *G. capensis*) typically have procumbent incisors and enlarged jaw muscles (Dubost, 1968; Hildebrand, 1985; Nevo, 1979).

In burrowing mammals that use their forelimbs for digging it is predicted that the long bones of the pectoral girdle should be thicker (Merritt, 2010). The maximum width of the distal end of the humerus relates to the intensity of the force of the digital flexors and extensors and should, therefore, be larger in mammals that dig (Goldstein, 1972).

Subterranean mammals should have bone – muscle systems with relatively large mechanical advantages. An important factor that affects the overall width of the long bones of the limbs is absolute body size. In order for mammals to compensate for increased size, there must be a disproportionate thickening of the limb bones. In order to compensate fully for body volume as overall size increases the leg width must increase in proportion to the power 1.5 of the increase of leg length (Gould, 1966).

Macro-anatomical investigations of skeletal systems in wild animals are fairly limited. Investigations have been published on insectivores (Özkan, 2004), wild ruminants (Siddiqui et al, 2008), lagomorphs (Özkan et al., 1997) and rodents (Özkan et al., 1997; Oulde et al., 2010). Within the order Rodentia the macro-anatomical skeletal system of mole-rats has been investigated, only in one species, the Mediterranean mole-rat, *Spalax leucodon* (Özkan, 2002). The various members of the Bathyergidae, the sub-Saharan hystricognath mole-rats of Africa, offer an ideal opportunity to examine the importance of morphological design as a determinant of behavioural and ecological patterns under natural conditions. The aim of the present study is to investigate the long bones of the forelimb in the skeletal system in three sympatric species of mole-rats and to contribute to the present level of knowledge.

Materials and methods

Study animals

Three sympatric species of mole-rat (*Bathyergus suillus, Georychus capensis* and *Cryptomys hottentotus hottentotus*) can occupy the same habitat in the Western Cape Province of South Africa. The Cape dune mole-rat, *Bathyergus suillus* is the largest truly subterranean mammal and exhibits sexual size dimorphism with males being significantly larger than females (Jarvis & Bennett, 1991; Thomas *et al*., 2009). Some individuals of 2.5 kg in body mass have been recorded (M. Scantlebury unpublished data). Indeed, the large size and the associated energy costs of digging appear to be factors confining this species to the sandy soil areas of the south and south-west of South Africa (Bennett & Faulkes, 2000; Thomas *et al*., 2009). The Cape dune mole-rat is one of two species of the Bathyergidae which excavates their burrow system predominantly using enlarged forepaws. *Bathyergus suillus* and its congener *B. janetta* are solitary species whose burrow systems remain fairly simple with one or two deep semi-permanent tunnels and numerous shallow side branches which are used for foraging for food and mates (Herbst & Bennett, 2006; Thomas et al., 2009).

The Cape mole-rat, *Georychus capensis* has a mean head and body length of 17.34cm for males, 18.5cm for females (Thomas *et al*., 2012) and mean body mass of 181g for males and 182g for females (Thomas *et al.,* 2012). *Georychus capensis* is a solitary species which constructs relatively simple burrow systems using its chisel like incisors. *Georychus capensis* burrow systems comprise of one or two main deep semi-permanent tunnels with numerous shallow foraging tunnels and chambers dedicated to the storage of faeces, food or rearing of offspring (Thomas *et al*., 2012).

The common mole-rat, *Cryptomys hottentotus hottentotus*, has a mean body mass of 83g for males and 58g for females (Davies & Jarvis, 1986). It occurs in social groups of up to 12 individuals which occupy a single burrow system that comprises one or more large nests, with latrines, bolt holes and food storage areas. As with *G. capensis*, it excavates the burrow systems using its chisel-like incisors.

The bones examined in this study were obtained from animals caught from a single study site during the summer and winter seasons of 2010 and 2011 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). A total of 20 specimens for *B. suillus*, 30 specimens for *G. capensis* and 40 specimens for *C. h. hottentotus* were observed. All specimens were of adult age (all 4 cheek teeth present).

The long bones used in this study were the ulna, radius, humerus and scapula. Bones were prepared using a process of maceration (Hooper & Ruysch, 1809; Bartels & Meyer, 1991).

