# The burrow structure, colony composition and reproductive biology of the giant mole-rat *(Fukomys mechowii)* Peters 1881 from the Copperbelt of Zambia.

By

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## Abstract

African mole-rats (Bathyergidae) are subterranean hystricomorph rodents offering an excellent system with which to test theories relating to the evolution and maintenance of sociality in mammals. The aridity food distribution hypothesis (AFDH) suggests that, within the bathyergids, sociality has evolved in response to patterns of rainfall, its effects on food distribution, and the subsequent costs and risks of foraging and dispersal. Here, in the first detailed study of burrow architecture in a social mole-rat species, with data from 32 burrows, we show that in the giant mole-rat *Fukomys mechowii,* burrow fractal dimension increases with colony size and is higher during the rainy season than during the dry season. The mass of food in the burrow increases with fractal dimension and is higher during the rainy season than during the dry season. These results link for the first time colony size, burrow architecture, rainfall and foraging success and provide support for two assumptions of the AFDH, namely that (1) in arid conditions burrowing may be severely constrained by the high costs of digging; and (2) the potential risks of failing to locate food may be mitigated by increases in colony size.

It was also fundamental in this study to assess whether the *Fukomys mechowii* is (1) An aseasonal or seasonal breeder (2) To investigate whether non-reproductive female giant mole-rats exhibit induced or spontaneous ovulation and finally (3) To estimate the age variation and sexual dimorphism of this little studied giant mole-rat species. Thus in a field study that involved the complete excavation of 32 burrow systems with a mean colony size of 9.9 individuals (range 7-16), it was evident that *Fukomys mechowii* is a cooperatively breeding mole-rat exhibiting a reproductive division of labour in which usually one, or occasionally two, females are responsible for procreation. Pregnant reproductive females

were found throughout the study period (September 2005 until June 2006), supporting preliminary evidence that reproduction occurs throughout the year. Of the 32 colonies sampled, 14 of 18 (87.5%) in which the reproductive female could be identified as pregnant contained a single reproductive female, while four (12.5%) had two females breeding simultaneously (plural breeding). The population sex ratio was skewed towards females at 1:1.46. Autopsy of pregnant reproductive females (n=18) revealed that the production of two (10/18 pregnancies) or three (7/18) offspring was the norm, with one case of four embryos being present. These new data increase our fragmentary knowledge of the natural history of this little studied species.

Six non-reproductive females were removed from their natal colonies and housed individually without a male for a period of 12 weeks as a control group. They were then subsequently housed for a further 6 weeks as experiment 1, on their own before being allowed non-physical contact in experiment 2, with a mature adult male for a further 6 weeks. The non-reproductive females were given a further period of isolation for a month prior to being physically paired with vasectomized males, in experiment 3. Urine was collected every second day for all three experiments and urinary progesterone profiles were generated. The progesterone values measured during the first part of Experiment 2 and 3 were markedly higher than those measured during the first part of Experiment 1 ($Z= -2.201$, $p=0.028$ for both comparisons), however, this was not significant after Bonferroni correction. Similarly progesterone values tended to be elevated during the second phase of Experiment 2 and 3 but not significantly so (Experiment 1 vs. 2: $Z=-1.782$, $p=0.075$, Experiment 1 vs. 3: $Z=-2.201$, $p=0.028$). Thus, chemical or physical stimulation by a male

does not appear to be necessary for ovulation in female giant mole-rats. The giant mole-rat is a spontaneous ovulator.

Due to difficulties in estimating absolute age in mammals, different methods for its estimation have been proposed, and among these, the degree of molar eruption and wear are considered to be one of the most reliable indicators of relative age. Consequently, maxillary molar tooth-row eruption and wear were used to assign individuals of the giant mole-rat, *Fukomys mechowii* (Peters, 1881) from two geographically proximal and ecologically similar localities in the Copper-belt Province of Zambia to 9 relative age classes. These were in turn used to assess the nature and extent of sexual dimorphism and age variation in this little-studied social mole-rat based on cranial morphometric data, reference to body mass and a series of both univariate and multivariate statistical analyses. Both univariate and multivariate analyses showed morphological differences between individuals of age classes 1–3 and those of age classes 5–9, while individuals of age class 4 were intermediate between these age class groupings, suggesting that this age class lies at a point on a hypothetical growth curve where it begins to stabilize. The analysis of the nature and extent of sexual dimorphism revealed its absence in the younger individuals of age classes 1–4 and its presence in older age classes 5–9. These results may allow an insight into our understanding of the population social structure, and reproductive strategies in the giant mole-rat**.**

In conclusion, it is worth mentioning that; (1) A number of studies have examined burrow architecture, although not necessarily fractal dimensions in the Bathyergidae but the majority of these have concentrated on solitary species in which when there is plural occupancy it is during the breeding season or when the mother has a litter. This study is thus the first to examine in detail the dynamic nature of social mole-rat burrows, with respect to

seasonal changes. The burrow fractal dimension is a good indication of the mole-rats ability to burrow to find food and thus results support the critical assumption which underlies the aridity food distribution hypothesis. The results accord well with previous data in social mole-rats indicating that larger colonies have greater survival and link colony size, burrow architecture and foraging success for the first time; (2) the giant mole-rat is an aseasonal breeder which in a few instances can have two queens per colony; (3) the giant mole-rat is a spontaneous ovulator and finally (4) the giant mole-rat *Fukomys mechowii* exhibits a sexual dimorphism amongst its older age classes 5-9. Suggesting that there are different growth curves in males versus females, whereby males attain much larger size (skull size and body mass) than females after puberty and finally intimating that opportunistic mating competition among males is very high.

# Preface

***"To get something you never had, you had to do something you never did! Thus, the will of God will never take you where the Grace of God will not protect and guide you!"***

**Zambia**

I collected the giant mole-rats *Fukomys mechowii* from 32 burrow systems, from Kakalo and Mushishima Farm blocks in Chingola District, Copperbelt Province of Zambia. I would like to thank my field Assistants; Timothy Salupeni and Fredrick Chama for their tireless work in excavating the burrow systems. I thank the District Veterinary and Nature conservation offices in Chingola for having provided my permit to capture mole-rats in Chingola. I am grateful to Dr. G. Monga, the Provincial Veterinary Officer in Copperbelt Province for providing all export permits that I needed for the shipment of live mole-rats from Zambia to South Africa.

**University of Pretoria**

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**Queen Mary University of London, UK**

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Finally, I would like to thank God for making me aware of nature and for providing me with good health, the opportunity to study and appreciate his creation.

***"We may be hard pressed on every side, but not crushed; perplexed, but not in despair; persecuted, but not abandoned; struck down but not destroyed. (1 Corinthians 4:8-9)"***

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mandibular-ramus height, from the dorsal edge of the coronoid process to the ventral edge of angular process; (20) UJI – upper jaw incisor length, measured from the tip of the incisors to the base, where the teeth connect to the skull; (21) LJI – lower jaw incisor length, measured from the tip of the incisor to the base, where the teeth connect to the skull; and (22) WI – width of the incisor where the incisor meets the premaxilae.

Fig. 3.1 Two burrows representing the observed differences in fractal dimension, from (a) the dry season (colony 24, fractal dimension =1.194) and (b) the rain season (colony 15, fractal dimension = 1.422). G = granary; N = nest; T = toilet chamber.

Fig. 3.2 The mass of food in the burrow as a function of burrow fractal dimension. Open circles: dry season, Filled circles: rainy season. Note the anomalous data point for colony 23, with 1310g of food.

Fig. 5.1 A plot of the first two principal components from a principal components analysis of the giant mole-rat, *Fukomys mechowii* of tooth-wear classes 1–9 from Kakalo and Mushishima farm blocks, Chingola, Copperbelt Province of Zambia. Minimum convex polygons enclose individuals of each tooth-wear class, which together with their associated sexes have been omitted.

Fig. 5.2 A distance phenogram from an unweighted pair-group method using arithmetic averages (UPGMA) cluster analysis male and female giant mole-rat, *Fukomys mechowii* of age tooth-wear-classes 1–9 from Kakalo and Mushishima farm blocks, Chingola, Zambia, showing 3 distinct clusters of individuals comprising the following sample sizes, tooth-wear classes and sexes (M = male; F = female), respectively: (1) Cluster 1 – 4:1F, 2:1M, 8:2F, 6:2M, 6:3F, 4:3M, 8:4F, 5:4M and 2:6F; (2)

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# Chapter 1

# General Introduction

## The Bathyergidae

The family Bathyergidae (derived from the Greek *bathys* meaning deep and *ergo* to work) comprises subterranean hystricomorph rodents that are endemic to the continent of Africa. The family shows a wide spectrum of social structure ranging from strictly solitary species such as those belonging to the genera *Bathyergus*, *Heliophobius* and *Georychus* through to social and truly social species in the genera *Cryptomys*, *Fukomys* and *Heterocephalus* (Jarvis and Bennett, 1990; 1991).

The bathyergids occupy a range of habitat types from mesic through to arid environments (Jarvis & Bennett, 1990). However, a common underlying prerequisite for their occurrence is the presence of the underground storage organs of geophytes, for which there is a propensity in Africa (Jarvis & Bennett, 1991; Faulkes *et al*., 2004). In mesic regions the soil is workable for much of the year and thus there is essentially no necessity for mole-rats to be social, however, in more arid regions the rainfall is sporadic and unpredictable and in such instances there are few opportunities available to successfully burrow towards the food resources. These brief windows of opportunity require a number of mole-rats to excavate and tunnel to locate and harvest sufficient food resources.

Indeed, sociality in the African mole-rats has been hypothesized to have evolved in response to patterns of rainfall, the subsequent effects on food distribution and size and the consequent costs and risks of foraging (Jarvis *et al*., 1994; Faulkes *et al*., 1997; Bennett & Faulkes, 2000; Burda *et al*., 2000).

The Aridity Food Distribution Hypothesis (AFDH) has been put forward in an attempt to explain how sociality in African mole-rats may have evolved among some mole-rat species but not in others. The premise is that cooperative behaviour arose in some mole-rat species where the energetic costs of burrowing increase as the rainfall pattern becomes more unpredictable and the available food resource more clumped (Jarvis *et al*., 1994). Although Burda *et al.,* (2000) argued against a causal relationship between cooperative foraging for food resources and the evolution of sociality in mole-rats [see Faulkes & Bennett (2007)] and O'Riain & Faulkes, (in press) for further commentary and debate), the AFDH has support from a number of empirical studies including long term field studies and associated molecular studies (Faulkes *et al*., 1997; Jarvis *et al*., 1998; Burland *et al*., 2002, Hess, 2004).

## *Sociality in mole-rats*

The solitary species of southern and eastern African mole-rats (*Georychus* and *Bathyergus*, *Heliophobius*) generally inhabit environments that exhibit a marked seasonality or higher rainfall pattern (Jarvis & Bennett, 1990, 1991; Bennett & Faulkes, 2000; Šumbera *et al.*, 2003a). A number of species of mole-rat that exhibit some degree of social behaviour may also occur in these mesic environments, but also in drier areas (Spinks *et al.*, 1999; Janse van Rensburg *et al*., 2002). The truly social mole-rats occur in semi-arid and arid regions where rainfall is sporadic and unpredictable and hence the times available for successful foraging are restricted and a large workforce is required to sufficiently excavate the tunnel system to locate these patchily distributed food resources.

The species belonging to the genus *Cryptomys* (restricted to southern Africa) are generally composed of small family groups that incorporate up to three successive litters (Bennett, 1989). Colonies are usually around 8-10 animals and are transient in nature, with animals exhibiting regular periods of dispersal from the natal colony Spinks, (1998). The use of microsatellite libraries have revealed that multiple paternity of litters and extra-pair copulations are common in these environments where ecological constraints are not great Bishop *et al*., (2004). In the more highly social mole-rat species *Fukomys damarensis*, colonies have been found to number up to 40 animals but are usually around 12 -14, with reproduction restricted to small cohorts of breeding animals that constitute a single reproductive female and a small group of reproductive males, which may or may not be present in the colony Burland *et al*., (2004).

## *Burrow structure*

Mole-rats are herbivorous and feed mainly on swollen tubers and underground storage organs of geophytes which are encountered and harvested during burrowing activity. Underground storage organs are an exceptional food resource to harvest since they have a long shelf life, they can be obtained throughout the year, are biologically stable and there is little competition from other consumers (Bennett & Faulkes, 2000). Geophytes which are harvested by mole-rats may be either consumed *in situ* or else they are stored in carefully sculptured food chambers which are periodically visited by mole-rats.

A number of studies have examined burrow architecture within various species of mole-rat (Hickman, 1977; Davies & Jarvis, 1986; Spinks *et al*., 2000a; Šumbera *et al*., 2003c; Herbst

& Bennett, 2006). The majority of these studies have concentrated on solitary species in which there is only plural occupancy of the burrow during the breeding season or when the mother has young. In general the burrow systems of solitary species are relatively simple being linear in nature with some sex differences in architecture [see Herbst *et al*., (2004)]. Relatively few studies have examined the burrow structure of social mole-rats, and where this has been done the sample sizes are typically very small. Spinks *et al*., (2000a) examined seven burrow systems of the common mole-rat, *Cryptomys hottentotus hottentotus* at two different trapping localities, whereas Le Comber *et al*., (2002) examined 25 burrow systems from seven species of which three were social ( viz. *C. h. hottentotus*, *Fukomys darlingi* and *Heterocephalus glaber*). The burrow architecture of social mole-rats shows a marked complexity with numerous tunnels radiating off from a central nest area [see Spinks *et al*., (2000a)].

There is absolutely no information pertaining to the changes that result in burrow architecture between the rainy and the dry seasons in social mole-rats. The only known study to investigate seasonal changes in burrow architecture is that of Šumbera *et al*., (2003c) who documented significant changes in the burrow systems of the solitary silvery mole-rat, *Heliophobius argenteocinereus*.

### *Burrow fractal dimensions*

Most studies of burrow architecture have examined metrics ranging from burrow shape, burrow system area, number of segments, linearity, turn angle, number of branches, segment length and branch length, (Romañach & Le Comber, 2004; Romañach *et al.*, 2005; Le

Comber *et al.*, 2006). However, due to the lacking of clarity in variables, recent studies have begun to use fractal dimension to provide a single measure sure of shape that has the advantage of being independent of burrow length Le Comber *et al.*, (2006). Fractal dimension is a formidable choice of measure of burrow shape because it is mainly a measure sure of the extent to which a one dimensional structure fills a plan with low fractal dimension (close to 1.0), describing a burrow that explores relatively little of surrounding area and high fractal dimension (close to 2.0) describing a burrow which explores the surrounding are more thoroughly Le Comber *et al*, 2006. In addition, it is an important tool in burrow system analysis because it further examines the relationship between burrow dimensions and demonstrates that burrows with high fractal dimension are more successful in locating food (Le Comber *et al.* 2002; Le Comber *et al.*, 2006). This detailed study in a single social mole-rat clarifies the assumptions underlying the Aridity Food Distribution Hypothesis (AFDH).

### *Colony size*

In the social mole-rats the size of a colony is dependent upon a number of factors, the size of the territory held by a colony, the degree of risk that the colony members face if attempting to disperse and establish their own colonies, the rainfall pattern and the time the substratum is workable. Colony size also does not remain static but is dynamic, with immigration and emigration occurring under suitable burrowing conditions. Usually following good rainfall, some colony members disperse and colony size is reduced or comprises newly established nascent pairs (Jarvis & Bennett, 1993).

In general the naked mole-rats of eastern Africa set the record with the largest colonies with a mean of around 80 animals from wild captured colonies (Brett, 1986), however, there are rare occasions of when up to three hundred individuals have been captured from a single burrow system, but these are normally in agricultural areas where abundant rootstocks are available Brett, (1986). In the genus *Fukomys*, colony size ranges from small groups of around 5 individuals (*Fukomys darlingi*) through to colonies exceeding 40 individuals (*Fukomys damarensis*), but colonies rarely exceed 20 individuals (Jarvis and Bennett, 1993; Bennett & Faulkes, 2000). In the genus *Cryptomys* colonies rarely exceed 14 animals in size (Bennett, 1989; Janse van Rensburg *et al.*, 2002). Spinks (1998) examined colony size in two populations of the common mole-rat, *Cryptomys hottentotus* that inhabit different regions with contrasting rainfall. Spinks (1998) found that the degree of aridity of the habitat did not affect the mean (5 animals) or range (2-14) of the colony size. The giant mole-rat is interesting in that it occurs in a mesic habitat where rainfall is high and predictable. Consequently it is hypothesized that colonies of these mole-rats should be smaller in size than their arid, but similar in size to their mesic counterparts of southern Africa.

## *Colony composition*

The use of tooth-wear on its own in mammals has been shown to be a poor ageing method (Hall *et al.* 1957; Keiss, 1969; Morris, 1972). However, by studying a single population where diet is fairly uniform the application of tooth-wear on the cusps of the molariform teeth can be used as a relative rather than absolute variable for ageing a population. The time of tooth eruption is less variable and can serve as a valuable marker of relative age. This method can in conjunction with skull morphometrics be used to investigate potential sexual

dimorphism and age in populations of mammals. Indeed, Bennett *et al*., (1990) successfully used this method to investigate sexual dimorphism in two species of social mole-rat, they found that within colonies it was absent in the common mole-rat, *C. h. hottentotus* but distinctly marked in the Damaraland mole-rat, *F. damarensis*.

Colonies of the social mole-rats belonging to the genera *Cryptomys*, *Fukomys* and *Heterocephalus* are generally familiar with some immigrants that have subsequently joined the colony over time. There is usually one, but very rarely two reproductive females that are responsible for the production of young that are recruited to the natal colony (Bennett & Faulkes, 2000). There may be between one to three putative reproductive males, these are usually the founding members of colonies (Bishop *et al*. 2004; Burland *et al*., 2002; Burland *et al*., 2004). A number of successive litters are incorporated into the colony of varying relative age structure, some of which may have opportunities to disperse and establish their own colonies (Bennett *et al*., 1990; Janse van Rensburg *et al*., 2004).

## *Reproductive strategies in the Bathyergidae*

Reproduction in mole-rats is ecologically constrained by the burrow environment (Jarvis & Bennett, 1990). In solitary dwelling mole-rats reproduction is predominantly seasonal. Instead of cueing into photoperiod the mole-rats use changes in temperature, changes in soil moisture content or sudden flushes of vegetation associated with precipitation to herald the onset of reproduction (Bennett, Gutjahr & Faulkes, 2007). Two social species of mole-rat show a marked seasonal component to reproduction. The common mole-rat, *Cryptomys hottentotus hottentotus* and the highveld mole-rat, *Cryptomys hottentotus pretoriae* are the

only two social species of bathyergid studied to date that exhibit a marked seasonality of reproduction (Spinks *et al*., 1997; Janse van Rensburg *et al*., 2002, 2003). These two species inhabit environments which are relatively mesic and have a predictable season of rainfall. In contrast, members of the genera *Fukomys* and *Heterocephalus* do not show a seasonal component to reproduction and produce young throughout the year (Bennett *et al*., 1991, 1994, Bennett & Aguilar, 1995). The majority of these findings have come from laboratory based studies where colonies of mole-rats have been housed under artificial lighting conditions and fed on *ad libitum* diets. To date there is a paucity of information that has arisen from field studies where postmortems have been performed on entire colonies throughout the calendar year (Bennett, Faulkes & Molteno, 2000).

## *Patterns of ovulation in the Bathyergidae*

Ovulation is essentially achieved through two methods either spontaneously (seasonally or continuously throughout the year) or by induction following mating behaviour and subsequent coitus (Milligan, 1980). The solitary species of mole-rats essentially employ induced ovulation where mechanical stimulation of the vagina and cervix by the penis of the male is essential for ovulation to take place. The solitary male mole-rats are characterized by a penis that has elaborate epidermal spines on the shaft and glans Parag *et al*., (2006). Interestingly, the loosely social mole-rats of the genus *Cryptomys* exhibit induced ovulation (Malherbe *et al*., 2004a; Jackson & Bennett, 2005) and the males possess penile protrusions (rounded, raised structures) rather than spines over the entire surface of the penis Parag *et al*., (2006). In the two eusocial species *Fukomys damarensis* and *Heterocephalus glaber* the penis lacks spines and protrusions altogether and possesses smooth ridges along the length

of the penis. Both of these eusocial species exhibit spontaneous ovulation (Faulkes *et al*., 1990; Snyman *et al*., 2006). As a result of the extreme natal philopatry that is experienced in these social mole-rats it may be of no selective advantage for induced ovulation and as a consequence not necessity for elaborate ornamentation to the penis Parag *et al*., (2006).

## *The giant mole-rat, Fukomys mechowii*

The giant mole-rat which was originally placed in the genus *Georychus*, is one of the largest of the social species and has the lowest chromosome number 2n=40, FN = 80 of all the mole-rats examined to date Macholan *et al*., (1993). It is a large stout mole-rat and is the largest species in the genus *Fukomys*. The pelage is short and dense in nature with a colour that is age dependent being dark slate grey (neonates), through to greyish-brown (weaned young), brown (juveniles and sub-adults) and golden ochre (adult animals). The head is large and may possess a white spot of forehead (except very small spot in some individuals). The giant mole-rat has a wide distribution being endemic to central Africa. The mole-rats are recorded from N. Zambia, S. and E. Zaire, central Angola (and perhaps N. Malawi). The mole-rats are found in Savanna bush-land, cultivated and abandoned fields, gardens, dambos (temporary swamps) and dense *Acacia* woodland. They burrow in a variety of soil types from quite stony to pure sand and clay. The area of distribution is characterized by an annual rainfall of more than 1,100 mm Scharff *et al*., (2001).

The giant mole-rat excavates extensive burrow systems comprising a deep nest (60-160 cm deep) with 3 or 4 entrances, food stores and toilet areas Scharff *et al*., (2001). Giant mole-rats have a low resting metabolic rate 0.6 $\pm$ 0.08 $cm^3O_2g^{-1}h^{-1}$ (96% of expected), low body

temperature 34 ± 0.4°C, and a low thermal conductance 0.09 ± 0.01 $cm^3O^2g^{-1}h^{-1o}C^{-1}$ (Bennett *et al*., 1994).

Food in non-cultivated areas includes grass rhizomes, roots, bulbs and tubers of diverse weeds, shrubs and trees; in cultivated areas; they probably feed on crop plants such as sweet potatoes, cassava and groundnuts Scharff *et al*., (2001]. Giant mole-rats are unusual amongst bathyergids, because they supplement their diet with invertebrate and vertebrate commensals found in their burrows (Burda & Kawalika, 1993; Scharff *et al*., 2001).