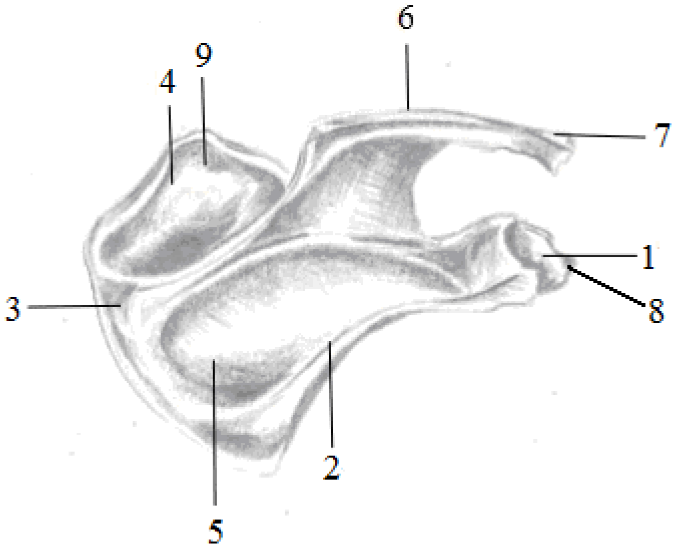
Results

Scapula

In *Bathyergus suillus* the scapula is roughly triangular in shape (Fig. 6.1). The anterior is narrow in shape and rapidly expands into a fan shaped posterior. The coracoid border is smooth in outline and as it extends towards the vertebral border it forms a slight rounded protuberance. The glenoid border is well-developed to receive the attachment of the triceps group of muscles (Fig. 6.1). In cross section the vertebral border is slightly convex. The dorsal surface of the scapula is slightly convex and is divided into the supraspinous and infraspinous fossae by the large mesoscapular spine (Fig. 6.1). The supraspinous fossa has a larger surface area than the infraspinous fossa. The acromion is small, robust and is angular in shape. The mesoscapular spine is well developed and is thicker than the acromion, and is more angled towards the vertebral border. The spine is robust and well developed passing almost central for most of the length of the scapula. The spine instead of being central towards the metacromium process connects to the coracoid process (Fig. 6.1). The edge of the spine is angled in cross section and is rotated towards the *m.teres major* process.

Figure 6.1

Bathyergus suillus, osteology of the pectoral girdle. The dorsal view of the scapula. 1: Glenoid border, 2: Coracoid border, 3: Vertebral border, 4: Supraspinous fossa, 5: Infraspinous fossa, 6: Meso-scapular spine, 7: Acromion, 8: Metacromion process 9: *Teres major* process.



In *G. capensis* the scapula is more triangular in shape than in *B. suillus*. The anterior is approximately one third of the size of the posterior. The anterior gradually expands in shape and almost forms a diagonal plane at the posterior. The coracoid border is smooth in outline and as it extends towards the vertebral border it forms a slight rounded protuberance at the posterior.The glenoid border is less developed than in *B. suillus* to receive the attachment of the triceps group of muscles. In cross section the vertebral border is flat and angled slightly towards the teres major process. The dorsal surface of the scapula is flat and is divided into the supraspinous and infraspinous fossae by the mesoscapular spine. The acromion is larger than in *B. suillus* and is triangular in shape. The mesoscapular spine is well developed and narrows from the enlarged acromion, and is located centrally compared to that of *B. suillus*. The spine is fairly fragile and passes centrally for the entire length of the scapula. The edge of the spine is flat in cross section.

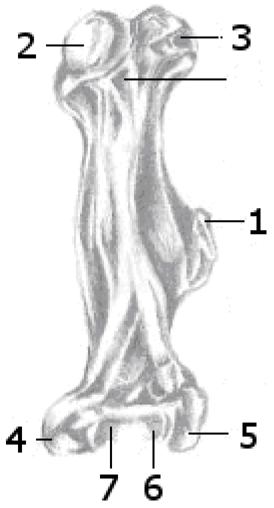
In *C. h. hottentotus* the scapula is virtually identical in shape to *G. capensis*, although there are a few differences. The anterior is approximately one half of the size of the posterior. The coracoid border is more angular in outline and as it extends towards the vertebral border and it does not form a protuberance at the posterior. The mesoscapular spine is almost cylindrical in shape and is the same in diameter as the acromion.