The mole-rats occur in colonies ranging from 2- 20 colony members strong. It has been suggested that the colonies can exceed 40 or more individuals (Burda & Kawalika, 1993; Scharff *et al*., 2001). Sex ratio within colonies appears to be in favour of females Scharff *et al*., (2001). The colony comprises a founding reproductive pair and non-reproductive offspring from several litters (Burda & Kawalika, 1993; Wallace & Bennett, 1998; Scharff *et al*., 2001). The reproductive animals are the most dominant, and the non-reproductive males are more dominant than females. The non-reproductive members of the colony cannot be placed into clearly defined work-related groups based on body mass (Wallace & Bennett, 1998). Giant mole-rats are very vocal compared to other species of *Cryptomys* and *Fukomys* (Burda & Kawalika, 1993; Credner *et al*., 1997).

Giant mole-rats appear to breed aseasonally from laboratory and fragmentary field observations, producing up to three litters per annum (Burda & Kawalika, 1993; Bennett & Aguilar, 1995; Scharff *et al*., 1999). The gestation period is long 112 (89-118) days. Mean

litter size is around 2-3 (range 1-4). At birth, young weigh around 19.6 (12.6-27.7) g. First solid foods eaten ca. Day 14 but the pups are weaned ca Day 90. Inter-sibling sparring begins at Day 10 (Bennett & Aguilar, 1995; Scharff *et al*., 1999).

Apart from humans, no predators are known which have specialized on giant mole-rats. Ectoparasites have not been found on animals or in the nests of giant mole-rats. Endoparasties include three species of cestodes (*Inermicapsifer madagascariensis*, *Raillietina* sp.,) and two species of nematodes (*Protospirura muricola*, *Cappilaria* sp.). Endoparasitic load (34%, n = 35) is relatively low compared to most other rodents (Scharff *et al*., 1997; Scharff *et al*., 2001).

**Plate 1.1 The giant mole-rat *Fukomys mechowii***

## Aims of study

The giant mole-rat (*Fukomys mechowii*) is one of the little studied species of bathyergid in sub-Saharan Africa, with earlier research focusing on the general biology and some laboratory studies on the sociality and reproduction based on small sample sizes with observations from few colonies. Many of the documented reports on colony composition of the giant mole-rat are based on hear say from local hunters.

The study first focused on providing a description of the general burrow architecture of the giant mole-rat from 32 burrow systems excavated in their entirety and the colony composition of the colonies captured during excavation. On average 3 burrows were excavated monthly for a period of one year. Fractal analysis was employed on the mapped burrow systems to answer three general questions relating specifically to the assumptions of the AFDH: (1) Is burrow fractal dimension higher in the rainy season, as might be predicted if either or both the energetic costs of digging, or differences in patterns of food distribution, vary between seasons? (2) Do larger colonies have burrows with higher fractal dimensions? This might be the case if, as the AFDH suggests, foraging is more efficient in larger, cooperatively foraging colonies. (3) Is higher fractal dimension associated with a greater mass of food in the burrow? (Le Comber *et al.,* 2006) showed, using computer simulations, that burrows with high fractal dimension located more food; here, we test whether this is reflected in larger food stores in a natural situation.

Postmortem examination of entire colonies collected during the project were used to investigate the mean colony size, relative age structure based on tooth wear and eruption

patterns of entire colonies over a period of one year. Furthermore, cranial morphometric analyses were performed to ascertain whether (i) the species is sexually dimorphic and (ii) if sexual dimorphism is evident does it arise early in the life history or following maturation and the attainment of adulthood. Using the animals collected from the study we further investigated whether the giant mole-rat is an aseasonal or seasonal breeder. The final component of the project investigated whether ovulation in non-reproductive females removed from the confines of the colony results from spontaneous or induced ovulation.

# Chapter 2

# Materials and methods

## Study site

### *Locations*

The study was undertaken over a period of 10 months from September 2005 to June 2006, on two adjacent farms, Kakalo and Mushishima, located 25km south of Chingola in the Copper Belt Province of Zambia ($10^{o}40$'S and $20^{o}85$'E). A total of 32 discrete burrow systems, out of c. 80, were excavated from areas of disturbed natural vegetation, that is, natural vegetation that is disturbed intermittently by agricultural practices. The mean (±SD) annual rainfall at Chingola is 1029.9 ± 233.8mm/year$^{-1}$, with 6.05 ± 0.94 months/year$^{-1}$ with more than 25mm of rain [the amount required to soften the soil at the depth of foraging tunnels (Jarvis *et al*., 1994)].

## Study animals

### *Burrow architecture*

Mole-rat burrow systems were located by the presence of discrete rows and groups of molehills on the surface. The distance between individually excavated colonies was deliberately maintained at 1000m to ensure that they represented separate burrow systems. The burrow systems were excavated in agricultural fields, grassland and dambos (shallow wetlands) within a variety of soil types ranging from clay to sandy loams. On average, 3 burrow systems were excavated every month using the hoe method Jarvis, (1991b) and the burrow was traced for its entire length. Capturing of mole-rats continued until the entire burrow system was excavated. The burrows were measured using a tape measure and string and plotted on graph paper relative to the magnetic north. The dimensions, depth and contents of the nesting areas, food stores and toilet chambers were also recorded.

Burrow excavations were assigned to either the rainy season or the dry season, according to the observed onset/end of the annual rains. The transition between seasons is abrupt and unambiguous and in some cases burrows that were excavated in the same month (November 2005; April 2006) were assigned to different seasons. The animals were captured by manually digging out the burrows leading to the centrally positioned nest, food stores and latrines. In most cases, the mole-rats retreated into the bolt holes (blind ending tunnels) from where they were captured; as the animals emerged, the tunnel was blocked and mole rats were captured by hand. Burrow systems took between 3-6 days to be excavated in their entirety. The positions of all tunnels and chambers were surveyed and mapped for each burrow.

### *Burrow fractal dimensions*

To quantify burrow shape in a way that was independent of size, we used fractal dimension, which offers a useful measure of the extent to which a burrow explores the surrounding area, especially in fossorial mammals in which the burrow is used for foraging (Le Comber *et al*., 2002, 2006; Šumbera *et al*., 2003a; Romañach & Le Comber, 2004). Burrow fractal dimension was estimated by calculating the box-counting or capacity dimension, DB (Block *et al.*, 1990), using methods adapted from Le Comber *et al*., (2002) and Romañach & Le Comber (2004). Burrow maps were photocopied to a standard size, h (256mm along the longest axis), and redrawn to ensure constant line thickness. Taking h=256mm, grids of h/20, h/21, h/22, h/23 . . . h/27 (the practical limit of resolution) were superimposed on the burrow maps, and the number of grid squares covering the burrow was counted for each grid size in turn. Thus, the grid size was successively halved, from a maximum of 256mm to a minimum of 2 mm. For a straight line, as the grid size is halved, the number of grid squares

required to cover the burrow increases by a factor of 21; that is, it doubles. For a plane, the number of grid squares increases by a factor of 22=4. This can be represented by regressing log N(e) against-log (1/e), where e is the length of the grid square and N(e) is the number of squares of length e required to cover the image, with the fitted line constrained to pass through the origin. For a perfectly linear structure, the slope of this line equals 1; for a perfectly planar structure, the slope equals 2. Thus, the slope of the fitted line corresponds to the line's fractal dimension. Variation in the depth of different parts of the burrows was ignored; this tends to be slight in comparison with burrow length (Bennett & Faulkes, 2000).

## Aseasonality

### *Climatology, animal composition and classification*

Zambia has 3 major seasons: (i) a cold dry season from mid-May to July; (ii) a hot dry season from August to October; and (iii) a wet season stretching from mid-November through April, sometimes extending to the second week of May. From the first to second week of November, just before rains commence, a minor dry/cool season occurs. Our sampling period thus covered all three seasons.

A total of 32 colonies comprising 317 animals were collected following complete excavation of the burrow systems. On capture, mole-rats were euthanased using chloroform (see 'Ethical Note'), weighed, toe-clipped for use in separate genetic studies and sexed. Their likely breeding status was determined, with breeding females identified by elongated teats and a perforate vagina and breeding males characterized by a stained mouth area, prominent, bulging abdominal testes and large body size (Bennett & Aguilar, 1995). Animals were categorised into three age classes based on laboratory studies of growth

(Bennett & Aguilar, 1995) as follows: (i) juveniles (weighing from 1-100g, aged approximately 100-150 days); (ii) sub-adults (101-200g, aged approximately 1 year); or (iii) adults (201g and above, aged approximately 1 year and above). Body masses of adults were compared statistically using a *t* test. After dissection, the genetic materials of kidney, liver and heart were sampled and stored in 70% Ethanol. The number of foetuses per pregnant female and juveniles per every colony were recorded throughout the capturing period.

## Sexual dimorphism and age variation

### *Tooth-wear age classes and cranial measurements*

Out of a total of three hundred and seventeen (317) animals captured, two hundred and sixty five (265) of which 151 were females and 114 males had undamaged skulls, on which the tooth-wear and eruption and cranial measurements were based. Molar teeth for animals were thoroughly cleaned and micrographs made for the assessment of age variation (Fig. 2.1). Twenty two (22) cranial measurements were also taken for the examination of sexual dimorphism of the animals (Fig. 5.2).

The estimation of relative age was adopted and modified from Janse van Rensburg *et al.* (2004) and Hart *et al.* (2007) as follows: *Tooth-wear class 1* – only two cheek teeth fully erupted; an emerging third cheek tooth still in a cavity; little sign of tooth-wear on teeth; *Tooth-wear class 2* – three cheek teeth fully erupted; only the first two cheek teeth showing signs of tooth-wear; *Tooth-wear class 3* – three cheek teeth fully erupted; an emerging fourth cheek tooth still in a cavity; *Tooth-wear class 4* – three cheek teeth fully erupted, with the fourth cheek tooth starting to surface; *Tooth-wear class 5* – all four cheek teeth erupted

with no sign of tooth-wear on the fourth cheek tooth; *Tooth-wear class 6* – all four cheek teeth erupted; fourth cheek tooth showing little signs of wear; *Tooth-wear class 7* – all four cheek teeth erupted; fourth cheek tooth showing a fair amount of wear; *Tooth-wear class 8* – all four cheek teeth erupted, with deeply scooped dentine on all four cheek teeth; and *Tooth-wear class 9* – all four cheek teeth erupted with deeply scooped dentine on all four cheek teeth that are also deformed and reduced in height due to heavy tooth-wear (Fig. 2.1).

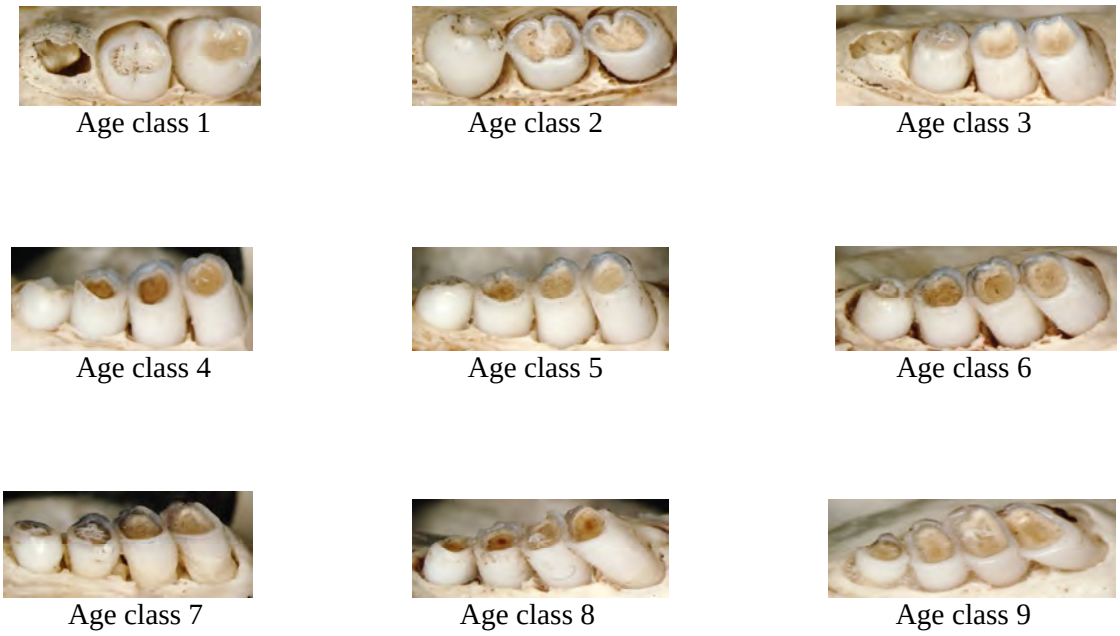


**Figure 2.1.** Right maxillary molar tooth row of the giant mole-rat *Fukomys mechowii* illustrating nine tooth-wear classes as adopted and modified from Janse van Rensburg *et al*., (2004) and Hart *et al.*, (2007) and described in the text.

The assessment of craniometric sexual dimorphism and variation in relative age within the giant mole-rat was based on 22 linear cranial measurements adopted and modified from Janse van Renseburg *et al.*, (2004) and Hart *et al.*, (2007) (Fig. 2.2). All cranial

measurements were recorded by a single observer (AMS) to the nearest 0.05mm using a pair of Mitutoyo digital calipers (Mitutoyo American Corporation, Aurora, Illinois, USA.).

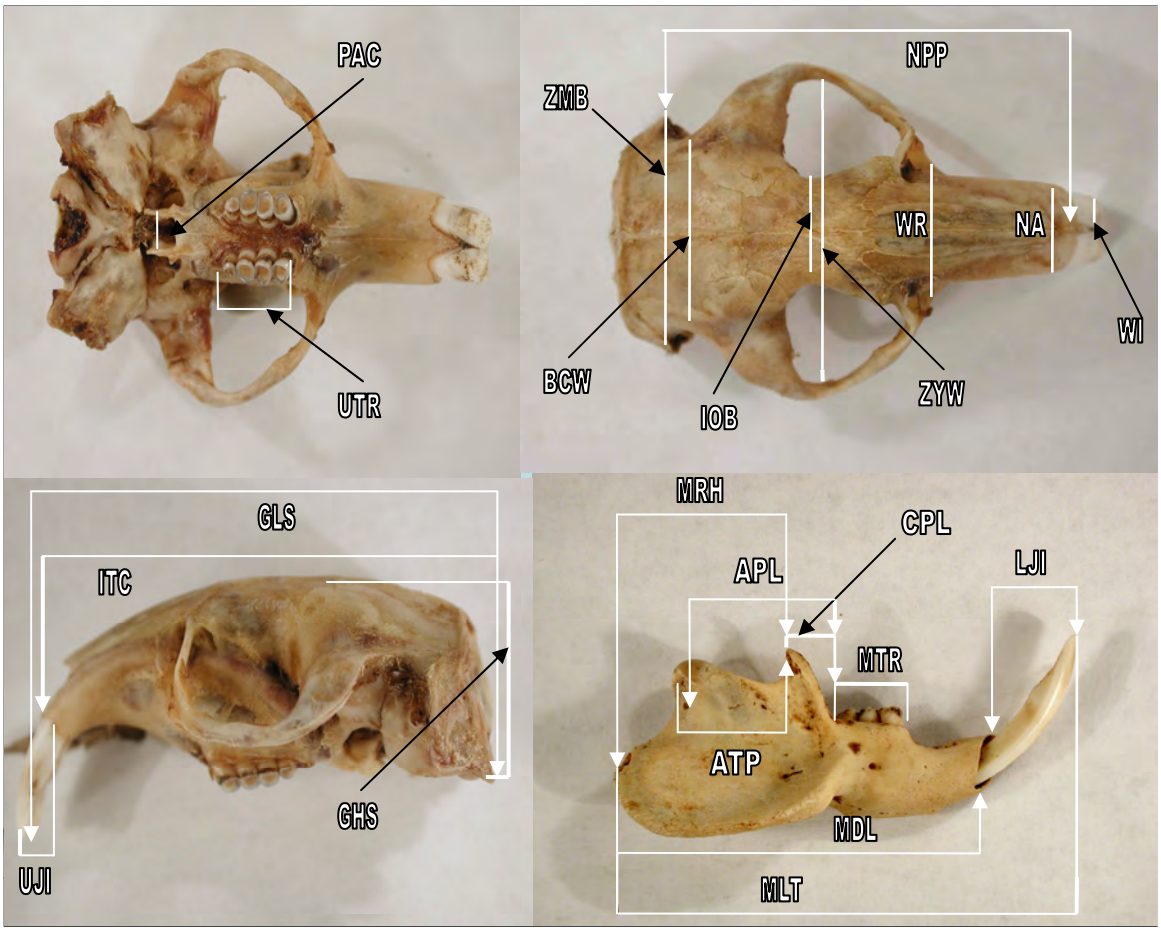


**Figure 2.2.** Abbreviations and reference points of 22 cranial measurements used in the present study as adopted and modified from those defined and illustrated by Janse van Rensburg *et al*., (2004) and Hart *et al.*, **(**2007) : (1) GLS – greatest length of skull, from the tip of the front of the incisors to the posterior part of the skull; (2) ITC – incisor to condyle length, from the anterior surface of the incisor at alveolus to the most posterior projection of the occipital condyle; (3) BCW – widest measurement of braincase breadth; (4) ZMB – zygomatic breadth - parietal width, (5) ZYW – greatest zygomatic width, between outer margins of the zygomatic arches, perpendicular to longitudinal axis of the skull; (6) IOB –

least breadth of the interorbital constriction; (7) WR – width of the rostrum ; (8) NA – anterior width of nasal where it joins with the premaxillae; (9) UTR – crown length of maxillary tooth row, from the anterior edge of the first molar to the posterior edge of the last molar; (10) PAC – hard plate width at point of constriction immediately posterior to the last molar; (11) NPP – the distance from anterior edge of nasals to the anterior edge of posterior part of the zygomatic arch; (12) GHS – greatest height of skull, perpendicular to horizontal plane through bullae; (13) MLT – greatest length of mandible, including teeth, from the posterior surface of condylar process to the tip of incisor; (14) MDL – greatest length of mandible (excluding teeth), from the posterior surface of condylar process to anteroventral edge of the incisor alveolus; (15) MTR – mandibular toothrow length, from the anterior edge of the first molar alveolus to the posterior edge of the last molar aveolus; (16) CPL-coronoid process length to posterior edge of fourth molar; (17) ATP – articular process length, from the ventral edge of mandibular foramen to mid-posterodosal edge of the coronoid process; (18) APL – angular process length of the middle mandible; (19) MRH – mandibular-ramus height, from the dorsal edge of the coronoid process to the ventral edge of angular process; (20) UJI – upper jaw incisor length, measured from the tip of the incisors to the base, where the teeth connect to the skull; (21) LJI – lower jaw incisor length, measured from the tip of the incisor to the base, where the teeth connect to the skull; and (22) WI – width of the incisor where the incisor meets the premaxilae.

Exploratory analyses of the derived craniometric measurements revealed the data to be normally distributed. The nature and extent of sexual dimorphism and age variation were first simultaneously univariately assessed by a two-way (ANOVA Zar, 1996) of samples of age classes 1–9 after establishing that tests for normality and homogeneity of variances satisfied the assumptions of ANOVA tests Zar, (1996). Where statistically significant age differences were detected by the ANOVA, non-significant subsets ($P > 0.05$) were identified by the *post hoc* Student-Newman-Keuls test (SNK; Gabriel & Sokal, 1969; Sokal & Rohlf, 1981) of ranked means. The derived two-way ANOVA table was in turn used to estimate the

%*SSQ* of the four potential sources of variation in the data, namely, sex, age interaction, and error (= residual) by dividing the *SSQ* associated with each source of variation by the total SSQ.

The nature and extent of sexual dimorphism and age variation within *F. machowii* was also multivariately assessed by an unweighted pair-group method using arithmetic averages (UPGMA) cluster analysis and principal component analysis (PCA) of standardized variables (Sneath & Sokal, 1973). UPGMA cluster analysis was based on Euclidean distances and correlation coefficients among groups, while the PCA was based on correlation coefficients among variables (Sneath & Sokal, 1973). Additional analyses included the computation of standard descriptive statistics. Since exploratory analyses showed that data on body mass were not normally distributed, body mass data within sexes and age classes were evaluated using the non-parametric Mann-Whitney *U* test Zar, (1996). All statistical analyses in the present study were based on all the 22 cranial measurements recorded, and were undertaken using the statistical software programme STATISTICA, version 8.0 (STatTSoft Inc. 2008).

## Ovulation methods

### *Experimental design, Creatinine and Progesterone determination*

The mole-rats used in the study were separately trapped from two farms, Kakalo and Mushishima, located 25 km south of Chingola in the Copper Belt province of Zambia ($10^{o}$ 40'S and $20^{o}$ 85'E). Animals were trapped by the hoe method (Bennett & Faulkes, 2000). All females used in the study had a mass exceeding 250g and males had a mass exceeding

350g to assure sexual maturity. Six non- reproductive females were collected from 6 different colonies, twelve adult males were also collected from 6 different colonies 1000m apart. Non-reproductive females were discerned by their non-perforate vagina and used for the experiment. Animals were then shipped to Pretoria and housed in a temperature-controlled room maintained at between 26 and 28$^{o}$C with a relative humidity of between 50 and 60% and a lighting regime of 12L: 12D. Wood shavings were used as nesting material. Mole-rats were fed sweet potatoes, chopped gem squash and apple daily; no free water was provided since they obtain all of their water requirements from the food resource to maintain a positive water balance.

Experimental manipulations and collection of urine took place from October 2006 until August 2007. In captivity, 6 non-reproductive females removed from their natal colonies were housed individually in plastic containers 1x0.5x0.5m, without a male for 18 weeks from 4$^{th}$ October, 2006 to 7$^{th}$ February, 2007. This same period included the first 6 weeks of acclimatization period from 4$^{th}$ October to 15$^{th}$ November, 2006 and experiment 1 (control), from 16$^{th}$ November, 2006 to 7$^{th}$ February, 2007. Subsequently, experiment 2 (chemical) started from 8$^{th}$ February through to 31$^{st}$ March, 2007 and was subdivided with the first 3.6 weeks (control) with females on their own and 3.7 weeks (chemical) with females being allowed non-physical contact with males but only separated by a mesh wire. The non-reproductive females were given a period of isolation for two and half months prior to commencement of the 12 weeks experiment 3 from 3$^{rd}$ June to 25$^{th}$ August 2007 and which inclusively covered the initial 6 weeks of control period with females alone and the subsequent 6 weeks when females were physically paired with vasectomised males. Urine

samples were collected every after one day for all experimental periods and urine profiles generated. This study was mainly aimed at elucidating the ovulation methods of the giant mole-rat.