Humerus

In *B. suillus* the straight shaft of the humerus is robust and approximately three times the length of the wide distal end. The entire shaft of the humerus is almost grained in appearance and is symmetrical in shape with a slight protrusion opposite the deltoid tuberosity (Fig. 6.2). The deltoid tuberosity is almost rough in appearance. The head of the humerus is large, almost hemispherical in form and protrudes from the proximal end of the bone and articulates with the glenoid fossae of the scapula (Fig. 6.1). The tuberosities on both sides of the humeral head are large. The greater tubercle sits lateral to the humeral head and is the smaller of the two tuberosities. The medial epicondyle is the site of origin for the forearm flexor and pronator muscles. The medial and lateral epicondyles are of equal size. The capitulum is separated from the trochlea by a distinct indentation and provides the point of articulation of the radius.

Figure 6.2

Bathyergus suillus, osteology of the pectoral limb. The anterior view of the humerus. 1: Deltoid tuberosity, 2: Humeral head, 3: Greater tubercle, 4: Medial epicondyle, 5: Lateral epicondyle, 6: Capitulum, 7: Trochlea.



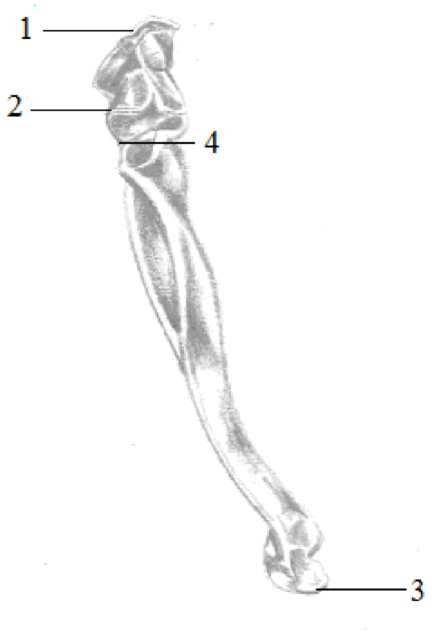
In *G. capensis* and *C .h. hottentotus* the appearance of the humerus is identical to *B. suillus* apart from a few exceptions. In *G. capensis* and *C. h.hottentotus* the distal end of the humerus is only a quarter of the shafts length. In *G. capensis* there is only a minute protrusion opposite the deltoid tuberosity and this is not visible at all in *C .h. hottentotus.*

Ulna

In *B. suillus*, the ulna is prismatic and angulated in shape and has numerous processes for muscle attachment. It is divisible into a body and two extremities (Fig. 6.3). The upper extremity presents two curved structures, the olecranon and the coronoid process. The olecranon is small accounting for approximately one eighth of the total length of the ulna. The olecranon is bent forward at the top to create a lip to allow attachment of the humerus (Fig. 6.3). Both the dorsal and ventral sides of the process serve for muscle attachment for the triceps and extensors of the wrist respectively. The shaft of the ulna is relatively long, being longer than that of the humerus. The shaft of the ulna tapers from the olecranon to the distal end which is angular in shape (Fig. 6.3). The shaft is grooved for its entire length. The styloid process is small and rounded and bears a facet for the cuboid and pisiform bones. In *G. capensis* and *C. h.hottentotus* the ulna varies in form from that of *B. suillus*. The olecranon and coronoid process account for approximately one third of the shaft's total length and the shaft grooves are less prominent in appearance.

Figure 6.3

Bathyergus suillus, osteology of the pectoral limb. The anterior view of the ulna 1: Olecranon, 2: Coronoid process, 3: Styloid process, Radial notch.

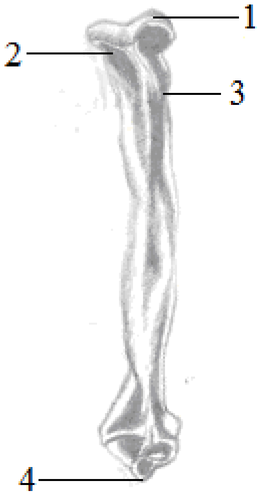


Radius

In *B. suillus*, *G. capensis* and *C. h. hottentotus* the radius is situated on the lateral side of the ulna. The radius is three quarters of the length of the ulna and is thick and robust. Both the proximal and distal ends of the bones are expanded for articulation with the humerus and ulna (Fig. 6.4). Both ends are of similar size, but are different in form. The head of the radius is rectangular in shape and the lower extremity of the radius is angular in shape. The shaft of the radius is grooved and angled for its entire length (Fig. 6.4). The shafted is angled approximately half way down, perhaps as a means of improving resistance to the medial forces of the attached muscles. There is a small protrusion one eighth of the way down the shaft of the radius. Along the posterior aspect of the shaft of the bone is a narrow groove in which lies a tendinous fibre that binds the shafts of the radius and ulna together (Fig. 6.4).

Figure 6.4

Bathyergus suillus, osteology of the pectoral limb. Lateral view of the radius. 1: Head of radius, 2: Neck of radius, 3: Radial tuberosity, 4: Styloid process.



Discussion

The influence of phenotypic evolution in the process of diversification is a broad question in evolutionary biology that can be investigated at different taxonomic levels. An understanding of how natural selection acts on the phenotypic traits as well as an understanding of the relationship between morphology and ecology is important in the realm of evolutionary morphology (Love, 2003).

Digging activity has caused diverse adaptations in subterranean rodents (Reig *et al*., 1990; Casinos *et al*., 1993). Compared to non-digging mammals, the humerus of subterranean rodents has a well developed humeral head with a pronounced deltoid tuberosity. The muscles are broader and their origins and insertions are relatively farther away from the articulations (Hildebrand, 1985; Lessa et al., 2008). The relationships between bone structures, origin, and inserts of the muscles can result in a mechanical advantage for muscles and an increased resistance of bone to muscular actions. In claw diggers, the forelimb system is adapted to produce strong forces of extension of the shoulder and elbow joint (Vassallo, 1998). In almost all comparative studies of diggers and non-diggers, bone resistance is demonstrated by the robustness of the shoulder and by an angulated deltoid tuberosity for the fixation of the extensor muscles (Vasallo 1998). This study supports the concept that claw diggers have robust scapula bones and angular deltoid tuberosities of the humerus unlike the chisel tooth diggers.

The present study demonstrates very little variation in osteology and morphology between different species of mole-rat despite the different methods of burrow excavation. The form of the scapula is affected by muscular action to a greater degree than any other bone in the body (Davis, 1964) and the major difference between claw diggers and chisel tooth diggers in the scapula appears to be the size of the acromion process. The acromion process forms part of the triradiate pectoral girdle and a larger process allows for a larger stride. Acromion processes are present in other rodents (Hebel & Stromberg, 1976; Özkan et al., 1997), guinea pigs (Özkan et al., 1997) and in rabbits (Özkan et al., 1997). The chisel tooth diggers in this study have a larger acromion process than the claw diggers suggesting that for manual excavation of soil it is more important to have extra strength in the forelimbs rather than dexterity. The thicker bones of *B. suillus* (claw digger) provide a greater surface area for extra muscle attachment than that of *G. capensis* and *C .h.hottentotus*. The humerus, ulna and radius of all three species of mole rat presented no distinct variations from the general type noted for mammals (Greene, 1968), but the ridges and tuberosities are more well-developed than in other terrestrial species. The one other study on the forelimb bones of subterranean rodents (Özkan, 2002) highlighted a different shaped humerus to the bathyergids, with prominent ridges and tuberosities. Although the three bathyergid species did have grooves and tuberosity sites present, the general shape of the humerus did not differ from that of other rodents. The deltoid tuberosity in all three bathyergid species was well developed but not as developed as in *Spalax leucodon* (Özkan, 2002) or in the Muridae family (Saunders & Manton, 1969).

Chapter 7

Synthesis

Bathyergids are unique in that they are a subterranean family with species that show a wide range of different socialities, including strictly solitary species (*Bathyergus suillus, B. janetta* and *Georychus capensis*), social species (*Cryptomys hottentotus*) and eusocial species (*Fukomys damarensis* and *Heterocephalus glaber*). They provide an ideal family model to investigate the influence of natural selection and social/sexual selection due to the diversity in sociality and the costs and limitations of a subterranean lifestyle. They live in a climatically stable environment that, although protected from the elements and predators, poses stringent energetic constraints. Foraging for food and searching for mates may be up to 3400 times more energetically expensive than searching on the surface (Vleck, 1981). Due to this energetically expensive lifestyle it is necessary for mole-rats to forage efficiently, especially during breeding season, or times of harsh environmental conditions that may affect food supply.