### *Experimental design*

**Experiment 1.** Six non-reproductive females of the giant mole-rat were identified from six separate colonies in Kakalo and Mushishima Farm blocks. Similarly twelve (12) matured males with dark colourations around the mouth were trapped from 6 other colonies located 1000m distant from where the females were collected. Females were constantly kept individually until they were shipped to Pretoria where they were placed individually in plastic containers (1 x 0.5 x 0.5m) and subsequently subjected to experimental manipulation. Urine samples were collected every second day for period of 83 days as described below. The samples collected for this period served to detect if the non-reproductive females were producing cyclical progesterone profiles.

**Experiment 2.** The same six females were then transferred to plastic containers sized (0.6 x 0.3 x 0.35m) and provided with a wire mesh (3mm grid) separation for preventing any physical contact but allowing chemical communication. A gonadally complete male was placed in the second compartment of the holding cage for the following 26 days. Urine samples were collected throughout this experiment every second day as described below and served to detect if the physical presence of a male stimulated spontaneous ovulation.

**Experiment 3.** After two and half months of isolation, the same six non-reproductive females were housed individually in plastic containers each with a vasectomised male and

allowed to physical contact and behavioural interactions. Urine samples were taken throughout this experiment every second day as described below.

### *Surgery*

Six males were vasectomized three months prior to being placed in physical contact with one of the six females. All vasectomies were completed three months prior to pairing up to ensure clearance of sperm from the vas deferens as well as a full recovery after surgery. Males were anaesthetized using iso-fluorane gas induction and maintenance with a mask. The vas deferens and epididymis were removed from each of the testis. Vasectomy was only performed to ensure that physical contact alone and not hormonal changes resulting from fertilization were recorded.

### *Sample collection*

The non-reproductive females were placed in urine collection chambers every second day between 08h00 and 14h00 during which urine samples were collected. The chambers were cylindrical and had a smooth mesh floor to allow urine to fall through to a collecting dish. This set up prevented faecal contamination of the urine. The mole-rats were checked hourly throughout the day and urine samples were collected by sterile pipette being stored in plastic epindorph tubes with the animal number and date. The plastic tubes were stored at -35$^{o}$C. On completion of collection the mole-rat was returned to the holding cage. The volume of urine varied between 500µl and 2500µl. The required amount for progesterone and subsequent creatinine determination was 240µl. In the event of no urine being voided by a mole-rat, it was treated as a missing point this happened very infrequently and had no effect on the overall progesterone profile.

***Creatinine determination***

Prior to hormone assay all urine samples were analysed for creatinine measurement Booney *et al.,* (1982). Expressing urine hormone concentrations per mmol creatinine takes into account that the concentration of urine may differ depending on the food intake of an animal. Creatinine concentration was determined by using a modified version of the Jaffe Reaction Folin, (1914). The process involves adding 10µl of standard or sample to the well of a microplate, in duplicate, and leaving two wells empty as duplicate control blank. A further 300µl of picrate reagent is added to the wells, including the blanks.

Fresh alkaline picrate was mixed and comprised a saturated picric acid solution, alkaline titron and deionised water (1:1:10). The alkaline triton is composed of 4.2ml triton x-100, 12.5 ml 1N NaOH and 66.0ml distilled deionised water. The microplate is then placed in the dark for a period of 1.5h, at room temperature to allow colour development to occur. A standard curve ($R^2$ >0.99) was used to determine all sample values.

***Progesterone determination.***

The hormone progesterone is an important indicator hormone because it rises with increasing follicular development and subsequent production of the corpora lutea of ovulation Espey & Lipner, (1994). The cyclical pattern of progesterone secretion in spontaneous ovulators provides the rationale behind the use of progesterone concentrations for detecting ovulation Bauman, (1981).

The concentration of progesterone in the urine samples was measured using the technique of Bennett *et al.,* (1994). The progesterone concentrations were measured using a coat-a-count kit (Diagnostic Products Corporation, Los Angeles, USA). The antiserum is highly specific for progesterone with a cross reactivity to all naturally occurring steroids <0.5%, with the

exception of 17α hydroprogesterone (3.4%), 11-eoxycorticosterone (2.4%), 5β-pregnan-3, 20-dione (3.2%) and 5α-pregnan-3, 20 dione (9.0%). The concentrations of the standards ranged from 0.3 to 127.2 nmol/l.

The assay has been validated for use in the mole-rat by testing the slope of the curve produced using serial dilutions of un-extracted mole-rat urine obtained from a pregnant female (over the range 1:1 to 1:64) against that of the standard curve. Following logit-log transformation of the data the slopes of the curve were compared using Statistica. The curves were parallel to and did not differ significantly from one another. The minimum detection limit of the assay was 0.36 nmol/l and intra- and inter-assay coefficient of variation was 5.1% (n=6) and 9.3% (n=6) respectively.

## Electrone micrograph

Penises were dissected out from frozen material of adult males, thawed and placed in 10% formalin on thawing. This fixing procedure was followed by a series of treatments with a 0.075M phosphate buffer, whereas post-fixation was achieved using a treatment of 1% osmium tetraoxide. Specimens were subjected to a series of dehydration steps using ethanol of increasing concentration (30-100%). Critical point drying (CPD) was reached (CPD from liquid $CO_2$) and the material was further dehydrated using the BIORAD 3000 critical point dryer (Watford, UK). At this point, the material is effectively coated with dehydrated cells that carry heavy metals (osmium and phosphate fixative) to which minute particles of gold can adhere. A Polaron E5200C (Watford, UK) sputter coater was used to sputter a few nanometers of gold, coating the fixed dehydrated material, which was mounted on a carbon

tape on a lead stage. The gold plated material was then viewed with a scanning electron microscope – J SM-840 (JEOL, Tokyo, Japan) and subsequent images were produced.

## Statistical analysis

### *Wilcoxon signed rank tests, Bonferroni correction and Statistica version 0.8*

Progesterone values were averaged for each individual female for the isolation periods and those with chemical contact, seismic communications or physical contact, respectively. For the first experiment, data were divided into two parts to obtain comparative data for both isolation and the contact phase of experiment 2 and 3. The cut-off point was chosen after 30 days corresponding to the length of the latter two experiments. Since data did not satisfy the assumptions for parametric tests, data for the two parts of each experiment where compared employing Wilcoxon signed rank tests. Likewise pairwise comparisons were made between the first part of the different experiments and the second parts. Bonferroni correction was applied to correct for sequential tests and all statistical tests were carried out with SPSS 15.0. However, the Statistica version 8.0 analysis was used in the pairwise comparison of all the 3 experiments for control and experimental.

## Ethical note

In this part of the Copper Belt, these animals are treated as pests (Bennett & Faulkes, 2000) and are also used by the local population as an important human food source, comprising a major source of protein. In this study, the animals were collected at the request of local farmers who would otherwise have eradicated them by other methods; after the study, the

remaining colonies from the area (including those in the grassland and dambos) were caught for food by local farmers.

Animals were euthanased with an overdose of chloroform on the evening of the day of capture by experienced workers, and stored in the interim in covered plastic containers with sand, nest material and food; sexing, weighing and tissue collection were carried out post mortem. Tissue from these animals was collected for a variety of other projects, including population genetics, craniometrics and studies of reproductive biology. Carcasses were eaten by trappers and farmers. The project was reviewed and passed by the Ethics Panel of the University of Pretoria (ref. AUCC06509/011). Capture of mole rats was authorized by the Department of Veterinary and Nature Conservation in the Copper Belt Province of Zambia, and all the necessary permits were obtained in Zambia.

All procedures followed the guidelines of the American Society of Mammalogists (ASM; Animal Care and Use Committee 1998; http://www.mammalogy.org/committees/index.asp) and the animal ethics committee of the University of Pretoria, Pretoria, South Africa. Standard data recorded from collected samples included sex and body mass (g) and all specimens were prepared as voucher specimens and will be deposited in the Natural History Museum, Lusaka, Zambia.

# CHAPTER 3

# Evolution of African mole-rat sociality: burrow architecture, rainfall and foraging in colonies of the cooperatively breeding *Fukomys mechowii*

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## Abstract

African mole rats (Bathyergidae) offer an excellent system with which to test theories relating to the evolution and maintenance of sociality in mammals. The aridity food distribution hypothesis (AFDH) suggests that, within the bathyergids, sociality has evolved in response to patterns of rainfall, its effects on food distribution, and the subsequent costs and risks of foraging and dispersal. Here, in the first detailed study of burrow architecture in a social mole-rat species, with data from 32 burrows, we show that in the giant mole-rat *Fukomys mechowii* burrow fractal dimension increases with colony size and is higher during the rainy season than during the dry season. The mass of food in the burrow increases with fractal dimension and is higher during the rainy season than during the dry season. These results link for the first time colony size, burrow architecture, rainfall and foraging success and provide support for two assumptions of the AFDH, namely that (1) in arid conditions burrowing may be severely constrained by the high costs of digging; and (2) the potential risks of failing to locate food may be mitigated by increases in colony size.

## Introduction

Sociality in African mole rats is thought to have evolved in response to patterns of rainfall, its effects on food distribution, and the subsequent costs and risks of foraging and dispersal (Jarvis, 1978; Bennett, 1988; Lovegrove & Wissel, 1988; Lovegrove, 1991; Jarvis *et al.*, 1994; Faulkes *et al.*, 1997; Jarvis *et al.*,,1998). In this scenario – the aridity food distribution hypothesis (AFDH) – sociality is adaptive as cooperative foraging spreads the energetic costs of burrowing and increases the chances of finding food which, because of its clumped nature, is sufficient, once found, to support large groups of animals.

Although Burda *et al.,* (2000) argue against a causal relationship between cooperative foraging for dispersed food resources and the evolution of sociality in mole-rats but see [Faulkes & Bennett (2007) and O'Riain & Faulkes (2008)] for further discussion and counter-argument], the AFDH is supported by evidence from a variety of sources, including long-term field studies, comparative analyses and molecular studies (Faulkes *et al.*, 1997; Jarvis *et al*., 1998; Spinks, Bennett & Jarvis, 2000b; Burland *et al.*, 2002; Hess, 2004). Other evidence has come from studies of burrow architecture, and specifically fractal dimension, which have shown that both habitat type and group size are reflected in burrow shape Le Comber *et al*., (2002). Fractal dimension is essentially a measure of the extent to which a one-dimensional structure fills a plane, with low fractal dimension (approaching a value of 1), reflecting burrows that explore relatively little of the area surrounding the burrow, and high fractal dimension (approaching a value of 2), reflecting burrows that explore the surrounding area more thoroughly.

A number of studies have examined burrow architecture– although not necessarily fractal dimension – in the Bathyergidae (Hickman, 1977; Davies & Jarvis, 1986; Zuri & Terkel, 1996; Rosi *et al.,* 2000; Spinks *et al*., 2000a; Šumbera *et al.,* 2003c; Herbst & Bennett, 2006), but the majority of these have concentrated on solitary species in which the only time there is plural occupancy of the burrow is during the breeding season or when the mother has young. Relatively few studies have examined burrows of social mole rats, and sample sizes are typically small; for example, Spinks *et al*., (2000a) examined seven *Cryptomys hottentotus hottentotus* burrows, at two sites, while Le Comber *et al*., (2002) examined 25

burrows from seven species, of which only three species (*C. h. hottentotus*, *Fukomys darlingi* and *Heterocephalus glaber*) were social or eusocial, with sample sizes of 10 (split between three sites), one and two, respectively. Our study is thus the first to examine in detail the architecture of a large number of burrows (n=32) of a social mole-rat species.

The giant mole rat *Fukomys mechowii* (formerly *Cryptomys mechowii*), is a social subterranean hystricomorph rodent that is restricted to the sub-tropical and tropical Miombo woodlands and grasslands of central Africa. It has been recorded in sub-equatorial central Africa, including the Democratic Republic of Congo, Angola and Zambia (Bennett & Faulkes, 2000) and is found in a wide variety of soil types ranging from pure sand through to clays. Annual rainfall across its range is 41100mm Scharff *et al.,* (2001). Like other bathyergids, giant mole rats are herbivorous, feeding mainly on geophytes and agricultural crops such as cassava and sweet potato tubers, which they encounter during burrowing (Sichilima *et al.,*, 2002). However, they are unusual within the Bathyergidae in that they supplement their diet with invertebrates and vertebrates found in their burrows, although this is the exception rather than the rule (Burda & Kawalika, 1993; Scharff *et al.,* 2001).

Colonies of *F. mechowii* contain eight to 20 animals, and could contain 40 or more (Burda & Kawalika, 1993; Scharff *et al*., 2001). There is reproductive division of labour, with breeding typically restricted to a single female and a number of male consorts (Bennett & Aguilar, 1995). In most cases, all other individuals are the offspring of the reproductive cohort (Wallace & Bennett, 1998).

It follows from the paucity of data relating to burrow architecture generally that very little information is available about temporal changes in burrow architecture between the rainy and dry seasons. A notable exception is Šumbera *et al*., (2003c), who reported significant differences in burrow architecture in the solitary silvery mole rat *Heliophobius argenteocinereus* at different times of year. However, to date there have been no equivalent data relating to social or eusocial species. This is of interest because a critical assumption of the AFDH is that, for large parts of the year, animals are effectively precluded from foraging by the hardness of the soil Jarvis, (1978). In *F. mechowii,* mole rats probably continue to excavate foraging tunnels, although to a much lesser extent than in the rainy season. The soil produced during these excavations may be used to backfill older tunnels, as is the case with the Damaraland mole rat *Fukomys damarensis* Jarvis *et al*., (1998), and the silvery mole rat [*H. argenteocinereus* Šumbera *et al.,* (2003)].

This study – which forms part of a larger study, some parts of which were published separately – had two principal objectives. First, we aimed to describe the burrow architecture and colony composition of 32 free-living colonies of the giant mole rat. Second, we used fractal dimension analysis to examine three questions relating specifically to the assumptions of the AFDH: (1) Is burrow fractal dimension higher in the rainy season, as might be predicted if either or both the energetic costs of digging, or differences in patterns of food distribution, vary between seasons? (2) Do colonies containing more animals have burrows with higher fractal dimension? This might be the case if, as the AFDH suggests, foraging is more efficient in larger, cooperatively foraging colonies. (3) Is higher fractal dimension associated with a greater mass of food within the burrow? (Le Comber,

Seabloom & Romañach 2006) showed, using computer simulations, that burrows with high fractal dimension located more food; here, this study tests whether this is reflected in larger food stores in real burrows.

## Materials and methods

During the trapping of animals in the field, occupants of 32 colonies were completely captured and each colony had the burrow systems mapped out and food contents recorded and weighed. Apart from root crops, cassava and sweet potatoes that were mainly common in burrows located near farmer's fields, some wild geophytes- roots, rhizomes and tubers found in burrows of the giant mole-rat were also identified. In total 317 animals were captured and necessary records were taken from each animal to fulfill the requirement of three chapters that were mainly based on the same colonies captured, except for one chapter that dealt with the investigation of the ovulation pattern used by the giant mole-rat we used new animals captured for this particular experiment. Skulls that were not damaged were carefully cleaned to remove tendons and kept dry. Later on, twenty two (22) measurements of each of the 265 skulls which were undamaged were taken and also the right molar tooth-raw for the same skulls undamaged were carefully cleaned and micrographs taken for the assessment of sexual dimorphism and age variations as further detailed in Chapter 5. In general, detailed and categorical information pertaining to the materials and methods for every Chapter is fully described in Chapter 2.

# Results

## *Colony composition*

In total, 317 giant mole-rats were captured from 32 colonies, comprising 79 adult males, 76 adult females, 12 sub-adult males, 25 sub-adult females, 40 male juveniles and 85 female juveniles. The mean mass of adult males was 570.7g (SD=20.7g) while that of adult females was 391.3g (SD=11.7g). Mean (±SD) colony size was 9.9±2.49 (range 7–16). No differences were detected in numbers of animals, adults, sub-adults or juveniles either between the two farms, Kakalo and Mushishima, or between seasons (two-sample t-tests: P=NS in all cases).

## *The burrow system*

Two representative burrow systems, one from the dry season and one from the rainy season, are shown in Fig. 3.1. The burrow system typically comprised a deep centrally positioned nest at a mean depth of 1.17±0.548m (range 0.40-2.50m) from which radiated a number of burrows that became more superficial and exhibited varying degrees of branching. Four of the burrow systems had two nests. Short blind ending branches were found towards the end of all burrow systems. Nests were apparently mainly used as sleeping areas, with only three nests containing one or two small wild bulbs and roots. The majority of the nest contents comprised fine crushed roots, pieces of grass and plastic paper. There was very little variation in the nest contents from the 32 excavated burrow systems.

Each burrow system contained one or occasionally two food stores at a mean depth of 1.03±0.458m (range 0.50-2.30m). Food stores were located close to the nesting chambers in a blind ending side branch passing the food store or ending in a food store. Only two burrow

systems had food stores located along the main burrow systems. In some instances, food was tightly packed at the end of store. The food stores typically contained naturally occurring geophytes as well as cassava and small sweet potatoes in areas that were close to agricultural land, with a variety of geophytes including root stocks of the Hypoxidaceae (e.g. *Hypoxis*), rhizomes of *Poaceae spp*., roots of the Asteraceae (e.g. *Senecio*) and corms of the Iridaceae (e.g. *Gladiolus*); several bulbs from species of the Liliaceae and those of Ordichidaceae (e.g. *Eulophia*) were also present. The total biomass of food averaged 260.8±264.59g per burrow system (Table 3.1). Food mass was greater during the rainy season (mean±SD: 349±322g) than during the dry season (161±128g) (t=2.10, d.f.=30, P=0.044). There was no sign of cropping of growing shoots and all tubers were dormant. Each burrow also contained one or more often two toilet chambers at a mean depth of 0.60±0.199m (range 0.30–1.00m).

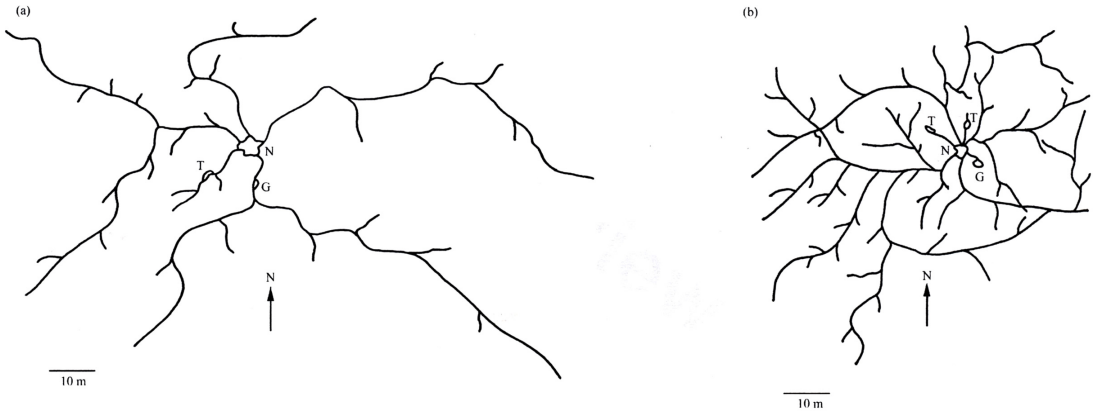


**Figure 3.1**. Two burrows representing the observed differences in fractal dimension, from (a) the dry season (colony 24, fractal dimension =1.194) and (b) the rain season (colony 15, fractal dimension = 1.422). G = granary; N = nest; T = toilet chamber.

**Burrow length**

Burrow length did not differ between the rainy season and the dry season (mean±SD: dry: 239±31.2m; rainy: 258±34.7m) or between sites (mean±SD: Kakalo: 240±33.1m; Mushishima: 260±33.0m) (two-way ANOVA: season: $F_{1,31}$=2.55, P=0.12; site: $F_{1,31}$=3.11, P=0.08; interaction: $F_{1,31}$=1.35, P=0.26), but increased with number of animals (linear regression: ANOVA: $F_{1,30}$=13.93, P=0.001, $r^2$=29.4%) although not number of adults (linear regression: ANOVA: $F_{1,30}$=0.37, P=0.548).