The thesis is divided into two major components; firstly an investigation into geometry and associated seasonal changes of the burrow systems of bathyergids, and secondly, the morphological adaptations of the mole-rats to the excavation of tunnel systems and mating strategies are investigated.

A study of the burrow geometry of three different, broadly sympatric, species of bathyergid showed some similarities and differences that appear to reflect social diversity rather than just foraging differences. The burrow systems possess one or two main central deep tunnels that we assume are more permanent than the foraging tunnels. These deeper tunnels often connect to nest chambers or food storage areas. It appears that the mole-rats do not have a preference of material for nesting (the nesting material usually comprises the husks or dried rhizomes of the geophytic food resources). Nests are present in both male and female burrow systems which implies that nests are not only used for rearing offspring but also as a refuge to sleep. Food stores were not present in the burrow systems of *B. suillus*, but were present in the burrow systems of *G. capensis* and the *C. h. hottentotus*. The absence in the former may be due to reliance on a larger proportion of above ground aerial vegetation in its diet. Bolt holes were only present in the burrow system of the common mole-rat suggesting that either they live in areas that are prone to flooding or that they have more predators than the other two species.

The two solitary species have different burrowing strategies. In burrow systems of *B. suillus* there is no effect of sex of the occupant on the burrow characteristics (eg. number of branches, burrow depth etc), however, males tended to explore the surrounding environment more efficiently than the females as indicated by a higher fractal dimension value. This implies that the males are either in search of females continuously through the year or that the cost of being large is so great they have to forage more efficiently to gain enough food to fuel the expensive subterranean lifestyle. The burrow systems of *B. suillus* do not change seasonally with respect to their tunnel dimensions or burrow geometry, in contrast to *G. capensis* whose burrow systems are shorter and cover a smaller area during the dry summer months but still explore the surrounding environment efficiently. The two solitary species not only have different burrowing strategies from each other but they also have different mating strategies. *Bathyergus suillus* is a seasonal breeder with males going in search of females, as indicated by the sex difference in burrow geometry and the sexual size dimorphism (SSD) in their external morphometrics (Hart *et al*., 2006; Thomas *et al*., 2009). In this study I found no apparent differences in burrow geometry between sexes as was observed in Thomas *et al*. (2009). There was also very limited SSD present in the animals caught. However, the SSD was present for head length and Zygomatic Arch Width (ZAW) both of which are typical in small mammals with a polygynous mating system involving male-male competition. *Georychus capensis* exhibits seasonal changes in burrow systems unlike that recorded for either *B. suillus* or *C. h. hottentotus* where a decrease in the length and the area covered is observed in summer. There is no difference in burrow geometry between males and females of *G. capensis*.

Cryptomy h. hottentotus burrow systems do not change seasonally but the burrow length is greatly affected by the number of animals present in a colony. In essence, the more individuals in the colony, the larger and more complex the burrow system. Previous studies (Spinks *et al*., 1999) in the more arid parts of this species distribution revealed similar burrow findings to its more mesic location; also the number of occupants from the colonies did not differ greatly from that of my study.

In contrast to *B. suillus*, although *G. capensis* shows some limited SSD, it is the females who are slightly larger. In *G. capensis* there was a higher ratio of females caught than males and this has also been observed at other localities in the western Cape (N.C. Bennett, pers. obs.)., this is in contrast to *B. suillus* where the sex ratio is parity. Female *G. capensis* are highly aggressive towards conspecifics and predators yet in *B. suillus* the males are generally more aggressive than the females especially during the breeding season (pers. obs.). *Georychus capensis* also has the greatest bite force of any of the five species of mole-rat measured (this study, Chap. 5). The high bite force combined with the heightened aggression and sexual dimorphism implies that *G. capensis* has an alternative mating strategy where a male burrow system is surrounded by numerous female burrow systems (polygyny). This alternative mating strategy is in contrast to that of *B. suillus* where one female burrow system is surrounded by numerous male burrow systems (polynandry).

Subterranean life results in anatomical as well as behavioural adaptations. Bathyergids are interesting in that the subfamily Bathyerginae (two species *Bathyergus janetta* and *Bathyergus suillus*) burrow by loosening soil with their front paws, while members of the subfamily Georychinae (*Heterocephalus, Heliophobius, Georychus, Cryptomys* and *Fukomys*) are 'chisel-tooth diggers', loosening soil by gnawing at it. Intuitively a higher bite force will allow more efficient chisel tooth digging, but social behaviour (e.g. male-male competition) may also have a role in selecting for high bite force. Bite force capacity values of five species of bathyergid were calculated from incisor measurements in an attempt to disentangle natural selection (digging efficiency) from sexual selection (intrasexual competition). This procedure has been validated in relation to the actual bite force of mole-rats determined via a force transducer (Freeman & Lemen, 2008). My results show that the species and degree of sociality influence bite force. Bathyergids can be divided into two subfamilies, the Bathyerginae and Georychinae. My results show that in the georychine bathyergids (chisel-tooth diggers), the Cape mole-rat *G. capensis* differs in its bite force from the common mole-rat, *C. h. hottentotus* and the Damaraland mole-rat, *F. damarensis*. Interestingly, the bathyergine mole-rat, the Namaqua dune mole-rat, *Bathyergus janetta* (a claw digger) does not differ from any of the other species analysed. These findings suggest that the differences in bite force are not phylogenetically constrained, but more likely environmentally influenced. With regards to sociality, the bite force results suggest that social animals have a smaller bite force regardless of body size implying a role for bite force in intrasexual competition.

In Chapter Six I expanded on the results of Chapter Five, by describing the forelimb bones (scapula, humerus, ulna and radius) of the three species with to the aim of unravelling the morphological adaptations that reflect the mole-rat being either a forelimb claw digger or a chisel-tooth digger. I predicted that the forelimb bones of the Cape dune mole-rat would be wider with a larger deltoid tuberosity relative to those of the Cape mole-rat and the common mole-rat, both of which are chisel-tooth diggers.

The influence of phenotypic evolution in the process of diversification is a broad question in evolutionary biology that can be investigated at different taxonomic levels. An understanding of how natural selection acts on morphological traits as well as an understanding of the relationship between morphology and ecology is important. Digging activity has caused diverse adaptations in subterranean rodents (Reig *et al*., 1990; Casinos *et al*., 1993). Compared to non-digging mammals, the humerus of subterranean rodents has a well-developed humeral head with a pronounced deltoid tuberosity. The muscles are broader and their origins and insertions are relatively further away from the articulations (Hildebrand, 1985; Lessa et al., 2008). The relationships between bone structures, origin, and inserts of the muscles can result in a mechanical advantage for muscles and an increased resistance of bone to muscular actions. In claw diggers, the forelimb system is adapted to produce strong forces of extension of the shoulder and elbow joint (Vassallo, 1998). In almost all comparative studies of diggers and non-diggers, bone resistance is demonstrated by the robustness of the shoulder and by an angulated deltoid tuberosity for the fixation of the extensor muscles (Vasallo, 1998). This study supports the concept that claw diggers have robust scapula bones and angular deltoid tuberosities of the humerus unlike those of chisel tooth diggers that were delicate and devoid of tuberosities.

This comparative study on the burrow geometry and the associated morphological adaptations of the three sympatric species has revealed that the *G. capensis* has a seasonal component to the geometry of its burrow that might relate to its life history pattern. *Bathyergus suillus* excavate in loose sands and loams predominantly using their claws and as a consequence may have access to their food resource and mates for longer periods of time than their solitary cousin *G. capensis*, which excavates using chisel tooth digging in soils that are seasonally workable may have limitation imposed on its excavation in the summer months. The social common mole-rat, *C. h. hottentotus* has a completely different life history strategy and dispersal of prospective reproductive animals occurs during the wet season when the soils are more friable and colony genesis is made more accessible.