**Table 3.1** Colony composition, burrow metrics and capture dates for each of the 32 colonies in the study.

| Colony | | Total animals | Adults M | Adults F | Sub-adults M | Sub-adults F | Juveniles M | Juveniles F | Borrow Length (m) | Fractal dimennsio | Food Mass (g) | Rain/Dry | Captured |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | K | 8 | 1 | 2 | 0 | 1 | 2 | 2 | 230 | 1.246 | 90 | Dry | September, 2005 |
| 2 | K | 7 | 1 | 1 | 0 | 0 | 2 | 3 | 250 | 1.276 | 65 | Dry | September, 2005 |
| 3 | K | 10 | 1 | 1 | 0 | 2 | 3 | 3 | 210 | 1.225 | 45 | Dry | October, 2005 |
| 4 | M | 9 | 1 | 1 | 0 | 1 | 2 | 4 | 260 | 1.210 | 120 | Dry | October, 2005 |
| 5 | M | 12 | 1 | 1 | 1 | 2 | 2 | 5 | 250 | 1.231 | 70 | Dry | November, 2005 |
| 6 | K | 9 | 1 | 1 | 0 | 1 | 2 | 4 | 290 | 1.270 | 145 | Dry | November, 2005 |
| 7 | M | 14 | 2 | 0 | 0 | 3 | 3 | 6 | 300 | 1.357 | 190 | Rainy | November, 2005 |
| 8 | K | 8 | 2 | 2 | 0 | 0 | 1 | 3 | 245 | 1.247 | 160 | Rainy | November, 2005 |
| 9 | K | 8 | 1 | 0 | 1 | 1 | 3 | 2 | 220 | 1.205 | 50 | Rainy | December, 2005 |
| 10 | M | 10 | 2 | 1 | 0 | 1 | 2 | 4 | 300 | 1.266 | 350 | Rainy | December, 2005 |
| 11 | M | 10 | 1 | 1 | 0 | 1 | 4 | 3 | 270 | 1.287 | 45 | Rainy | December, 2005 |
| 12 | K | 7 | 1 | 0 | 0 | 1 | 2 | 3 | 210 | 1.260 | 110 | Rainy | December, 2005 |
| 13 | M | 9 | 4 | 3 | 2 | 0 | 0 | 0 | 230 | 1.368 | 545 | Rainy | February, 2006 |
| 14 | K | 11 | 3 | 6 | 0 | 1 | 0 | 1 | 280 | 1.354 | 630 | Rainy | March, 2006 |
| 15 | M | 16 | 6 | 4 | 0 | 0 | 3 | 3 | 310 | 1.422 | 455 | Rainy | March, 2006 |
| 16 | K | 16 | 5 | 2 | 2 | 3 | 0 | 4 | 300 | 1.373 | 745 | Rainy | March, 2006 |
| 17 | K | 7 | 1 | 3 | 0 | 0 | 2 | 1 | 210 | 1.294 | 340 | Rainy | March, 2006 |
| 18 | M | 10 | 2 | 6 | 0 | 0 | 1 | 1 | 250 | 1.318 | 200 | Rainy | March, 2006 |
| 19 | M | 10 | 4 | 4 | 0 | 1 | 0 | 1 | 260 | 1.154 | 250 | Rainy | April, 2006 |
| 20 | M | 11 | 2 | 4 | 0 | 0 | 0 | 5 | 280 | 1.331 | 340 | Rainy | April, 2006 |
| 21 | K | 10 | 5 | 5 | 0 | 0 | 0 | 0 | 210 | 1.324 | 95 | Rainy | April, 2006 |
| 22 | K | 9 | 1 | 3 | 1 | 1 | 0 | 3 | 240 | 1.266 | 110 | Rainy | April, 2006 |
| 23 | K | 15 | 4 | 4 | 0 | 0 | 1 | 6 | 280 | 1.252 | 1310 | Rainy | April, 2006 |
| 24 | K | 10 | 1 | 2 | 1 | 0 | 0 | 6 | 230 | 1.194 | 240 | Dry | April, 2006 |
| 25 | M | 8 | 4 | 0 | 1 | 1 | 0 | 2 | 230 | 1.208 | 345 | Dry | April, 2006 |
| 26 | M | 10 | 5 | 2 | 0 | 0 | 1 | 2 | 205 | 1.278 | 65 | Dry | April, 2006 |
| 27 | K | 7 | 5 | 2 | 0 | 0 | 0 | 0 | 190 | 1.249 | 380 | Dry | April, 2006 |
| 28 | M | 9 | 3 | 2 | 1 | 1 | 0 | 2 | 215 | 1.213 | 95 | Dry | May, 2006 |
| 29 | K | 8 | 2 | 3 | 0 | 0 | 1 | 2 | 260 | 1.243 | 420 | Dry | May, 2006 |
| 30 | K | 12 | 3 | 4 | 1 | 1 | 1 | 2 | 205 | 1.234 | 210 | Dry | May, 2006 |
| 31 | K | 7 | 2 | 2 | 1 | 2 | 0 | 0 | 270 | 1.222 | 45 | Dry | May, 2006 |
| 32 | M | 10 | 2 | 5 | 0 | 0 | 2 | 1 | 280 | 1.288 | 85 | Dry | June, 2006 |

**K= Kakalo; M = Mushishim or M = Male; F = Female**

**Burrow fractal dimension**

Burrow fractal dimension was strongly affected by season (mean±SD: dry: 1.24±0.029; rainy: 1.30±0.067), but did not differ between the two farms (mean±SD:Kakalo: 1.26±0.048; Mushishima: 1.28±0.074) (two-way ANOVA: season: $F_{1,31}$=9.41, P=0.005; site: $F_{1,31}$=0.88, P=0.35; interaction: $F_{1,31}$=0.57, P=0.46). Fractal dimension increased with burrow length (linear regression: ANOVA: $F_{1,30}$=6.77, P=0.014, $r^2$=15.7%), with total number of animals (linear regression: ANOVA: $F_{1,30}$=10.41, P=0.003, $r^2$=23.3%) and with total number of adults (linear regression: ANOVA: $F_{1,30}$=7.39, P=0.011, $r^2$=17.1%). The mass of food in the burrow was generally greater in burrows of higher fractal dimension but this not significant (linear regression: ANOVA: $F_{1,30}$=3.45, P=0.073, $r^2$=7.3%). However, this result was strongly affected by a single, anomalous burrow (colony 23) with a large food mass and a low fractal dimension. If this colony was excluded, the relationship between fractal dimension and food mass was highly significant (linear regression: ANOVA: $F_{1,29}$=11.12, P=0.002, $r^2$=25.2%; Fig. 3.2).

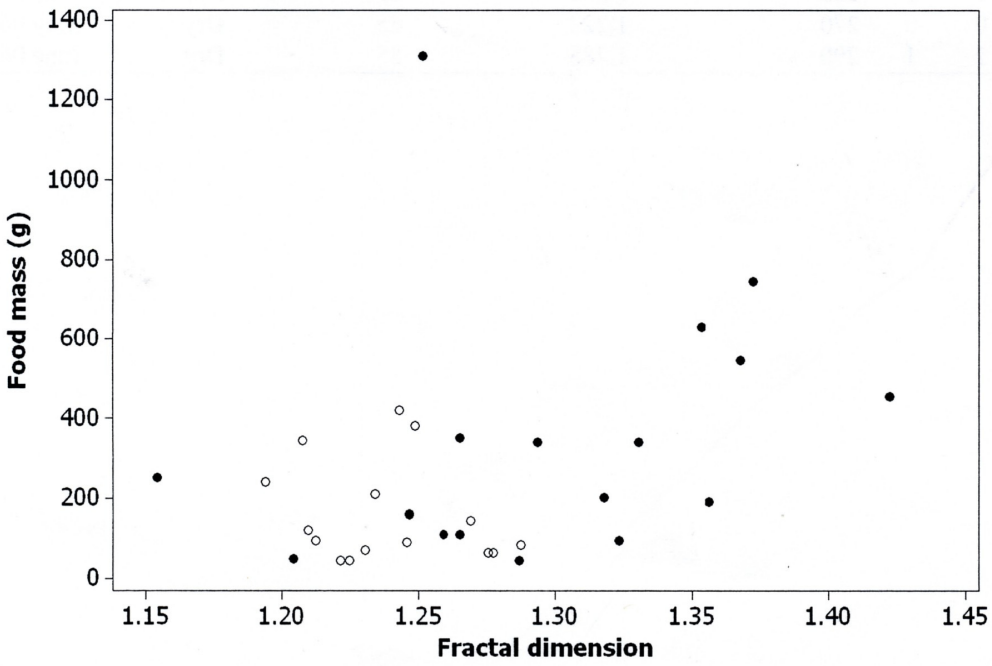


**Figure 3.2.** The mass of food in the burrow as a function of burrow fractal dimension. Open circles: dry season, Filled circles: rainy season. Note the anomalous data point for colony 23, with 1310g of food.

## Discussion

Our results provide support for two critical assumptions of the AFDH, namely (1) that patterns of burrowing are likely to vary between seasons, because in arid conditions burrowing may be severely constrained by the increased energetic demands of digging in hard soil, possibly coupled with the resulting reductions in food abundance, and (2) that the potential risks of failing to locate food may be mitigated by increases in the number of animals foraging. Our results are in line with previous data in social mole-rats indicating that larger colonies have greater survival Jarvis *et al*., (1998) and make for the first time the link between colony size, burrow architecture and foraging success. We demonstrate for the first time the dynamic nature of the social mole-rat burrow with respect to changes in

season, specifically rainfall, and the effects of seasonal changes in burrow architecture on the mass of food in the burrow. We show that burrow fractal dimension – a good indication of the extent to which a burrow explores the surrounding area Le Comber *et al*., (2006) – increases with the number of animals, and especially adults, in the colony, and is higher during the rainy season than during the dry season. The mass of food in the burrow tended to increase with fractal dimension and was higher during the rainy season than during the dry season.

These results are also interesting in the light of other work on New World rodents, and support the idea that sociality is an important determinant of burrow architecture in disparate taxa. In *Microtus ochrogaster,* differences in burrow morphology were related primarily to the type of social group inhabiting the burrow, with burrows of communal groups exhibiting greater complexity than burrows of male –female pairs, although there were no effects of season (Mankin & Getz, 1994). The constraints of burrow digging have also been linked to the evolution of sociality in other species, for instance *Microtus pinetorum* (Powell & Fried, 1992) and a variety of New World hystricognath rodents (Ebensperger & Blumstein, 2006).

The burrow system of the giant mole rat is extensive, with total length ranging from 190 to 310m. This falls within the range of values reported for solitary species [e.g. *Bathyergus suillus*: mean 162m, range 107–420m (Davies & Jarvis, 1986); *Bathyergus janetta*: mean 127m, range 71–165m (Herbst & Bennett, 2006); *H. argenteocinereus*: mean 72.7±35.9m, range 22–114m Šumbera *et al*., (2003c)]; in fact, burrow fractal dimension probably offers a more useful burrow metric than burrow length, because of its relationship to foraging

success Le Comber *et al*.,(2006). This is supported by work showing that, even when values for burrow lengths do not differ in solitary and social species, there may be significant differences in fractal dimension Le Comber *et al*., (2002). Interestingly, while fractal dimension was greater in the rainy season, we found no differences in total burrow length. This might arise because the excavation of relatively short side tunnels can lead to substantial increases in fractal dimension without increasing total burrow length to the same extent. In fact, very large burrow systems may not always be advantageous, because any breaches in the system by predators must be monitored and the relevant section repaired as quickly as possible. Indeed, breached sections of burrow are usually visited by inhabiting mole-rats within an hour of being opened and are subsequently plugged with soil. An additional complication is that, in the absence of detailed studies tracking changes in individual burrows over time, it is not clear to what extent there is a time lag between changes in environmental conditions and changes in burrow architecture. Further work in this area would be of interest. During periods in which the soil has been softened by rainfall and geophytes begin to proliferate, mole-rats must find and store sufficient food to last them through the dry season. Thus, the main limiting factors for burrow excavation in mole-rats are twofold: (1) amount and periodicity of rainfall and (2) number of animals in the burrow system available for digging. Results in this study provide evidence in support of each of these factors. During the dry season, burrows had lower fractal dimension and contained less stored food. Also the study provided evidence that foraging is more efficient when colony size is larger: burrows of larger colonies had higher fractal dimension and contained more food. These results fit well with the foraging models of [(Lovegrove & Wissel, 1988) and Spinks & Plaganyi (1999)], which suggested that colony size is important in foraging risk.

Increased group size reduces the risk of starvation, particularly for mole-rat species occurring in arid environments. To summarize, these results are important because they link for the first time rainfall, colony size, burrow architecture and foraging success in a single social mole-rat species, and thus support the critical assumptions that underlies the aridity food distribution hypothesis.

# CHAPTER 4

## Field evidence for aseasonality of reproduction and colony size in the Afrotropical giant mole-rat *Fukomys mechowii* (Rodentia: Bathyergidae)

*African Zoology (in press)*

## Abstract

The giant mole-rat, *Fukomys mechowii* is a cooperatively breeding subterranean mole-rat exhibiting a reproductive division of labour in which usually one, or occasionally two, females are responsible for procreation. In a field study that involved complete excavation of 32 burrow systems, mean colony size was 9.9 individuals (range 7-16). Pregnant reproductive females were found throughout the study period (September 2005 until June 2006), supporting preliminary evidence that reproduction occurs throughout the year. Of the 32 colonies sampled, 10 of 14 in which the reproductive female could be identified as pregnant contained a single reproductive female, while four had two females breeding simultaneously (plural breeding). The population sex ratio was skewed towards females at 1:1.46. Autopsy of pregnant reproductive females (n=18) revealed that the production of two (10/18 pregnancies) or three (7/18) offspring was the norm, with one case of four embryos being present. These new data increase our fragmentary knowledge of the natural history of this little studied species.

## Introduction

The giant mole-rat *Fukomys mechowii* (Peters, 1881; formally *Cryptomys mechowi*) is an Afrotropical subterranean rodent that occurs in the Miombo woodland and Savannas of Zambia, Democratic Republic of the Congo and Angola (Bennett & Aguilar, 1995; Scharff *et al*., 2001). The existence of two genetically divergent clades within *Cryptomys* has been known for some time e.g. Faulkes *et al.,* (1997), and it has been proposed that the genus *Cryptomys* should be taxonomically subdivided into *Cryptomys* and *Coetomys* Ingram *et al.,* (2004) or, more recently, *Cryptomys* and *Fukomys* Kock *et al.,* (2006). For this paper we

adopt the latter nomenclature. The social lifestyle of *F. mechowii* is thought to be typical of the mole-rat genera *Fukomys* and *Cryptomys*, which exhibit cooperative breeding and reproduction highly skewed towards a single female and a number of male consorts (Bennett & Aguilar, 1995). Delayed dispersal of offspring gives rise to family groups (simple and/or extended). However, the exact kin structure of groups and the incidence of unrelated immigrants remain unknown for this species.

Colony size is an important parameter in comparative studies of African mole-rats, because it is a crucial component of sociality and an indirect measure of the degree of dispersal/philopatry. Social group size has been previously reported to frequently exceed 60 individuals (Burda & Kawalika, 1993), although these data were based on interviews with local hunters and not systematic trapping from distinct colonies. In a later study, Scharff *et al*., (2001) captured six complete colonies, five of which ranged from 3-12 in group size, but with the sixth possibly numbering 40 or more animals. However, we speculate that the animals from the latter colony may have been caught from neighbouring burrows, as the area in question was difficult to survey. Thus, maximum colony size remains uncertain for this species.

Sex ratio in the wild has previously been reported to be skewed towards females, and the sexes are dimorphic, with males being larger than females Scharff *et al*., (2001). Studies in captivity suggest that the reproductive individuals are the most dominant in each respective sex, with non-reproductive males generally more dominant than non-reproductive females. Furthermore, unlike in *F. damarensis*, non-reproductive individuals cannot be placed into

clearly defined work-related groups based on body mass (Wallace & Bennett, 1998; Scantlebury *et al.,* 2006).

Laboratory studies have also shown that the giant mole-rat can breed throughout the year, the long gestation period of 97-111 days means the production of more than two litters per annum is uncommon (Bennett & Aguilar, 1995; Scharff *et al*., 2001). In an attempt to clarify some of the confusion over group size and reproduction (in terms of group structure and number of reproductive individuals), we undertook an extensive field survey of the colony size, age composition and reproductive status of 317 animals from 32 wild colonies of giant mole-rats.

## Materials and methods

The study was conducted over a 10 month period (September 2005 – June 2006 inclusive).The total of 317 animals were captured and records of pregnant females, number of foetuses and juveniles from each colony were taken. Animals were finally sacrificed as described in Chapter 2.

## Results

In total, 317 mole-rats from 32 colonies comprising 131 males and 186 females, categorized into 125 juveniles (21.0% of population), 37 sub-adults (22.2%) and 155 adults (56.8%) were captured over the study period. Mean colony size was 9.9 (range 7-16). There was a highly significant difference in body mass between adult males and females ($t=7.6$; $p < 0.0001$; d.f.=153): mean ± s.e.m. mass of adult males was 570.7 ± 20.7g (range 220-995;

*n*=79) whilst that of adult females was 391.8 ± 11.7g (range 240-650; *n*=76). Among the adult females, in most cases the breeding females were the heaviest. The average mass of reproductive females was 424.7g (pregnant: range 235-650; *n*=18) and 400.8g (non-pregnant: range 250-600; *n*=18), while the average mass of non-reproductive adult females was 381.5g (range 240-600; *n*=58). The sex ratio of the population captured was skewed towards females at 1.46:1 (female: male).

**TABLE 4.1**. Date of capture and site localities of colonies of *F. mechowii* from Kakalo and Mushishima farms in Chingola, Copperbelt Province, Zambia, together with the respective incidence of reproduction and litter sizes.

| Colony no. | Colony size (*n*) | No. Pregnant reproductive females | No. Foetuses present | Year/month captured | Farm block Area | Prevailing season, condition of soil and vegetation at time of capture |
|---|---|---|---|---|---|---|
| 1 | 8 | 0 | 0 | Sept. 05 | Kakalo | Hot/dry season, soil very hard, vegetation dry/burnt |
| 2 | 7 | 1 | 2 | Sept. 05 | Kakalo | |
| 3 | 10 | 1 | 2 | Oct. 05 | Kakalo | |
| 4 | 9 | 0 | 0 | Oct. 05 | Mushishima | |
| 5 | 12 | 0 | 0 | Nov. 05 | Mushishima | Short cool/dry season, onset of rains, vegetation sprouting |
| 6 | 9 | 0 | 0 | Nov. 05 | Kakalo | Rainy season, soil soft, green vegetation all over. |
| 7 | 14 | 0 | 0 | Nov. 05 | Mushishima | |
| 8 | 8 | 0 | 0 | Nov. 05 | Kakalo | |
| 9 | 8 | 1 | 2 | Dec. 05 | Kakalo | |
| 10 | 10 | 1 | 2 | Dec. 05 | Mushishima | |
| 11 | 10 | 0 | 0 | Dec. 05 | Mushishima | |
| 12 | 7 | 0 | 0 | Dec.05 | Kakalo | |
| 13 | 9 | 0 | 0 | Feb. 06 | Mushishima | |
| 14 | 11 | 1 | 2 | March 06 | Kakalo | |
| 15 | 16 | 2 | 3/3 | March 06 | Mushishima | |
| 16 | 16 | 0 | 0 | March 06 | Kakalo | |
| 17 | 7 | 1 | 2 | March 06 | Kakalo | |
| 18 | 10 | 1 | 3 | March 06 | Mushishima | |
| 19 | 10 | 2 | 3/2 | April 06 | Mushishima | Rainy season slowly reducing, Soil still soft, green vegetation. |
| 20 | 11 | 0 | 0 | April 06 | Mushishima | |
| 21 | 10 | 2 | 2/4 | April 06 | Kakalo | |
| 22 | 9 | 0 | 0 | April 06 | Kakalo | |
| 23 | 15 | 0 | 0 | April 06 | Kakalo | |
| 24 | 10 | 0 | 0 | April 06 | Kakalo | |
| 25 | 8 | 0 | 0 | April 06 | Mushisima | |
| 26 | 10 | 2 | 2/3 | April 06 | Mushishima | |
| 27 | 7 | 0 | 0 | April 06 | Kakalo | |
| 28 | 9 | 1 | 2 | May 06 | Mushishima | Rain season diminishes, soil still soft, green vegetation. |
| 29 | 8 | 0 | 0 | May 06 | Kakalo | Cool/dry season, soil hard, vegetation dried up. |
| 30 | 12 | 1 | 3 | May 06 | Kakalo | |
| 31 | 7 | 0 | 0 | May 06 | Kakalo | |
| 32 | 10 | 1 | 3 | June 06 | Mushishima | |

Despite large variation in the prevailing environmental and ecological conditions, pregnant females were found throughout the study period (Table 4.1). Modal litter size was two (10/18 pregnancies), with seven cases of triplets and a single example of a female carrying four offspring (Table 4.1). Mean litter size was thus 2.5 pups. The majority of colonies in which the breeding female was identified as being pregnant (10/14) had a single reproductive female, but four out of 32 colonies had two reproductive females.

## Discussion

This study is the most extensive to date to investigate colony size in *F. mechowii*. The mean colony size of approximately ten animals is not dissimilar to that reported for *F. damarensis*, the closest species studied extensively in the wild, where the mean group size is around 12 animals (Bennett & Faulkes, 2000). However, the maximum of sixteen animals in *F. mechowii* reported here is substantially less than two colonies of forty-one recorded for *F. damarensis*. The range in group size of 7-16 animals is in keeping with the study by Scharff *et al*., (2001), and the absence of very large group size may indicate that the group of 40+ animals caught by Scharff *et al*. was from two or more neighbouring colonies rather than a single burrow. The results also question the reliability of the data gleaned from local hunters in (Burda and Kawalika, 1993), where groups were reported to frequently consist of over 60 animals.

An increasing body of evidence has been collected on the seasonality of reproduction in African mole-rats for both solitary species e.g. *Georychus capensis*, *Bathyergus suillus, Bathyergus janetta* and *Heliophobius argenteocinereus* (Šumbera *et al*., 2003b; Hart *et al.,*

2006; Oosthuizen & Bennett, 2007) and social, e.g. *Cryptomys* and *Fukomys* (Bennett & Jarvis, 1988a; Bennett, 1989; Burda, 1989; Spinks *et al*., 1997, 1999; Janse van Rensburg *et al*., 2002, 2004). Until recently, the only published information on the reproduction of the giant mole-rat was derived from laboratory studies (Bennett & Aguilar, 1995; Scharff *et al.,* 1999) and one small field study Scharff *et al.,* (2001) in which reproduction was suggested to take place throughout the year, or from anecdotal reports from Ansell (1978) who captured young animals throughout the year. The sample sizes, period of collection and the number of colonies involved were limited in these studies. Our field data clearly support the laboratory findings that giant mole-rats do indeed breed continuously throughout the year. To date all the studied species within the genus *Fukomys* have been reported to be aseasonal breeders producing offspring throughout the year: [*F. damarensis* (Bennett & Jarvis, 1988b; Bennett & Faulkes, 2000)], [*F. darlingi* (Bennett *et al*., 1994)] and [*F. anselli* (Burda, 1989)]. In contrast, within the more southerly occurring genus *Cryptomys*, reproduction appears to be more seasonal, e.g. [*Cryptomys h. hottentotus* (Spinks *et al*., 1997, 1999)] and [*Cryptomys h. pretoriae* (Janse van Rensburg *et al.,* 2002)].

The small litter size (two to four pups) produced by *F. mechowii* is also characteristic of other species of both [*Fukomys* (Bennett & Jarvis, 1988b; Burda, 1989; Bennett *et al*., 1994; Bennett & Aguilar, 1995; Scharff *et al*., 2001)] and [*Cryptomys* (Bennett, 1989; Malherbe *et al*., 2004b, Oosthuizen *et al.,* 2007)]. Among the social bathyergid genera *Fukomys* and *Cryptomys*, the species so far investigated all have relatively small litters (2 to 6 pups; Bennett *et al.,* 1991), compared to solitary species, e.g. *Bathyergus suillus*, *B. janetta* and *Georychus capensis*, where litter size ranges are 1-4, 1-7 and 4-10 respectively. The eusocial

naked mole-rat (*Heterocephalus glaber*) is exceptional in the family in having litters of up to 27 (see Bennett & Faulkes, 2000 for review). The significance of this variation in litter sizes among bathyergids remains unclear, and there are no clear trends with regard to social system or habitat. The skew towards females in the sex ratio of colonies in the giant mole-rat Scharff *et al.,* (2001, this study) differs from those of *F. damarensis*, *C. hottentotus* (dwelling in mesic habitats) and the more divergent naked mole-rat where sex ratio is skewed towards males among adults (Bennett & Faulkes, 2000). Again, the significance of these observations and species differences remains unclear.

In all social *Cryptomys* and *Fukomys* species and in *Heterocephalus* there is a marked reproductive skew characteristic of cooperative breeders, whereby breeding is normally restricted to a single reproductive female and one or a few male consorts (Bennett & Jarvis, 1988; Burda, 1989; Bennett *et al*., 1994; Bennett & Aguilar, 1995; Bennett & Faulkes, 2000; Scharff *et al*., 2001). A significant result in this study is the observation of plural breeding, with two breeding females present (and pregnant) in four of the 32 colonies. In the bathyergid species that have been studied to date, plural breeding of females within colonies appears to be very uncommon. In an extensive field study of common mole-rats, 49 colonies surveyed at two geographic locations all had a single reproductive female Spinks *et al*., (2000) and many other small studies have also failed to detect more than one reproductive female per colony (e.g. Bennett, 1989). In only one case has plural breeding been observed, and that was in two out of 30 colonies caught at Somerset West, South Africa over a two-year period (N.C. Bennett, unpublished data). Plural breeding among females in colonies of Damaraland mole-rats has not been observed, either in captivity (in more than 60 colonies),

or in the wild (in over 150 colonies caught over a 15 year period from several geographic locations; J.U.M. Jarvis and N.C. Bennett, unpublished data). In naked mole-rats, Braude (1991) recorded two instances of plural breeding among a total of 2051 naked mole-rats from 23 colonies in Meru National Park, Kenya. Colonies maintained by Jarvis at the University of Cape Town are the only captive naked mole-rats so far reported to have contained two queens Jarvis, (1991b). If one accepts that *F. mechowii*, like all *Cryptomys* and *Fukomys* species studied to date, has an outbreeding system of mating, then the incidence of plural breeding implies that the queens have an unrelated male or males to mate with and raises interesting questions about the kin structure and dynamics of groups. The highly significant dimorphism in body mass between males and females may also imply sexually selection and competition among males.

There are currently only two published long term field studies on *F. damarensis* and *C. h. hottentotus* that have provided insights into the turnover of reproductive animals and lifetime reproductive success of "non-reproductive" animals (Jarvis & Bennett, 1993; Spinks *et al.,* 2000; Burland *et al.,* 2004; Bishop *et al.,* 2004). Further research using mark recapture studies and molecular genetic techniques on long term marked populations of *F. mechowii* are required to further unravel the interesting life history strategy of this central African mole-rat.

# CHAPTER 5

## Sexual dimorphism and age variation in the social giant mole-rat, *Fukomys mechowii* (Rodentia: Bathyergidae) from Zambia, Central Africa: An analysis based on traditional cranial morphometric data

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## Abstract

Due to difficulties in estimating absolute age in mammals, different methods for its estimation have been proposed, and among these, the degree of molar eruption and wear are considered to be at least one of the reliable indicators of relative age. Consequently, maxillary molar tooth-row eruption and wear were used to assign individuals of the giant mole-rat, *Fukomys mechowii* (Peters, 1881) (Rodentia: Bathyergidae) from two geographically proximal and ecologically similar localities in the Copper-belt Province of Zambia, Central Africa to nine relative age classes. These were in turn used to assess the nature and extent of sexual dimorphism and age variation in this little-studied social mole-rat based on cranial morphometric data with reference to body mass, and a series of both univariate and multivariate statistical analyses. Both univariate and multivariate analyses showed morphological differences between individuals of age classes 1–3 and those of age classes 5–9, while individuals of age class 4 were intermediate between these two age class groupings, suggesting that this age class lies at a point on a hypothetical growth curve where it begins to stabilize. The analysis of the nature and extent of sexual dimorphism revealed its absence in the younger individuals of age classes 1–4 and its presence in older age classes 5–9, and these results are supported by the data on body mass. These results may allow an insight into our understanding of the population and social structures, and reproductive strategies in this little-studied giant mole-rat.

## Introduction

Numerous studies have been undertaken to assess the nature and extent of non-geographic variation in rodents, particularly at the level of sexual dimorphism and age variation. These include studies on rats [(*Niviventer cominga)* – Yu & Lin, 1999]; *Dasymys* – Mullin *et al.,* 2004; mole-rats [(*Cryptomys hottentotus*, *F. damarensis*, *F. mechowii*, and *Heterocephalus glaber* Begall & Burda, 1998]; Bennett *et al*., 1990; Davies and Jarvis, 1986; Hagen, 1985; Scharff *et al.,* 1999; mice [(*Peromyscus maniculatus)* – Schulte-Hostedde *et al.,* 2001]; tuco-tucos [(*Ctenomys talarum* – Zenuto *et al.,* 1999]; the highveld mole-rat (common name) [(*Cryptomys hottentotus pretoriae*)– Janse van Rensburg *et al*., 2004] and Cape dune mole-rat [(*Bathyergus suillus*)– Hart *et al*., 2007].

However, due to difficulties in estimating absolute age in mammals, various methods for its estimation have been proposed Hart *et al*., (2007). While body mass has been used in the past for example, in subterranean mole-rats (Bennett, 1988; Bennett *et al.,* 1990; Janse van Rensburg *et al.,* 2004), it is considered to be affected by soil type, the availability and quality of food, and in social species, by the social rank of an individual [Bennett 1988, 1989]; [Jacobs *et al*., 1991; Janse van Rensburg *et al*., 2004; Jarvis, 1979; Morris, 1972; Wallace & Bennett, 1998]. The estimation of relative age based on molar eruption and wear is considered to be at least more reliable, particularly if a sample emanates from a homogenous sample in an attempt to reduce the potential influence of geographic variation (Chaplin & White, 1969; Chimimba & Dippenaar, 1994; Dippenaar & Rautenbach, 1986; Janse van Rensburg *et al.,* 2004; Taylor *et al.,* 1985; Hart *et al.,* 2007).

Consequently, in the present study, the degree of molar eruption and wear is used to assess the nature and extent of sexual dimorphism and age variation in the giant mole-rat, *Fukomys mechowii* Peters, (1881) from geographically proximal and ecologically similar localities in the Copper-belt Province of Zambia, Central Africa based on traditional cranial morphometric data and a range of both univariate and multivariate analyses. Nevertheless, body mass which has previously been used to assess the nature and extent of sexual dimorphism and age variation in other social species such as the highveld mole–rat, [(*Cryptomys hottentotus pretoriae*) Janse van Rensburg *et al*., 2004] was also used in the present study for comparative purposes.

However, of fundamental importance in the assessment of non-geographic variation in general is how the derived data are statistically analyzed during its evaluation. Although previous assessments of non-geographic variation largely involved the use of a range of univariate analyses (reviewed in Chimimba & Dippenaar, 1994), the partitioning of the percent contribution of the sum of squares (%*SSQ*) of each source of variation to the total *SSQ* which can be computed directly from a two-way analysis of variance table ANOVA; Zar, (1996) is considered to be the most appropriate method (Leamy, 1983; Hart *et al.,* 2007). However, the use of this univariate %*SSQ* approach alone in the assessment of non-geographic variation has limitations because of the number of variables that must be statistically significant before unequivocally deciding on the presence of overall statistically significant non-geographic variation Willig *et al.,* (1986). Instead, multivariate analysis of variance (MANOVA; Zar, 1996) which uses rather than ignores correlations among

variables has been recommended as the most appropriate method for evaluating overall statistical differences in the analysis of non-geographic Willig *et al.,* (1986).

Consequently, the present study is based on samples from two geographically proximal and ecologically similar localities, and uses ANOVA, %*SSQ*, and a series of multivariate analyses of traditional cranial morphometric data in order to assess the nature and extent of sexual dimorphism and age variation in the giant mole-rat from Zambia. The giant mole-rat is a social subterranean hystricomorph rodent that is restricted to the sub-tropical and tropical Miombo woodlands and grasslands of Central Africa (Bennett & Aguilar, 1995; Sichilima *et al.,* 2008). Given that most studies on mole-rats in Africa have been undertaken in the southern parts of the continent, our study of which part of the results are interpreted with reference to the reproductive biology of the species, forms part of a broader investigation of this little-studied species of mole-rat from the central part of Africa.

Exploratory analyses of the derived craniometric measurements revealed the data to be normally distributed. The nature and extent of sexual dimorphism and age variation were first simultaneously univariately assessed by a two-way ANOVA (Zar, 1996) of samples of age classes 1–9 after it was established that tests for normality and homogeneity of variances satisfied the assumptions of ANOVA tests (Zar, 1996). Where statistically significant age differences were detected by the ANOVA, non-significant subsets ($P > 0.05$) were identified by the post hoc Student-Newman-Keuls test SNK; (Gabriel & Sokal, 1969; Sokal & Rohlf, 1981) of ranked means. The derived two-way ANOVA table was in turn used to estimate the %*SSQ* of the four potential sources of variation in the data, namely, sex, age, sex age

interaction, and error (= residual) by dividing the *SSQ* associated with each source of variation by the total SSQ.

The nature and extent of sexual dimorphism within *F. mechowii* was also multivariately assessed by an unweighted pair-group method using arithmetic averages (UPGMA) cluster analysis and principal component analysis (PCA) of standardized variables (Sneath & Sokal, 1973). UPGMA cluster analysis was based on Euclidean distances and correlation coefficients among groups, while the PCA was based on correlation coefficients among variables (Sneath & Sokal, 1973). Additional analyses included the computation of standard descriptive statistics. Since exploratory analyses showed that data on body mass were not normally distributed, body mass data within sexes and age classes were evaluated using the non-parametric Mann-Whitney *U* test (Zar, 1996). All statistical analyses in the present study were based on all the 22 cranial measurements recorded, and were undertaken using the statistical programme (STATISTICA, version 8.0 StatSoft Inc. 2008).

## Materials and methods

Two hundred and sixty five (265) animals out of the total of three hundred and seventeen (317) that were captured in the field had their skulls undamaged hence 22 measurements of each skull were taken for the assessment of the sexual dimorphism in the giant mole-rat. Further more the right molar row of each of the 265 skulls was thoroughly cleaned and micrographs were taken on them for the assessment of age variation as detailed in Chapter 2.

## Results

The ANOVA results showed that all 22 measurements were highly statistically significant ($P < 0.001$) with reference to age, while 19 of the 22 measurements were all highly statistically significant due ($P < 0.001$) to sexual dimorphism and one measurement (AFL), was statistically significant at $P < 0.01$ (Table 5.1). Fourteen out of the 22 measurements showed statistically significant interaction between sexual dimorphism and age at either $P < 0.001$ or $P < 0.01$) (Table 5.1), while one measurement (AFA), was statistically significant at $P < 0.05$. Although there was unequivocal statistically significant sexual dimorphism, the largest *F*-values were mainly associated with age variation rather than either sexual dimorphism or the interaction between these two components of variation (Table 5.1).

The significant contribution of age to the total variation is also evident from the generally high %*SSQ* values for age (%*SSQ*: $\bar{x}$ = 54.62%; range = 28.44–81.25%) than that for sex (%*SSQ*: $\bar{x}$ = 4.40; range = 0.15–3.69%) and the interaction (%*SSQ*: $\bar{x}$ = 2.97; range 1.39–3.83%) between age variation and sexual dimorphism (Table 5.1). Although all the 22 measurements were statistically significant at either $P < 0.001$ or $P < 0.01$ and also with higher %*SSQ* values, the %*SSQ* values for the error component (= residual) for all 22 measurements and their associated means were also relatively high (%SSQ: $\bar{x}$ = 40.01; range = 13.54–64.98%) (Table 5.1) particularly so with reference to the %*SSQ* values for sexual dimorphism and the interaction between sexual dimorphism and age variation. This suggests that apart from the presence of sexual dimorphism and age variation, there are other factors that may be influencing the nature and extent of non-geographic variation within the giant mole-rat.

**Table 5.1.** *F*-values and percent *SSQ* of each source of variation derived from a two-way analysis of variance (ANOVA) of nine age classes (1–9) based on the degree of tooth eruption and wear in male and female giant mole-rats, *Fukomys mechowii*, from Kakalo and Mushishima farm blocks in Chingola, Copperbelt Province of Zambia. Statistical significance: * = $P < 0.05$; ** = $P<0.01$; *** = $P < 0.001$. Measurements are defined and illustrated in Fig. 2.2.

| Measurement | *F*-Value | | | *%SSQ* | | | |
|---|---|---|---|---|---|---|---|
| | Age A) | Sex (S) | A x S | Age (A) | Sex (S) | A x S | Error |
| GLS | 52.74*** | 24.53*** | 2.12** | 59.39 | 3.45 | 2.39 | 34.77 |
| ITC | 62.67*** | 29.37*** | 2.34** | 62.95 | 3.69 | 2.35 | 31.01 |
| BCW | 28.60*** | 17.96*** | 1.69 | 45.11 | 3.54 | 2.66 | 48.69 |
| ZMB | 46.47*** | 21.67*** | 2.64** | 56.19 | 3.28 | 3.19 | 37.34 |
| ZYW | 52.48*** | 18.01*** | 3.13*** | 59.14 | 2.54 | 3.53 | 34.79 |
| IOB | 13.68*** | 11.68*** | 1.51 | 28.78 | 3.07 | 3.17 | 64.98 |
| WR | 44.50*** | 22.04*** | 2.92*** | 54.93 | 3.40 | 3.60 | 38.07 |
| NA | 46.81*** | 15.66*** | 2.72** | 56.83 | 2.38 | 3.31 | 37.48 |
| UTR | 185.45*** | 40.18*** | 6.90*** | 81.25 | 2.20 | 3.01 | 13.54 |
| PAC | 13.65*** | 12.72*** | 1.88 | 28.44 | 3.31 | 3.92 | 64.33 |
| NPP | 64.49*** | 16.87*** | 3.04*** | 64.16 | 2.09 | 3.03 | 30.72 |
| GHS | 39.81*** | 16.76*** | 1.12 | 53.31 | 2.81 | 2.53 | 41.35 |
| MLT | 103.32*** | 29.29*** | 4.91*** | 72.37 | 2.56 | 3.44 | 21.63 |
| MDL | 51.03*** | 16.08*** | 2.40** | 59.12 | 2.33 | 2.78 | 35.77 |
| MTR | 167.87*** | 30.72*** | 6.26*** | 80.38 | 1.84 | 3.00 | 14.78 |
| AFL | 23.11*** | 7.20** | 0.77 | 41.52 | 1.62 | 1.39 | 55.47 |
| MAF | 24.33*** | 12.38*** | 1.62 | 41.67 | 2.65 | 2.79 | 52.89 |
| AFA | 28.35*** | 13.39*** | 1.96* | 45.10 | 2.66 | 3.12 | 49.12 |
| MRH | 46.64*** | 9.09*** | 2.03** | 57.81 | 1.40 | 2.53 | 38.26 |
| UJI | 33.45*** | 2.64 | 2.46** | 49.84 | 0.49 | 3.68 | 45.99 |
| LJI | 28.13*** | 0.71 | 1.29 | 46.58 | 0.15 | 2.15 | 51.12 |
| WI | 45.99*** | 8.85*** | 3.10** | 56.73 | 1.36 | 3.83 | 38.08 |
| Mean | | | | 54.62 | 4.40 | 2.97 | 40.01 |

The results of the *post hoc* SNK tests that were undertaken in order to identify statistically non-significant subsets ($P > 0.05$) of age class groupings of the 22 measurements revealed three contrasting patterns of ranked means (Table 5.2). The first and major and major pattern

which involved 11 of the 22 measurements (BCW, ZMB, IOB, WR, PAC, GHS, MTR, AFA, MRH, UJI and LJI) showed an orderly increase in size with increasing age (Table 5.2). This pattern is also evident in standard descriptive statistics (Table 5.3) where there is a direct relationship between measurement magnitude and age. The second trend in the SNK tests which involved eight of the 22 measurements (ZYW, NA, UTR, NPP, MDL, AFL, MAF and WI) grouped individuals of the younger age classes 1–4, and those of the older age classes 5–9 into two different non-overlapping non-significant subsets (Table 5.2). The third pattern that involved three measurements only (GLS, ITC and MLT) showed statistically significant differences between all the nine age classes of the giant mole-rat examined (Table 5.2).

**Table 5.2**. *Post hoc* Student-Newman-Keuls (SNK) tests of tooth-wear classes (AC) 1–9 of the giant mole-rat, *Fukomys mechowii* from Kakalo and Mushishima farm blocks, Chingola, Copperbelt Province of Zambia. Non-significant subsets ($P > 0.05$) are indicated by vertical lines, while NS = no significant difference; AS = all means significantly different. Measurements are defined and illustrated in Fig. 2.2.

| GLS | AC | *N* | SD | Means | |
|---|---|---|---|---|---|
| | I | (18) | 3.17 | 31.60 | |
| | II | (22) | 3.00 | 36.71 | |
| | III | (26) | 3.77 | 39.35 | |
| | IV | (21) | 5.25 | 41.53 | |
| | V | (41) | 6.80 | 44.95 | AS |
| | VII | (15) | 5.55 | 47.00 | |
| | VI | (28) | 4.44 | 47.31 | |
| | VIII | (33) | 5.00 | 49.60 | |
| | IX | (61) | 5.43 | 53.40 | |

| UTR | AC | *N* | SD | Means |
|---|---|---|---|---|
| | I | (18) | 0.72 | 4.57 |
| | II | (22) | 0.39 | 6.31 |
| | III | (26) | 0.62 | 6.81 |
| | IV | (21) | 0.62 | 7.44 |
| | V | (41) | 0.72 | 8.30 |
| | VII | (15) | 0.78 | 8.54 |
| | VI | (28) | 0.66 | 8.83 |
| | VIII | (33) | 0.64 | 9.24 |
| | IX | (61) | 0.72 | 9.45 |

| MAF | AC | *N* | SD | Means |
|---|---|---|---|---|
| | I | (18) | 1.09 | 7.26 |
| | II | (22) | 1.54 | 9.89 |
| | IV | (21) | 1.82 | 10.19 |
| | III | (21) | 3.15 | 10.39 |
| | VII | (15) | 1.75 | 11.56 |
| | V | (41) | 1.68 | 11.61 |
| | VI | (28) | 1.70 | 11.65 |
| | VIII | (33) | 2.67 | 13.04 |
| | IX | (61) | 1.72 | 13.71 |

| ITC | AC | *N* | SD | Means | |
|---|---|---|---|---|---|
| | I | (18) | 2.81 | 30.00 | |
| | II | (22) | 3.21 | 34.92 | |
| | III | (26) | 3.91 | 37.39 | |
| | IV | (21) | 5.25 | 39.57 | |
| | V | (41) | 4.25 | 43.80 | AS |
| | VII | (15) | 5.58 | 44.86 | |
| | VI | (28) | 5.09 | 45.21 | |
| | VIII | (33) | 4.77 | 47.63 | |
| | XI | (61) | 5.39 | 51.41 | |

| PAC | AC | *N* | SD | Means |
|---|---|---|---|---|
| | I | (18) | 0.32 | 3.00 |
| | III | (26) | 0.36 | 3.49 |
| | II | (22) | 0.45 | 3.50 |
| | IV | (21) | 0.65 | 3.58 |
| | VII | (15) | 0.69 | 3.84 |
| | V | (41) | 0.49 | 3.88 |
| | VI | (28) | 0.50 | 3.96 |
| | IX | (61) | 0.56 | 4.33 |
| | VIII | (33) | 1.08 | 4.36 |

| AFA | AC | *N* | SD | Means |
|---|---|---|---|---|
| | I | (18) | 1.81 | 9.84 |
| | II | (22) | 2.03 | 11.89 |
| | IV | (21) | 2.45 | 12.53 |
| | III | (26) | 2.55 | 12.54 |
| | V | (41) | 1.52 | 14.10 |
| | VII | (15) | 1.95 | 14.16 |
| | VI | (28) | 2.56 | 14.51 |
| | VIII | (33) | 2.50 | 15.75 |
| | IX | (61) | 2.71 | 17.28 |

| BCW | AC | *N* | SD | Means |
|---|---|---|---|---|
| | I | (18) | 1.27 | 15.08 |
| | II | (22) | 0.87 | 16.33 |
| | III | (26) | 1.88 | 16.51 |
| | IV | (21) | 1.11 | 17.17 |
| | V | (41) | 1.21 | 18.12 |
| | VII | (15) | 1.23 | 18.24 |
| | VI | (28) | 1.46 | 18.30 |
| | VIII | (33) | 1.11 | 18.53 |
| | IX | (61) | 1.16 | 19.37 |

| NPP | AC | *N* | SD | Means |
|---|---|---|---|---|
| | I | (18) | 2.99 | 28.05 |
| | II | (22) | 2.56 | 33.45 |
| | III | (26) | 2.56 | 34.95 |
| | IV | (21) | 3.31 | 37.37 |
| | V | (41) | 4.93 | 41.70 |
| | VII | (15) | 5.11 | 41.78 |
| | VI | (28) | 5.14 | 43.16 |
| | VIII | (33) | 4.36 | 45.08 |
| | IX | (61) | 5.27 | 48.44 |

| MRH | AC | *N* | SD | Means |
|---|---|---|---|---|
| | I | (18) | 0.88 | 5.76 |
| | IV | (21) | 1.27 | 7.93 |
| | III | (26) | 1.08 | 8.10 |
| | II | (22) | 1.40 | 8.27 |
| | V | (41) | 1.46 | 8.91 |
| | VII | (15) | 1.98 | 9.52 |
| | VI | (28) | 1.76 | 10.00 |
| | VIII | (33) | 2.38 | 10.88 |
| | IX | (61) | 2.03 | 11.52 |

| ZMB | AC | *N* | SD | Means |
|---|---|---|---|---|
| | I | (18) | 1.74 | 17.52 |
| | II | (22) | 1.36 | 19.01 |
| | III | (26) | 1.15 | 20.07 |
| | IV | (21) | 2.00 | 20.79 |
| | V | (41) | 2.07 | 22.41 |
| | VI | (28) | 2.33 | 22.75 |
| | VII | (15) | 2.61 | 23.44 |
| | VIII | (33) | 2.27 | 23.95 |
| | IX | (61) | 2.27 | 25.70 |

| GHS | AC | *N* | SD | Means |
|---|---|---|---|---|
| | I | (18) | 1.05 | 13.51 |
| | II | (22) | 1.26 | 15.59 |
| | III | (26) | 1.30 | 16.09 |
| | IV | (21) | 1.41 | 16.61 |
| | V | (41) | 1.53 | 18.00 |
| | VI | (28) | 1.78 | 18.39 |
| | VII | (15) | 2.04 | 18.40 |
| | VIII | (33) | 1.87 | 19.06 |
| | IX | (61) | 2.65 | 20.70 |

| UJI | AC | *N* | SD | Means |
|---|---|---|---|---|
| | I | (18) | 0.64 | 3.87 |
| | III | (26) | 0.69 | 4.65 |
| | II | (22) | 0.44 | 4.66 |
| | IV | (21) | 0.60 | 4.97 |
| | VI | (28) | 0.74 | 5.42 |
| | VII | (15) | O.85 | 5.56 |
| | V | (41) | O.80 | 5.58 |
| | VIII | (33) | 0.88 | 6.41 |
| | IX | (61) | 1.04 | 6.54 |