Although sympatric, an analysis of the seasonal changes in burrow geometry has shed light on the potentially different mating strategies that are operational within this family of mole-rats. Hard dry soils in the summer may inhibit extensive burrow extension, whereas mole-rats species occurring in softer sands and loams may still have an opportunity to extend their tunnel systems during the drier and more unfavourable summer months.

Despite the energetic costs and environmental limitations there is still a paucity of data regarding burrow systems and morphology of bathyergids. This is due to the timely and difficult process in manually acquiring accurate data for burrow systems. With technology becoming more advanced and more easily accessible it may be possible to observe seasonal changes of a burrow system without having to extract the animal from its system. Possible technical approaches include the use of Ground Penetrating Radar (GPR) which has already proved to be successful for observing burrow systems of other mammals (Stott, 1996). Other possible methods of investigating burrow systems include robotic cameras (A. Legeza, pers. com.) and fibrescopes. These mentioned tecniques would allow a non invasive approach to observing mating systems, animal behaviour and seasonal influences.

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Appendix

Appendix 1

Burrow data for 23 *B. suillus* burrows in two seasons, summer and winter

Ref	Season (0=winter, 1=summer)	Site	Sex (0=female, 1=male)	Burrow length (m)	Burrow area (m²)	Fractal dimension	Mounds	Old mounds	Fresh mounds	Branch number	Depth (cm)	Tunnel height (cm)	Tunnel width (cm)	Nest	Food store	Bolt hole	Latrine
S21	0	B	0	57.4	1050	1.013	19	12	7	2	29.9	11.8	10.6	0	0	0	0
S22	0	C	0	56.83	374.4	1.094	55	3	52	9	23.3	14.8	12.8	1	0	0	1
S6	0	D	0	31.2	645.98	1.0624	22	13	9	2	38.16	14.26	19.8	1	0	0	1
S3	0	A	0	43.4	234.52	1.1511	38	19	19	5	19.09	13.69	17.6	0	0	0	0
S4	0	B	0	29.8	124	1.0444	28	26	2	1	21.14	10	20.4	0	0	0	0
S5	0	C	0	50.2	112.06	1.1475	39	29	10	8	25.38	15.3	16.7	0	0	0	0
S7	0	D	0	33.2	134.74	1.0889	40	31	9	5	17.03	10.78	19.4	0	0	0	1
S23	0	A	1	55	237.6	1.104	20	12	8	0	21	10.2	11.8	0	0	0	0
S24	0	B	1	31.65	470.4	1.103	76	65	11	15	32.2	13.7	12.7	0	0	0	0
S25	0	C	1	40.25	372.4	1.102	68	47	21	7	21.4	11.2	11	0	0	0	0
S1	0	A	1	66.6	1368	1.1533	49	22	27	3	34.78	13.87	19.5	0	0	0	0
S2	0	B	1	172.5	3800	1.1748	170	82	88	24	30.59	17.53	18.6	0	0	0	0
S8	0	D	1	62.2	1509.52	1.1814	50	25	25	7	21	12.54	19.3	1	0	0	0
Suillus 2	1	A	0	26.2	30	1.036	74	62	12	0	22.3	15.08	13.73	0	0	0	0
Suillus 1	1	A	0	29.8	110.75	1.066	156	147	9	4	22.65	18.24	17.41	0	0	0	0
S31	1	C	0	6.02	5.304	1.067	4	1	3	1	22	11.5	11.25	0	0	0	0
S32	1	B	0	5.55	5.808	1.045	3	1	2	1	35.25	12.75	10.75	0	0	0	1
S41	1	A	0	7.63	3.6	1.012	4	1	3	7	28.8	13.9	14.5	0	0	0	0
S42	1	B	1	29.09	86.4	1.197	19	16	3	10	30.4	18.3	17.4	1	0	0	0
Suillus 5	1	C	1	21.55	90.5	1.118	16	14	2	6	26.5	17.6	16.6	0	0	0	0
Suillus 4	1	C	1	21.66	112	1.104	9	7	2	5	30.17	15.9	14.1	1	0	0	0
Suillus 3	1	D	1	21.5	168	1.105	15	13	2	4	41.2	16.4	15.1	0	0	0	0
S33	1	D	1	49.77	264	1.188	98	94	4	11	28.5	16.8	18	0	0	0	0