| ZYW | AC | *N* | SD | Means |
|---|---|---|---|---|
| | I | (18) | 3.07 | 21.88 |
| | II | (22) | 3.35 | 26.28 |
| | III | (26) | 2.92 | 26.48 |
| | IV | (21) | 4.22 | 28.24 |
| | V | (41) | 3.91 | 32.45 |
| | VII | (15) | 5.04 | 33.66 |
| | VI | (28) | 4.75 | 33.68 |
| | VIII | (33) | 4.65 | 36.10 |
| | IX | (61) | 5.43 | 39.66 |

| MLT | AC | *N* | SD | Means | |
|---|---|---|---|---|---|
| | I | (18) | 2.59 | 31.78 | |
| | II | (22) | 2.30 | 33.75 | |
| | III | (26) | 2.25 | 34.56 | |
| | IV | (21) | 2.75 | 35.93 | |
| | V | (41) | 3.10 | 40.34 | AS |
| | VI | (28) | 5.66 | 43.04 | |
| | VII | (15) | 5.49 | 45.01 | |
| | VIII | (33) | 5.07 | 47.77 | |
| | IX | (61) | 6.05 | 52.57 | |

| LJI | AC | *N* | SD | Means |
|---|---|---|---|---|
| | I | (18) | 0.88 | 5.76 |
| | IV | (21) | 1.27 | 7.93 |
| | III | (26) | 1.08 | 8.10 |
| | II | (22) | 1.40 | 8.27 |
| | V | (41) | 1.46 | 8.91 |
| | VII | (15) | 1.98 | 9.52 |
| | VI | (28) | 1.76 | 10.00 |
| | VIII | (33) | 2.38 | 10.88 |
| | IX | (61) | 2.03 | 11.52 |

| IOB | AC | *N* | SD | Means |
|---|---|---|---|---|
| | I | (18) | 0.70 | 9.34 |
| | IX | (61) | 0.72 | 9.45 |
| | III | (26) | 0.41 | 9.75 |
| | II | (22) | 0.77 | 9.81 |
| | IV- | (21) | 0.48 | 9.85 |
| | V | (41) | 0.99 | 10.33 |
| | VII | (15) | 0.70 | 10.47 |
| | VI | (28) | 0.97 | 10.58 |
| | VIII | (33) | 0.76 | 10.59 |

| MDL | AC | *N* | SD | Means |
|---|---|---|---|---|
| | I | (18) | 3.00 | 21.57 |
| | II | (22) | 4.31 | 28.10 |
| | III | (26) | 4.35 | 28.75 |
| | IV | (21) | 3.10 | 29.31 |
| | V | (41) | 4.91 | 35.07 |
| | VII | (15) | 4.53 | 35.10 |
| | VI | (28) | 4.88 | 35.97 |
| | VIII | (33) | 5.67 | 40.55 |
| | IX | (61) | 5.74 | 41.27 |

| WI | AC | *N* | SD | Means |
|---|---|---|---|---|
| | I | (18) | 0.41 | 1.51 |
| | II | (22) | 0.45 | 2.29 |
| | III | (26) | 0.51 | 2.55 |
| | IV | (21) | 0.55 | 2.62 |
| | V | (41) | 0.61 | 3.05 |
| | VII | (15) | 0.56 | 3.22 |
| | VI | (28) | 0.53 | 3.28 |
| | VIII | (33) | 0.57 | 3.48 |
| | IX | (61) | 0.65 | 3.83 |

| WR | AC | *N* | SD | Means |
|---|---|---|---|---|
| | I | (18) | 0.66 | 6.57 |
| | II | (22) | 0.96 | 8.15 |
| | III | (26) | 0.87 | 8.52 |
| | IV | (21) | 1.16 | 8.91 |
| | V | (41) | 1.19 | 8.95 |
| | VI | (15) | 1.75 | 10.66 |
| | VII | (28) | 1.96 | 10.69 |
| | VIII | (33) | 1.61 | 11.36 |
| | IX | (61) | 2.63 | 12.61 |

| MTR | AC | *N* | SD | Means |
|---|---|---|---|---|
| | I | (18) | 0.48 | 4.52 |
| | II | (22) | 0.79 | 6.63 |
| | III | (26) | 0.57 | 6.71 |
| | IV | (21) | 0.65 | 7.36 |
| | V | (41) | 0.68 | 8.21 |
| | VII | (15) | 0.79 | 8.62 |
| | VI | (28) | 0.69 | 8.90 |
| | VIII | (33) | 0.61 | 9.22 |
| | IX | (61) | 0.74 | 9.36 |

| NA | AC | *N* | SD | Means |
|---|---|---|---|---|
| | I | (18) | 0.96 | 4.82 |
| | II | (22) | 1.00 | 6.50 |
| | III | (26) | 0.86 | 6.67 |
| | IV | (21) | 1.22 | 7.16 |
| | V | (41) | 1.21 | 8.31 |
| | VII | (15) | 1.53 | 8.56 |
| | VI | (28) | 1.27 | 8.66 |
| | VIII | (33) | 1.43 | 9.23 |
| | IX | (61) | 1.82 | 10.41 |

| AFL | AC | *N* | SD | Means |
|---|---|---|---|---|
| | I | (18) | 0.60 | 4.81 |
| | III | (26) | 0.95 | 6.26 |
| | II | (22) | 1.13 | 6.27 |
| | IV | (21) | 1.42 | 6.55 |
| | VII | (15) | 1.30 | 7.47 |
| | V | (41) | 1.41 | 7.85 |
| | VI | (28) | 1.55 | 7.89 |
| | VIII | (33) | 1.67 | 9.00 |
| | IX | (61) | 2.55 | 9.44 |

**Table 5.3.** Standard descriptive statistics of 22 [craniometric] measurements of male and female giant mole-rat, *Fukomys mechowii* from Kakalo and Mushishima farm blocks in Chingola, Copperbelt Province of Zambia. $\bar{x}$ = arithmetic mean; *SD* = standard deviation; *2SE* = two standard errors; *n* = sample size. Measurements are defined and illustrated in Fig. 2.2.

| Sex | Tooth wear class (*n*) | | Measurement | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | GLS | ITC | BCW | ZMB | ZYW | IOB | WR | NA | UTR | PAC | NPP |
| ♂ | I (7) | $\bar{x}$ | 42.27 | 29.69 | 16.33 | 17.69 | 20.57 | 9.25 | 6.59 | 4.89 | 4.70 | 3.13 | 27.58 |
| | | *SD* | 6.42 | 3.19 | 1.10 | 1.63 | 1.81 | 0.34 | 0.76 | 1.10 | 0.82 | 0.27 | 3.12 |
| | | *2SE* | 1.85 | 1.20 | 0.42 | 0.61 | 0.68 | 0.13 | 0.29 | 0.40 | 0.31 | 0.10 | 1.18 |
| | II (5) | $\bar{x}$ | 47.96 | 35.80 | 16.74 | 19..97 | 26.11 | 9.90 | 8.06 | 6.41 | 6.35 | 3.36 | 33.60 |
| | | *SD* | 5.54 | 3.73 | 0.66 | 1.25 | 2.66 | 0.61 | 0.81 | 0.87 | 0.15 | 0.28 | 3.13 |
| | | *2SE* | 1.75 | 1.67 | 0.29 | 0.56 | 1.19 | 0.27 | 0.36 | 0.39 | 0.07 | 0.12 | 1.40 |
| | III (7) | $\bar{x}$ | 48.67 | 40.54 | 17.42 | 20.87 | 27.35 | 9.80 | 8.44 | 6.59 | 6.71 | 3.56 | 34.73 |
| | | *SD* | 4.88 | 5.53 | 0.90 | 1.41 | 2.11 | 0.31 | 0.41 | 0.51 | 0.36 | 0.29 | 2.67 |
| | | *2SE* | 1.30 | 2.09 | 0.34 | 0.53 | 0.80 | 0.12 | 0.15 | 0.19 | 0.14 | 0.11 | 1.00 |
| | IV (12) | $\bar{x}$ | 51.58 | 40.33 | 17.23 | 20.78 | 28.71 | 9.93 | 9.17 | 7.41 | 7.37 | 3.53 | 37.77 |
| | | *SD* | 6.04 | 6.52 | 1.32 | 2.40 | 5.20 | 0.51 | 1.45 | 1.36 | 0.57 | 0.73 | 4.11 |
| | | *2SE* | 2.47 | 1.88 | 0.38 | 0.69 | 1.50 | 0.15 | 0.42 | 0.39 | 0.16 | 0.21 | 1.19 |
| | V (10) | $\bar{x}$ | 50.41 | 46.96 | 18.03 | 22.64 | 35.23 | 10.69 | 10.62 | 8.94 | 8.37 | 4.06 | 43.85 |
| | | *SD* | 4.98 | 4.47 | 1.03 | 2.12 | 3.81 | 0.59 | 1.37 | 1.26 | 0.48 | 0.59 | 4.14 |
| | | *2SE* | 1.17 | 1.41 | 0.33 | 0.67 | 1.20 | 0.19 | 0.43 | 0.40 | 0.15 | 0.19 | 1.31 |
| | VI (14) | $\bar{x}$ | 56.36 | 46.73 | 19.09 | 23.58 | 35.20 | 11.08 | 11.37 | 9.07 | 9.39 | 4.16 | 45.05 |
| | | *SD* | 4.08 | 5.40 | 1.50 | 2.80 | 5.03 | 0.99 | 2.03 | 1.36 | 0.30 | 0.48 | 5.57 |
| | | *2SE* | 0.69 | 1.44 | 0.40 | 0.75 | 1.34 | 0.27 | 0.54 | 0.36 | 0.08 | 0.13 | 1.49 |
| | VII (6) | $\bar{x}$ | 31.60 | 49.31 | 19.12 | 25.54 | 37.74 | 11.03 | 11.84 | 9.66 | 9.29 | 4.37 | 46.19 |
| | | *SD* | 3.17 | 5.94 | 1.16 | 2.44 | 5.42 | 0.44 | 2.07 | 1.81 | 0.51 | 0.73 | 4.69 |
| | | *2SE* | 0.75 | 2.43 | 0.47 | 0.99 | 2.21 | 0.18 | 0.85 | 0.74 | 0.21 | 0.30 | 1.92 |
| | VIII(18 | $\bar{x}$ | 36.71 | 48.25 | 18.64 | 24.18 | 37.05 | 10.69 | 11.84 | 9.44 | 9.73 | 4.66 | 45.57 |
| | | *SD* | 2.99 | 4.86 | 1.25 | 2.31 | 4.80 | 0.82 | 1.68 | 1.50 | 0.15 | 1.34 | 4.29 |
| | | *2SE* | 0.64 | 1.14 | 0.29 | 0.54 | 1.13 | 0.19 | 0.40 | 0.35 | 0.03 | 0.32 | 1.01 |
| | IX (35) | $\bar{x}$ | 39.35 | 54.19 | 19.83 | 26.88 | 42.32 | 11.63 | 13.58 | 11.26 | 9.87 | 4.61 | 50.97 |
| | | *SD* | 3.77 | 4.40 | 1.05 | 1.86 | 4.52 | 1.20 | 1.72 | 1.48 | 0.52 | 0.56 | 4.36 |
| | | *2SE* | 0.74 | 0.74 | 0.18 | 0.31 | 0.76 | 0.20 | 0.29 | 0.25 | 0.08 | 0.09 | 0.74 |
| | | | | | | | | | | | | | |

| Sex | Tooth wear class (*n*) | | Measurement | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | GHS | MLT | MDL | MTR | AFL | MAF | AFA | MRH | UJI | LJI | WI |
| ♂ | I (7) | $\bar{x}$ | 13.32 | 31.38 | 20.07 | 4.63 | 4.69 | 6.94 | 9.18 | 10.50 | 5.16 | 3.52 | 1.29 |
| | | *SD* | 1.18 | 3.30 | 1.91 | 0.65 | 0.77 | 1.01 | 0.59 | 0.87 | 0.57 | 0.35 | 0.33 |
| | | *2SE* | 0.45 | 1.25 | 0.72 | 0.25 | 0.29 | 0.38 | 0.22 | 0.33 | 0.21 | 0.13 | 0.12 |
| | II (5) | $\bar{x}$ | 15.51 | 33.11 | 28.32 | 6.56 | 6.48 | 10.21 | 12.60 | 15.11 | 8.13 | 4.81 | 2.16 |
| | | *SD* | 0.92 | 2.86 | 1.62 | 0.49 | 0.21 | 1.01 | 1.23 | 1.57 | 1.48 | 0.28 | 0.34 |
| | | *2SE* | 0.41 | 1.28 | 0.72 | 0.22 | 0.09 | 0.45 | 0.55 | 0.70 | 0.66 | 0.13 | 0.15 |
| | III (7) | $\bar{x}$ | 16.81 | 35.36 | 29.98 | 6.58 | 6.51 | 12.46 | 13.22 | 15.56 | 8.32 | 4.71 | 2.46 |
| | | *SD* | 1.80 | 2.39 | 3.70 | 0.24 | 0.62 | 5.41 | 2.34 | 2.46 | 0.97 | 0.78 | 0.27 |
| | | *2SE* | 0.68 | 0.90 | 1.40 | 0.09 | 0.24 | 2.05 | 0.88 | 0.93 | 0.37 | 0.30 | 0.10 |
| | IV (12) | $\bar{x}$ | 16.80 | 36.30 | 30.19 | 7.31 | 6.85 | 10.15 | 12.72 | 15.95 | 7.76 | 4.71 | 2.74 |
| | | *SD* | 1.78 | 2.94 | 3.03 | 0.59 | 1.71 | 2.08 | 3.14 | 3.28 | 1.13 | 0.50 | 0.68 |
| | | *2SE* | 0.51 | 0.84 | 0.87 | 0.17 | 0.49 | 0.60 | 0.90 | 0.94 | 0.32 | 0.14 | 0.19 |
| | V (10) | $\bar{x}$ | 18.87 | 41.83 | 38.04 | 8.26 | 8.76 | 12.57 | 14.73 | 19.87 | 9.02 | 6.15 | 3.45 |
| | | *SD* | 1.42 | 2.06 | 5.17 | 0.42 | 1.99 | 2.36 | 1.83 | 2.69 | 1.07 | 0.68 | 0.73 |
| | | *2SE* | 0.45 | 0.65 | 1.64 | 0.13 | 0.63 | 0.75 | 0.58 | 0.85 | 0.34 | 0.21 | 0.23 |
| | VI (14) | $\bar{x}$ | 19.21 | 45.08 | 36.92 | 9.45 | 8.17 | 11.85 | 15.20 | 18.17 | 10.6 | 5.44 | 3.38 |
| | | *SD* | 1.99 | 4.49 | 5.04 | 0.29 | 1.17 | 1.68 | 2.07 | 3.82 | 1.8 | 0.78 | 0.59 |
| | | *2SE* | 0.53 | 1.20 | 1.35 | 0.08 | 0.31 | 0.45 | 0.55 | 1.02 | 0.5 | 0.21 | 0.16 |
| | VII (6) | $\bar{x}$ | 20.03 | 50.14 | 38.36 | 9.36 | 8.48 | 12.85 | 15.54 | 21.07 | 9.8 | 6.02 | 3.63 |
| | | *SD* | 2.28 | 5.18 | 4.23 | 0.52 | 1.59 | 1.73 | 2.33 | 2.90 | 2.0 | 1.08 | 0.57 |
| | | *2SE* | 0.93 | 2.12 | 1.73 | 0.21 | 0.65 | 0.71 | 0.95 | 1.18 | 0.8 | 0.44 | 0.23 |
| | VIII(18 | $\bar{x}$ | 19.28 | 49.42 | 42.25 | 9.66 | 8.97 | 13.33 | 16.41 | 21.05 | 10.8 | 6.58 | 3.60 |
| | | *SD* | 1.96 | 5.06 | 5.99 | 0.19 | 1.89 | 3.34 | 2.52 | 3.86 | 2.6 | 0.84 | 0.60 |
| | | *2SE* | 0.46 | 1.19 | 1.41 | 0.04 | 0.45 | 0.79 | 0.60 | 0.91 | 0.6 | 0.20 | 0.14 |
| | IX (35) | $\bar{x}$ | 21.70 | 55.80 | 44.07 | 9.77 | 9.84 | 14.37 | 18.52 | 24.70 | 12.0 | 6.79 | 4.13 |
| | | *SD* | 2.80 | 4.96 | 4.75 | 0.54 | 1.57 | 1.42 | 2.58 | 2.82 | 2.1 | 1.14 | 0.53 |
| | | *2SE* | 0.47 | 0.84 | 0.80 | 0.09 | 0.27 | 0.24 | 0.44 | 0.48 | 0.3 | 0.19 | 0.09 |

| Sex | Tooth wear class (*n* | | Measurement | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | GLS | ITC | BCW | ZMB | ZYW | IOB | WR | NA | UTR | PAC | NPP |
| ♀ | I (11) | $\bar{x}$ | 40.53 | 30.13 | 14.93 | 17.40 | 27.71 | 9.39 | 6.55 | 4.78 | 4.49 | 2.99 | 28.35 |
| | | *SD* | 3.22 | 2.69 | 1.40 | 1.87 | 3.48 | 0.88 | 0.62 | 0.92 | 0.68 | 0.34 | 3.02 |
| | | *2SE* | 1.07 | 0.81 | 0.42 | 0.57 | 1.05 | 0.26 | 0.19 | 0.27 | 0.20 | 0.10 | 0.91 |
| | II (17) | $\bar{x}$ | 43.98 | 34.66 | 16.20 | 18.73 | 26.33 | 9.78 | 8.17 | 6.53 | 6.30 | 3.54 | 33.40 |
| | | *SD* | 6.96 | 3.13 | 0.90 | 1.28 | 3.60 | 0.83 | 1.02 | 1.06 | 0.44 | 0.49 | 2.06 |
| | | *2SE* | 1.25 | 0.76 | 0.22 | 0.31 | 0.88 | 0.20 | 0.25 | 0.26 | 0.10 | 0.12 | 0.50 |
| | III (19) | $\bar{x}$ | 45.96 | 36.24 | 16.18 | 19.77 | 26.15 | 9.73 | 8.56 | 6.71 | 6.84 | 3.46 | 35.03 |
| | | *SD* | 3.61 | 2.40 | 2.05 | 0.91 | 3.16 | 0.46 | 0.99 | 0.96 | 0.69 | 0.38 | 2.16 |
| | | *2SE* | 0.97 | 0.55 | 0.47 | 0.21 | 0.72 | 0.11 | 0.23 | 0.22 | 0.16 | 0.08 | 0.50 |
| | IV (9) | $\bar{x}$ | 43.93 | 38.54 | 17.11 | 20.82 | 27.61 | 9.74 | 8.58 | 6.83 | 7.53 | 3.65 | 36.84 |
| | | *SD* | 2.17 | 2.89 | 0.83 | 1.44 | 2.57 | 0.43 | 0..52 | 0.98 | 0.72 | 0.57 | 1.91 |
| | | *2SE* | 0.72 | 0.96 | 0.28 | 0.48 | 0.85 | 0.14 | 0.17 | 0.32 | 0.24 | 0.19 | 0.64 |
| | V (31) | $\bar{x}$ | 48.63 | 42.78 | 18.15 | 22.33 | 31.55 | 10.21 | 9.73 | 8.11 | 8.28 | 3.82 | 40.99 |
| | | *SD* | 4.99 | 3.70 | 1.29 | 2.09 | 3.55 | 1.06 | 1.06 | 1.14 | 0.79 | 0.45 | 5.02 |
| | | *2SE* | 1.29 | 0.66 | 0.23 | 0.38 | 0.64 | 0.19 | 0.19 | 0.21 | 0.14 | 0.08 | 0.90 |
| | VI (14) | $\bar{x}$ | 49.41 | 43.68 | 17.51 | 21.93 | 32.15 | 10.09 | 9.94 | 8.25 | 8.27 | 3.76 | 41.27 |
| | | *SD* | 4.39 | 4.43 | 0.92 | 1.40 | 4.06 | 0.67 | 1.05 | 1.07 | 0.38 | 0.46 | 4.04 |
| | | *2SE* | 0.86 | 1.16 | 0.24 | 0.37 | 1.08 | 0.18 | 0.28 | 0.29 | 0.10 | 0.12 | 1.08 |
| | VII (9) | $\bar{x}$ | 31.09 | 41.90 | 17.65 | 22.04 | 30.93 | 10.10 | 9.31 | 7.83 | 8.04 | 3.49 | 38.84 |
| | | *SD.* | 3.37 | 2.78 | 0.91 | 1.65 | 2.33 | 0.60 | 0.61 | 0.74 | 0.45 | 0.40 | 2.76 |
| | | *2SE* | 1.27 | 0.93 | 0.30 | 0.45 | 0.78 | 0.20 | 0.21 | 0.25 | 0.15 | 0.13 | 0.92 |
| | VIII(15 | $\bar{x}$ | 38.09 | 46.88 | 18.40 | 23.68 | 34.97 | 10.47 | 10.78 | 0.98 | 8.65 | 4.00 | 44.38 |
| | | *SD* | 2.88 | 4.71 | 0.93 | 2.27 | 4.34 | 0.68 | 1.36 | 1.35 | 0.49 | 0.47 | 4.50 |
| | | *2SE* | 1.89 | 1.22 | 0.24 | 0.59 | 1.12 | 0.18 | 0.35 | 0.35 | 0.13 | 0.12 | 1.16 |
| | IX (26) | $\bar{x}$ | 42.11 | 47.66 | 18.76 | 24.11 | 36.07 | 10.76 | 11.31 | 9.26 | 8.88 | 4.07 | 45.03 |
| | | *SD* | 5.94 | 4.25 | 1.02 | 1.76 | 4.45 | 0.96 | 2.19 | 1.60 | 0.55 | 0.42 | 4.45 |
| | | *2SE* | 2.24 | 0.83 | 0.20 | 0.34 | 0.87 | 0.19 | 0.43 | 0.31 | 0.11 | 0.08 | 0.87 |

| Sex | Tooth wear class (*n*) | Measurement | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | GHS | MLT | MDL | MTR | AFL | MAF | AFA | MRH | UJI | LJI | WI |
| ♀ | I (11) | $\bar{x}$ | 13.62 | 32.03 | 22.53 | 4.45 | 4.88 | 7.46 | 10.26 | 11.19 | 4.10 | 6.14 | 1.65 |
| | | *SD* | 1.00 | 2.20 | 3.23 | 0.36 | 0.48 | 1.13 | 2.20 | 1.44 | 0.70 | 0.84 | 0.42 |
| | | *2SE* | 0.30 | 0.65 | 0.97 | 0.10 | 0.15 | 0.34 | 0.66 | 0.43 | 0.21 | 0.25 | 0.13 |
| | II (17) | $\bar{x}$ | 15.61 | 33.94 | 28.04 | 6.66 | 6.21 | 9.80 | 11.69 | 14.75 | 4.61 | 8.31 | 2.33 |
| | | *SD* | 1.37 | 2.17 | 4.75 | 0.87 | 1.29 | 1.68 | 2.20 | 2.91 | 0.47 | 1.42 | 0.47 |
| | | *2SE* | 0.33 | 0.53 | 1.15 | 0.21 | 0.31 | 0.41 | 0.53 | 0.71 | 0.11 | 0.35 | 0.12 |
| | III (19) | $\bar{x}$ | 15.82 | 34.27 | 28.30 | 6.76 | 6.16 | 9.62 | 12.29 | 14.17 | 4.63 | 8.02 | 2.58 |
| | | *SD* | 0.99 | 2.18 | 4.57 | 0.65 | 1.05 | 1.32 | 2.63 | 2.99 | 0.52 | 1.13 | 0.58 |
| | | *2SE* | 0.23 | 0.50 | 1.04 | 0.15 | 0.24 | 0.31 | 0.60 | 0.69 | 0.12 | 0.26 | 0.13 |
| | IV (9) | $\bar{x}$ | 16.37 | 35.44 | 28.16 | 7.44 | 6.16 | 10.26 | 12.29 | 15.78 | 5.33 | 8.16 | 2.45 |
| | | *SD* | 0.69 | 2.56 | 3.46 | 0.75 | 0.86 | 1.53 | 1.13 | 2.25 | 0.57 | 1.47 | 0.25 |
| | | *2SE* | 0.23 | 0.85 | 1.15 | 0.25 | 0.29 | 0.51 | 0.38 | 0.75 | 0.19 | 0.49 | 0.08 |
| | V (31) | $\bar{x}$ | 17.66 | 39.86 | 34.12 | 8.19 | 7.55 | 11.30 | 13.89 | 17.71 | 5.39 | 8.88 | 2.91 |
| | | *SD* | 1.46 | 3.35 | 4.51 | 0.76 | 1.04 | 1.30 | 1.38 | 2.82 | 0.75 | 1.58 | 0.51 |
| | | *2SE* | 0.26 | 0.60 | 0.80 | 0.14 | 0.19 | 0.23 | 0.24 | 0.51 | 0.13 | 0.28 | 0.09 |
| | VI (14) | $\bar{x}$ | 17.56 | 40.99 | 35.01 | 8.36 | 7.60 | 11.45 | 13.82 | 18.02 | 5.40 | 9.40 | 3.18 |
| | | *SD* | 1.08 | 3.35 | 4.71 | 0.51 | 1.86 | 1.76 | 2.31 | 2.54 | 0.71 | 1.45 | 0.45 |
| | | *2SE* | 0.29 | 0.89 | 1.26 | 0.13 | 0.50 | 0.47 | 0.62 | 0.68 | 0.19 | 0.38 | 0.12 |
| | VII (9) | $\bar{x}$ | 17.31 | 41.79 | 32.94 | 8.13 | 6.80 | 10.70 | 13.24 | 17.77 | 5.26 | 9.33 | 2.95 |
| | | *SD* | 0.83 | 2.80 | 3.38 | 0.49 | 0.70 | 1.15 | 0.96 | 1.78 | 0.50 | 2.05 | 0.36 |
| | | *2SE* | 0.28 | 0.94 | 1.13 | 0.16 | 0.23 | 0.38 | 0.32 | 0.59 | 0.17 | 0.68 | 0.12 |
| | VIII(15 | $\bar{x}$ | 18.81 | 45.80 | 38.50 | 8.69 | 9.04 | 12.70 | 14.95 | 20.57 | 6.20 | 10.86 | 3.35 |
| | | *SD* | 1.79 | 4.48 | 4.66 | 0.51 | 1.42 | 1.61 | 2.31 | 2.52 | 0.91 | 2.10 | 0.52 |
| | | *2SE* | 0.46 | 1.15 | 1.20 | 0.13 | 0.37 | 0.41 | 0.60 | 0.65 | 0.23 | 0.54 | 0.13 |
| | IX (26) | $\bar{x}$ | 19.55 | 48.23 | 37.50 | 8.81 | 8.91 | 12.82 | 15.60 | 21.20 | 6.20 | 10.79 | 3.44 |
| | | *SD* | 1.86 | 4.49 | 4.75 | 0.60 | 2.89 | 1.70 | 1.85 | 2.75 | 0.77 | 1.65 | 0.58 |
| | | *2SE* | 0.36 | 0.88 | 0.93 | 0.12 | 0.57 | 0.33 | 0.36 | 0.54 | 0.15 | 0.32 | 0.11 |

The first principal components axis from the PCA which represents size-related variation explains 77.57% of the total variance and had high negative loadings in all the 22 measurements used in the analysis (Table 5.4). Only two measurements (UTR and MTR)

had relatively high positive loadings on the second principle components axis which represents shape-related variation and explains 4.05% of the total variance (Table 5.4).

**Table 5.4.** Relative loadings of measurements from the first two principal components of a principal components analysis of the giant mole-rat, *Fukomys mechowii* of tooth-wear classes 1–9 from Kakalo and Mushishima farm blocks in Chingola, Copperbelt Province of Zambia. Measurements are defined and illustrated in Fig. 2.2.

| | **Principal components axes** | |
|---|---|---|
| **Measurement** | I | II |
| GLS | -0.95 | -0.00 |
| ITC | -0.97 | -0.02 |
| BCW | -0.83 | -0.02 |
| ZMB | -0.93 | -0.04 |
| ZYW | -0.97 | -0.10 |
| IOB | -0.77 | -0.32 |
| WR | -0.96 | -0.15 |
| NA | -0.96 | -0.10 |
| UTR | -0.83 | 0.46 |
| PAC | -0.72 | -0.22 |
| NPP | -0.97 | -0.03 |
| GHS | -0.95 | -0.13 |
| MLT | -0.95 | -0.00 |
| MDL | -0.86 | 0.12 |
| MTR | -0.83 | 0.46 |
| AFL | -0.85 | -0.22 |
| MAF | -0.83 | -0.06 |
| AFA | -0.89 | -0.14 |
| MRH | -0.89 | 0.02 |
| UJI | -0.74 | 0.33 |
| LJI | -0.75 | 0.21 |
| WI | -0.91 | 0.02 |
| % variance explained | Axis 1 = 77.57% | Axis 2 = 4.05% |

A plot of the first two principal components axis (Fig. 5.1), which for clarity does not show individuals, reveal that although individuals of tooth-wear classes 2 and 3 overlap extensively, there is a clear separation between individuals of tooth-wear classes 1–3 and those of extensively overlapping tooth-wear classes 5–9 on the first principal components axis. Individuals of tooth-wear class 4 lie intermediate between individuals of tooth-wear classes 1–3 and those of tooth-wear classes 5–9 (Fig. 5.1).

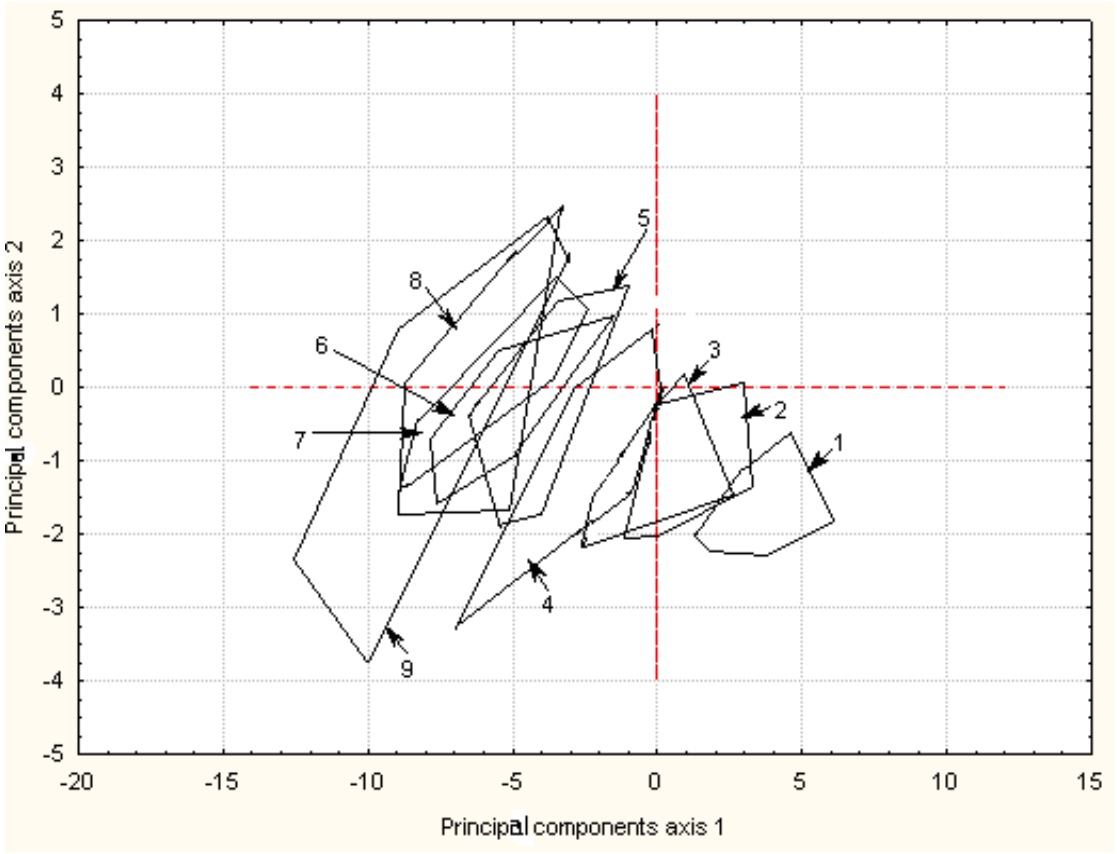


**Figure 5.1.** A plot of the first two principal components from a principal components Analysis of the giant the mole-rat, *Fukomys mechowii* of tooth-wear classes 1–9 from Kakalo and Mushishima farm blocks, Chingola, Copperbelt Province of Zambia. Minimum convex polygons enclose individuals of each tooth-wear class, which together with their associated sexes have been omitted.

A distant phenogram from the UPGMA cluster analysis (Fig. 5.2) showed three biologically meaningful clusters of individuals in multivariate space. The first cluster (1) mainly comprised a combination of male and female individuals of the younger age classes 1–4 with two females of age class 6. This strongly suggests the absence of sexual dimorphism within these younger age classes. While the second cluster (2), predominantly comprised individuals of the older age classes 5–9 with some females of age class 3 and males of age class 4, and some minor sub-clusters of individuals of the same sex. Apart from three females of age class 6, the third cluster (3) mainly comprised males of the older age classes 5–9. These males, which are larger than females, strongly suggest the presence of sexual dimorphism in the older age classes of the giant mole-rat.


**Figure 5.2.** A distance phenogram from an unweighted pair-group method using arithmetic averages (UPGMA) cluster analysis male and female giant mole-rat, *Fukomys mechowii* of age tooth-wear classes 1–9 from Kakalo and Mushishima farm blocks, Chingola, Zambia, showing 3

distinct clusters of individuals comprising the following sample sizes, tooth-wear classes and sexes (M = male; F = female), respectively: 1) Cluster 1 – 4:1F, 2:1M, 8:2F, 6:2M, 6:3F, 4:3M, 8:4F, 5:4M and 2:6F; 2) Cluster 2 – 13:5F, 6:5M, 7:6F, 3:6M, 5:7F, 3:7M, 11:8F, 7:8M, 18:9F, 8:9M, 2:3F and 3:4M; and 3) Cluster 3 – 2:5M, 3:6F, 8:8M, 5.7M, 9:9M.

A confirmation on the absence of sexual dimorphism in the younger age classes and its presence in the older age classes was assessed by two independent ANOVAs and %*SSQ* of individuals of age classes 1–4 and age classes 5–9. All the 22 measurements differed statistically significantly for age (20 measurements at $P < 0.001$, one at $P < 0.01$, and one at $P < 0.05$) (Table 5.5). None of the measurements differed significantly for sex while one measurement only (UJI) differed significantly for the interaction between sexual dimorphism and age at $P < 0.05$ (Table 5.5). The importance of age variation rather than sexual dimorphism in the younger age classes 1–4 was also shown by the higher %*SSQ* values for age (%*SSQ*: $\bar{x}$ = 37.38; range = 9.75–77.58%) than for sex (%*SSQ*: $\bar{x}$ = 0.80; range = 0.00–2.99%) or the interaction between age and sex (%*SSQ*: $\bar{x}$ = 2.07; range = 0.30–6.26%) (Table 5.5). The analysis of %*SSQ* of age classes 1-4 also showed higher mean %*SSQ* values for the error component than for age (%*SSQ*: $\bar{x}$ = 59.75), sex or the interaction between age and sex (Table 5.5) suggesting that other factors may be responsible for non-geographic variation in the giant mole-rat rather sexual dimorphism and age variation alone.

**Table 5.5.** *F*-values and percent *SSQ* of each source of variation derived from a two-way analysis of variance (ANOVA) of four age classes (1–4) based on the degree of tooth eruption and wear in male and female giant mole-rats, *Fukomys mechowii*, from Kakalo and Mushishima farm blocks, Chingola, Copperbelt Province of Zambia. Statistical significance: * = $P < 0.05$; ** = $P<0.01$; *** = $P < 0.001$. Measurements are defined and illustrated in Fig. 2.2.

| Measurement | | *F*-Value | | | | *%SSQ* | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Age A) | Sex (S) | A x S | | Age (A) | Sex (S) | A x S | Error |
| GLS | | 24.23*** | 3.22 | 1.13 | | 45.92 | 2.04 | 2.13 | 49.91 |
| ITC | | 22.65*** | 3.55 | 1.25 | | 44.05 | 2.30 | 2.43 | 51.22 |
| BCW | | 7.73*** | 3.22 | 0.62 | | 21.61 | 2.99 | 1.74 | 73.66 |
| ZMB | | 15.66*** | 3.14 | 0.75 | | 35.76 | 2.40 | 1.70 | 60.14 |
| ZYW | | 12.10*** | 0.00 | 0.94 | | 30.89 | 0.00 | 2.37 | 66.74 |
| IOB | | 2.88* | 0.16 | 0.24 | | 9.75 | 0.18 | 0.82 | 89.25 |
| WR | | 20.62*** | 0.20 | 0.62 | | 43.29 | 0.15 | 1.30 | 55.26 |
| NA | | 16.96*** | 0.24 | 0.49 | | 38.66 | 0.18 | 1.12 | 60.04 |
| UTR | | 74.35*** | 0.00 | 0.36 | | 73.58 | 0.00 | 0.36 | 26.06 |
| PAC | | 4.41** | 0.02 | 0.48 | | 14.10 | 0.02 | 1.55 | 84.33 |
| NPP | | 37.83*** | 0.00 | 0.33 | | 58.65 | 0.00 | 0.51 | 40.84 |
| GHS | | 22.32*** | 0.73 | 0.98 | | 44.76 | 0.49 | 1.96 | 52.79 |
| MLT | | 9.61*** | 0.04 | 0.73 | | 26.19 | 0.04 | 1.99 | 71.78 |
| MDL | | 17.52*** | 0.18 | 1.30 | | 38.75 | 0.13 | 2.88 | 58.24 |
| MTR | | 63.51*** | 0.14 | 0.27 | | 70.44 | 0.05 | 0.30 | 29.21 |
| AFL | | 9.81*** | 1.17 | 0.53 | | 26.46 | 1.06 | 1.42 | 71.06 |
| MAF | | 11.60*** | 1.80 | 2.57 | | 28.21 | 1.46 | 6.26 | 64.07 |
| AFA | | 6.69*** | 0.30 | 0.75 | | 19.75 | 0.30 | 2.23 | 77.72 |
| MRH | | 13.34*** | 0.26 | 0.52 | | 33.12 | 0.22 | 1.28 | 65.38 |
| UJI | | 16.39*** | 3.24 | 2.79* | | 35.20 | 2.32 | 5.94 | 56.54 |
| LJI | | 19.12*** | 1.32 | 0.94 | | 40.82 | 0.94 | 2.01 | 56.23 |
| WI | | 20.62*** | 0.61 | 1.58 | | 42.30 | 0.42 | 3.25 | 54.03 |
| Mean | | | | | | 37.38 | 0.80 | 2.07 | 59.75 |

The ANOVA of the older age classes 5–9 (Table 5.6) showed 21 of the 22 measurements to be statistically significant for age (20 at $P < 0.001$ and one at $P < 0.05$), 20 were statistically significant for sexual dimorphism (all at $P < 0.001$) where males are larger than females, and five were statistically significant for the interaction between sex and age (two at $P <$

0.01 and three at $P < 0.05$). Of particular significance is that the ANOVA of the older age classes 5–9 generally had higher *F*-values for sex than for age, and is also evident in the higher %*SSQ* values for sex (*SSQ*: $\bar{x}$ = 14.99%; range = 1.67–22.19%) than that of either the age component (*SSQ*: $\bar{x}$ = 9.97%; range = 2.17–27.46%) or the interaction between age and sex (*SSQ*: $\bar{x}$ = 2.64%; range = 1.44–5.33%) (Table 5.6). Similar to the analysis of the younger age classes 1–4, the analysis of %*SSQ* of the older age classes 5-9 also showed higher mean %*SSQ* values for the error component (%*SSQ*: $\bar{x}$ = 72.40%; range = 62.47–91.55%) than for age (*SSQ*: $\bar{x}$ = 9.97%; range = 2.17–27.46%), sex (*SSQ*: $\bar{x}$ = 2.64%; range = 1.44–5.33%) or the interaction between age and sex (*SSQ*: $\bar{x}$ = 2.64%; range = 1.44–5.33%) (Table 5.6), suggesting that factors other than sexual dimorphism and age variation may be responsible for non-geographic variation in the giant mole-rat.

**Table 5.6.** *F*-values and percent *SSQ* of each source of variation derived from a two-way analysis of variance (ANOVA) of four age classes (5–9) based on the degree of tooth eruption and wear in male and female giant mole-rats, *Fukomys mechowii*, from Kakalo and Mushishima farm blocks, Chingola, Copperbelt Province of Zambia. Statistical significance: * = $P < 0.05$; ** = $P<0.01$; *** = $P < 0.001$. Measurements are defined and illustrated in Fig. 2.2.

| Measurement | *F*-Value | | | *%SSQ* | | | |
|---|---|---|---|---|---|---|---|
| | Age A) | Sex (S) | A x S | Age (A) | Sex (S) | A x S | Error |
| GLS | 12.25*** | 28.38*** | 2.05 | 11.19 | 19.32 | 3.24 | 66.25 |
| ITC | 14.09*** | 34.97*** | 2.40* | 13.00 | 20.96 | 3.57 | 62.47 |
| BCW | 7.66*** | 18.94*** | 3.06** | 8.24 | 13.33 | 5.33 | 73.10 |
| ZMB | 14.65*** | 24.38*** | 3.28** | 9.23 | 22.19 | 4.97 | 63.61 |
| ZYW | 13.66*** | 35.13*** | 1.80 | 13.26 | 20.62 | 2.72 | 63.40 |
| IOB | 4.66*** | 18.33*** | 0.96 | 8.78 | 8.94 | 1.84 | 80.44 |
| WR | 12.99*** | 34.69*** | 1.55 | 13.30 | 19.92 | 2.38 | 64.40 |
| NA | 11.89*** | 25.32*** | 2.31* | 10.12 | 19.02 | 3.70 | 67.16 |
| UTR | 2.27** | 5.91 | 0.69 | 3.18 | 4.88 | 1.48 | 90.46 |
| PAC | 3.86*** | 24.95*** | 0.84 | 7.29 | 11.78 | 1.58 | 79.35 |
| NPP | 11.29*** | 29.40*** | 2.07 | 11.72 | 18.00 | 3.30 | 66.98 |
| GHS | 10.95*** | 23.64*** | 1.35 | 9.81 | 18.19 | 2.25 | 69.75 |
| MLT | 11.67*** | 22.91*** | 1.69 | 9.38 | 19.10 | 2.77 | 68.75 |
| MDL | 12.30*** | 15.88*** | 1.83 | 6.60 | 20.47 | 3.04 | 69.89 |
| MTR | 1.00 | 10.38*** | 0.29 | 2.17 | 5.65 | 0.63 | 91.55 |
| AFL | 5.64*** | 8.00*** | 0.85 | 3.95 | 11.51 | 1.68 | 82.86 |
| MAF | 8.26*** | 14.26*** | 0.90 | 6.52 | 15.09 | 1.64 | 76.75 |
| AFA | 13.13*** | 24.14*** | 1.59 | 9.62 | 20.92 | 2.53 | 66.93 |
| MRH | 18.17*** | 14.39*** | 2.39* | 27.46 | 5.44 | 3.62 | 63.48 |
| UJI | 10.52*** | 11.49*** | 0.81 | 5.11 | 18.72 | 1.44 | 74.73 |
| LJI | 10.02*** | 3.58 | 0.88 | 18.62 | 1.67 | 1.64 | 78.07 |
| WI | 8.10*** | 24.87*** | 1.52 | 10.75 | 14.01 | 2.62 | 72.62 |
| Mean | | | | 9.97 | 14.99 | 2.64 | 72.40 |

Evidence for the lack of sexual dimorphism in the younger age classes 1–4 and its presence in the older age classes 5–9 is apparent in independent PCAs of these age class groupings (Figs 5.3 and 5.4, respectively). This is also evident if these results are compared with the

PCA of the total sample indicated in Fig. 5.1 and also in standard descriptive statistics (Table 5.3) where there are differences in size between the sexes in the older age classes.

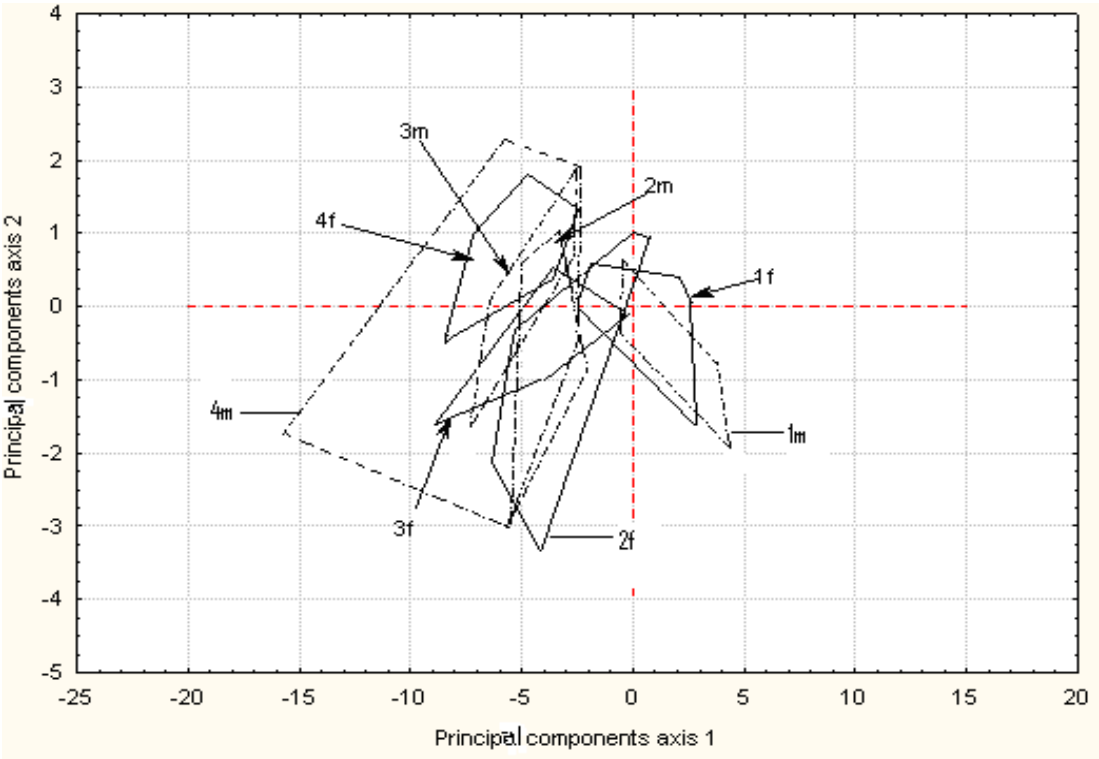


**Figure 5.3**. A plot of the first two principal components from a principal components analysis of giant mole-rats, *Fukomys mechowii* of younger tooth-wear classes 1–4 from Kakalo and Mushishima Farm Blocks, Chingola, Copperbelt Province of Zambia. Dashed and continuous minimum convex polygons enclose male (m) and female (f) individuals of each age class (1–4), respectively.

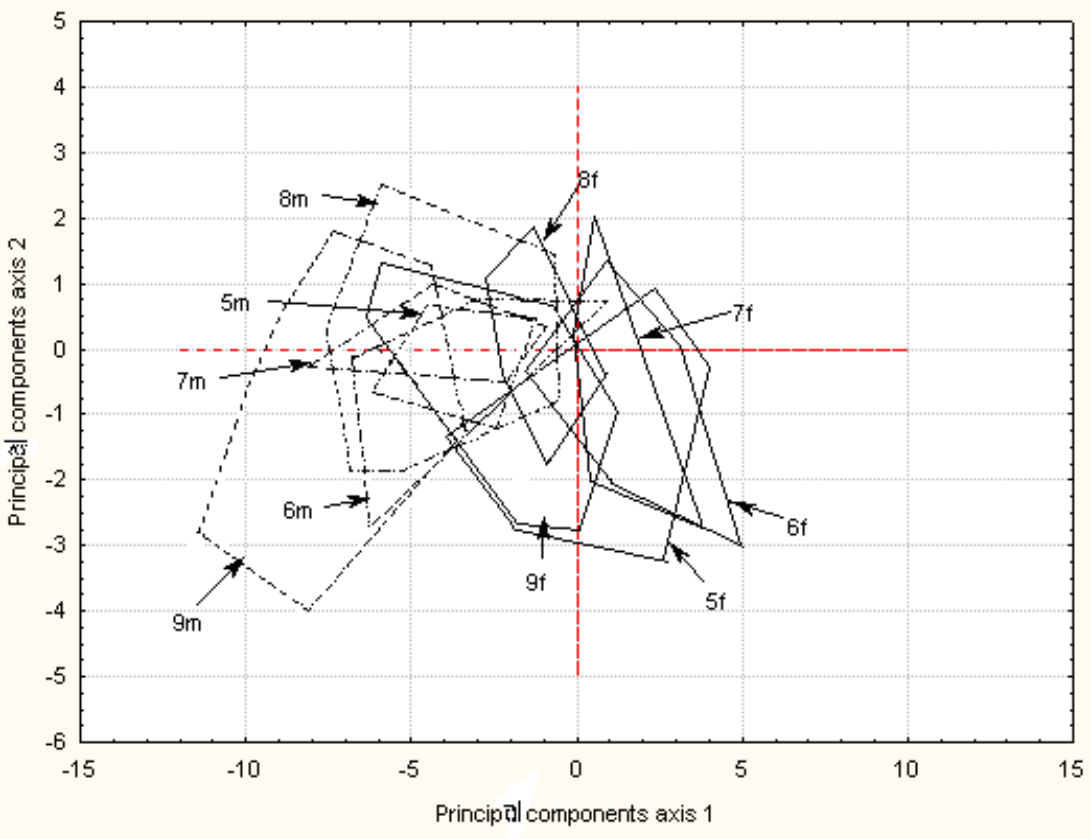


**Figure 5.4.** A plot of the first two principal components from a principal components analysis of the giant mole-rat, *Fukomys mechowii* of older tooth-wear classes 5–9 from Kakalo and Mushishima farm blocks, Chingola, Copperbelt Province of Zambia. Dashed and continuous minimum convex polygons enclose male (m) and female (f) individuals of each age class, respectively.

The absence of sexual dimorphism in younger age classes 1–4 and its presence in older age classes 5–9 of the giant mole-rat shown by the craniometric data in the present study was independently tested using data on body mass. There is a distinct increase in body mass as a function of relative age in both sexes (Fig. 5.5). Of particular relevance however, is that in broad similarity with craniometric data in the present study, individuals of the younger age

classes 1–5 showed no sexual dimorphism in body mass, while males and females of the older age classes 6–9 differed statistically significantly in body mass

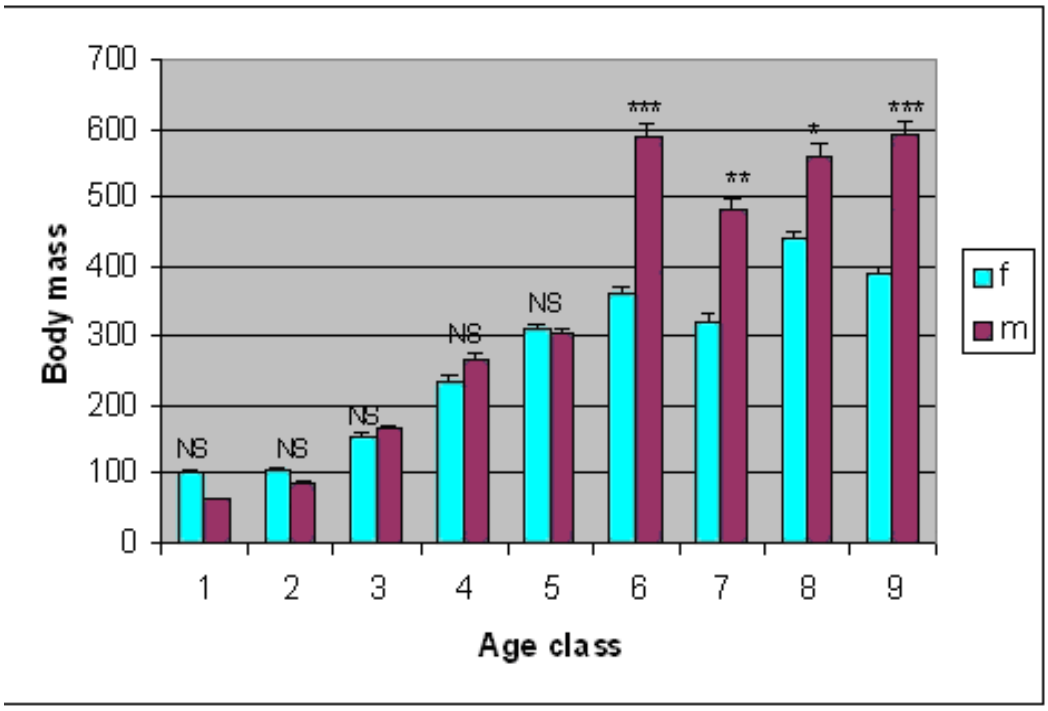


**Figure 5.5.** A plot of nine relative age classes (1–9) defined and illustrated in Fig. 2 and body mass (g) (± 2 standard errors of the mean (*SE*)) of male (m) and female (f) giant mole-rats, *Fukomys mechowii* from Kakalo and Mushishima farm blocks, Chingola, Copperbelt Province of Zambia. Statistical significance: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not statistically significant.

## Discussion

Both the univariate (ANOVA, *post hoc* SNK tests, and %*SSQ*) and multivariate (UPGMA cluster analysis and PCA) analyses undertaken in the present study showed the presence of statistically significant age variation, but a lack of sexual dimorphism in younger individuals of age classes 1–4 within the giant mole-rat. However, while these analyses also showed the

presence of statistically significant age variation in the older age classes 5–9, these age class groupings also revealed the presence of sexual dimorphism. Overall, these two age class groupings (i.e., age classes 1–4 vs 5–9) are also morphometrically distinct from each other in multivariate space, where individuals of age class 4 lie intermediate between those of age classes 1–3 and age classes 5–9. This suggests that intermediately placed individuals of age class 4 lie at a point on a hypothetical growth curve where it begins to stabilize.

The results in the present study are similar to those found in the Zambian mole-rat, *Fukomys anselli* where Begall & Burda (1998) demonstrated that the growth rate in both sexes was constant up until $18^{th}$–$20^{th}$ weeks, after which, males were observed to grow faster than females. Similarly, Yu & Lin (1999) showed that the body mass of the spiny rat, *N. coxingi* was sexually dimorphic in older individuals than in juveniles and sub-adults. In addition, Hart *et al.,* (2007) also reported that the body mass and length of the Cape dune mole-rat, *Bathyergus suillus* was also sexually dimorphic in older rather than young individuals.

In contrast, body mass and sexual dimorphism has been demonstrated in other small mammals regardless of age. These include the subterranean social [Damaraland mole-rat, *Fukomys damarensis*; (Bennett *et al*., 1990)], the [Talas, tuco-tuco *Ctenomys talarum* (Zenuto *et al*., 1999)] and the solitary [Namaqua dune mole-rat, *Bathyergus janetta* (Davies & Jarvies, 1986)]. Other studies on subterranean rodents in which sexual dimorphism occurs regardless of age include the bushy-tailed wood rat (*Neotoma cinerea*), the deer mouse (*Peromyscus maniculatus*), and the red-backed *Clethionomys gapperi* Schulte-Hostedde *et al.*, (2001). In contrast, a lack of sexual dimorphism has also been reported in other

subterranean rodents. These include the social common mole-rat [*Cryptomys hottentotus hottentotus* Bennett *et al*., (1990)], the highveld mole-rat, [*C. h. pretoriae* Janse van Rensburg *et al*., (2004)], the solitary Cape mole-rat [*Georychus capensis* Taylor *et al*., (1985)] and the silvery mole-rat [*Heliophobius argenteocinereus* Scharff *et al*., (1999)].

The results of the PCA in the present study showed that the difference between males and females in the social giant mole-rat was mainly due to overall size rather than shape. Similar results were found in the social [Damaraland mole-rat *F. damarensis* (Bennett & Faulkes, 2000)] as well as in solitary Cape dune mole-rat [*Bathyergus suillus* Hart *et al.,* (2007)]. However, these authors suggested that this may be due to an increase in male–male interactions during reproduction when males compete for reproductive opportunities. Hart *et al*., (2007) suggested that massive fat deposits around the necks of male Cape dune mole-rats may act as a cushion from incisor bites during aggressive interactions between males which have been observed under laboratory conditions and from inter-locked skulls in the wild. Giant mole-rats have also been observed fighting aggressively during male–male contacts (A.M. Sichilima, pers. obs).

Dispersing males of naked mole-rats (*Heterocephalus glaber*) are usually found larger than non-dispersing males of similar age (O'Riain *et al.,* (1996). The lone dispersing male of the giant mole-rat has similarly been observed to be usually large in body size (A. M. Sichilima, pers. obs). O'Riain *et al*., (1996) suggested that fat reserves associated with dispersing large body-sized male naked mole-rats may serve a nutritional function in order to avoid starvation during dispersal and the establishment of colonies.

It is interesting to note that in monogamous social mole-rats, two reproductive pairs have been reported to be responsible for procreation within a colony (Jarvis & Bennett, 1993; Gayland *et al.,* 1998), while in polygamous systems, two potential reproductive males are responsible for controlling the recruitment of unrelated pups into the colony Greenwood, (1980). Consequently, the monogamous system has either none or insignificant male–male competition for mates while in the polygamous system, there is male–male competition for mates among older males and possibly among younger unrelated maturing males. However, evidence of the presence of: (1) a single male and a single queen, (2) 2–5 adult males, and (3) two queens in some colonies (A. M. Sichilima, pers. obs.) suggests that the social *F. mechowii* may be both monogamous and polygamous.

Although other studies have argued that the estimation of age in mammals based on molar eruption and wear may not be suitable in some species such as bats *Myotis lucifugus* Hall *et al.,* (1957), the elk *Cervus elephus* Keiss (1969) and white tailed deer *Odocoileus virginianus* (Gilbert & Stolt, 1990), our study suggests that this may not be the case in *F. mechowii*. Our data suggest that in the absence of data on absolute ageing, the estimation of age based on molar eruption and wear may be appropriate for the giant mole-rat.

In addition, the use of body mass to estimate absolute age in mammals has also been considered to be inappropriate. However, similar to the results found in the solitary Cape dune mole-rat Hart *et al*., (2007), the results in our study on the social giant mole-rat also found a general trend of an increasing body mass with increasing age. More importantly,

similar to the cranial morphometric data, sexual dimorphism in body mass was absent in the younger age classes but present in the older age classes. It is interesting to note that body mass can be a good indicator of sexual dimorphism and relative age in both the social giant mole-rat (the present study) as well as in the solitary Cape dune mole-rat where Hart *et al.,* (2007) argued that there may not be an additional constraint on body mass (and body length) due to the social rank of an individual as has been reported in other social mole-rats Bennett *et al*., (1990).

Of additional relevance in the present study is that the results of our variance partitioning showed a very large error (= residual) component in the derived %*SSQ* values. This suggests that apart from the presence of sexual dimorphism and age variation in the giant mole-rat, there are other factors that may be influencing non-geographic variation within the species. These other potential influences of non-geographic variation in the giant mole-rat need to be investigated further in order to allow a better insight into the understanding of the population and social structures, and reproductive strategies in this little-studied mole-rat species.

### *Conclusion*

Sexual dimorphism and relative age variation in nine age classes estimated from the degree of molar tooth-row eruption and wear in the giant mole-rat, *Fukomys mechowii* from Zambia, Central Africa were assessed using traditional cranial morphometric data and body mass, and a range of univariate and multivariate analyses. All analyses revealed craniometric differences between individuals of age classes 1–3 and those of age classes 5–9, with those of age class 4 being intermediate between these two age class groupings, suggesting that age class 4 is at a point on a hypothetical growth curve where it begins to

stabilize. In contrast, the analyses revealed the absence of sexual dimorphism in the younger individuals of the giant mole-rat of age classes 1–4 and its presence in older age classes 5–9, and these results are supported by the analysis of the data on body mass. The sexual dimorphish in giant mole-rasts has therefore, demonstrated that there are different growth curves in males versus females, whereby males attain much larger size (skull size and body mass) than females after puberty. In conclusion, it is this factor that has been responsible for ANOVA significant interaction results in the older age classes 5-9.

# CHAPTER 6

## Do non-reproductive female giant mole-rats, *Fukomys mechowii* removed from the confines of their natal colony exhibit induced or spontaneous ovulation?

***Journal of Zoology, London (to submit).***

## Abstract

The giant mole-rat is a social subterranean rodent that exhibits aseasonal breeding. Non-reproductive females do not show physiological suppression of reproduction while in the confines of the natal colony. The study aimed to investigate if non-reproductive female giant mole-rats exhibit induced or spontaneous ovulation. Six non-reproductive females were removed from their natal colonies and housed individually without a male for a period of 18 weeks of which the first 6 weeks were for acclimatisation and the subsequent 12 weeks for a control experiment 1. They were then later housed for a further 7.3 weeks for a chemical contact experiment 2, which had females on their own for the first 3.6 weeks before being allowed to non-physical contact with a mature adult male for a further 3.7 weeks. The non-reproductive females were given a further period of isolation for two and half months prior to being paired physically with vasectomized males for 6 weeks, as experiment 3 which inclusively covered 12 weeks together with the earlier 6 weeks of control period. Urine was collected every second day for all three experiments and urine profiles generated. Progesterone values were markedly higher during the second part of Experiment 1 (4.43 ± 2.9 ng /mg Cr, n=6) compared to the first part (1.43 ± 0.5ng Progesterone/mg creatinine, n=6). Similarly, the progesterone values measured during the first part of Experiment 2 and 3 tended to be higher (Z= -2.201, p=0.028 for both comparisons) than those measured during the first 83 days of Experiment 1. However, this was not significant after Bonferroni correction. The progesterone values were also elevated during the second phase of Experiments 2 and 3 but not significantly so (Experiment 1 vs. 2: Z=-1.782, p=0.075, Experiment 1 vs. 3: Z=-2.201, p=0.028). Pairwise comparisons of progesterone concentrations between the control and experimental manipulation for 3 experiments, using

Statistica version 8.0, revealed non significant results between Experiments 1 ($P$ = 0.8707, $F$ = 0.348736) and 2 (P =0.361606, $F$ = 1.25244) but experiment 3 was significant at $P$ = 0.00238, $F$ =9.2374 (Fig 6.4). However, the varying differences noticed in the progesterone concentration of experiments 1-3, for the control period were not significant i.e. experiment 1, $P$ = 0.939319, with $F$ = 0.205787, experiment 2, $P$ = 0.588757, with $F$ = 0.86161 and experiment 3, $P$ = 0.393088, with $F$ = 1.4964 (Fig 6.4). Thus, chemical or physical stimulation by a male does not appear to be necessary for ovulation in female giant mole-rats but concentrations are enhanced when a non-breeding female is in chemical or physical contact with a vasectomised male. In captivity, the first rise in the urinary progesterone concentrations of the non-breeding females was only observed after 79 days. These results imply that although the giant mole-rat *F. mechowii* is a spontaneous ovulator and that recrudescence of ovulation requires a period of time to occur.

## Introduction

In female eutherian mammals ovulation may take place by one of two means, namely spontaneous or induced ovulation Milligan, (1972). Females exhibiting induced ovulation have spontaneous development of the primordial follicles to the Graafian follicle stage, but without copulation and the subsequent vaginal and cervical stimulation that is required the female fails to ovulate. In contrast, females, especially of aseasonal breeders undergoing spontaneously ovulation characteristically possess continuous cycling of the reproductive hormones and subsequent ovulation and the production of corpora lutea of ovulation without the physical and or chemical contact of the male. In induced ovulation the cycling of reproductive hormones and subsequent ovulation only occurs in the physical presence of a

male (vaginal stimulation, tactile or olfactory). In induced ovulation the physical presence always involves coitus.

In subterranean animals the cost of finding a mating partner is largely increased during the dry periods compared to those for species that live above ground due to high energetic costs of digging Vleck, (1979). Rainfall can affect soil hardness and thus the costs of mate searching may be reduced during high rainfall periods as members of the colony are more relaxed due to easier foraging. This may select for induced ovulation in subterranean species and indeed in a number of solitary subterranean rodents exhibiting seasonal reproduction (Bennett & Jarvis 1988a; Herbst *et al*., 2004; Hart *et al*., 2006) and the optimal strategy in choice is induced ovulation (van Sandwyk & Bennett 2005). In solitary members of the subterranean Southern African mole-rats (Bathyergidae-*Bathyergus suillus* and *Georychus capensis*) which are seasonal breeders and induced ovulators, elaborate penile structures further facilitate this mode of ovulation Parag *et al*., (2006).

Apart from some solitary species, the family Bathyergidae contains some representatives that occur socially with a distinct reproductive skew, with reproduction partitioned to a single female and a number of putative breeding males (Bennett & Jarvis, 1988b; Bennett, 1989; Burda, 1989; Bennett *et al*., 1994; Bennett & Aguilar, 1995). Some of these social bathyergids occur in mesic habitats with high seasonal rainfall that is likely to facilitate frequent dispersal of non-breeders. Females of these species remain anovulatory whilst in the confines of the natal colony but after dispersal and subsequently pairing with unrelated males they exhibit induced ovulation (Malherbe *et al*., 2004a; Jackson & Bennett, 2005)

facilitating colony foundation by dispersing individuals. This typical induced ovulation is complemented by males with numerous epidermal spines on the penis Parag *et al*., (2006).

In contrast, the two eusocial species of mole-rat, the Damaraland mole-rat, *Fukomys damarensis* and the naked mole-rat, *Heterocephalus glaber* experience strong ecological constraints in their arid habitats that provide non-breeders with little or no opportunity to disperse Jarvis *et al*., (1994). In the habitats occupied by these mole-rats, rainfall is unpredictable and sporadic, and years may pass before soil properties are ideal for dispersal. The non-reproductive females of the naked and Damaraland mole-rats are physiologically suppressed whilst in the confines of the colony. In the presence of the reproductive female, the concentrations of luteinizing hormone are low and the rest of females remain anovulatory (Bennett *et al*.,1993; Molteno & Bennett, 2002). Removal of the queen from the colony removes the suppression of reproduction in the Damaraland mole-rat yet the non-reproductive females will only reproduce if unrelated males reside in the colony (Rickard & Bennett, 1997). In contrast, queen succession from within can occur in the naked mole-rat, however, as in the Damaraland mole-rat non-breeding females are physiologically suppressed in the presence of a female breeder Faulkes *et al.*, (1990). When removed from the influence of the breeding female non-reproductive females of both species are relieved of suppression and subsequently pair with genetically unrelated males to form new colonies. However, in captivity the appearance of first elevation of progesterone for the non-breeding females is dependent on the species with others producing elevations within 7 days Faulkes *et al*., (1990). Males of both species lack the elaborate ornamentation of the penis found in the other Bathyergidae Parag *et al.*, (2006) and female Damaraland mole-rats exhibit

spontaneous ovulation Snyman *et al.*, (2006). This mode of ovulation may have arisen or persisted in these two species because colony turnover is less frequent compared to the species in mesic habitats. As a consequence of extreme natal philopatry and the more prolonged mating opportunities, there may be no selective advantage to induced ovulation.

Recent molecular phylogenies place another member of the Bathyergidae, the giant mole-rat (*Fukomys mechowii*) in close relationship with the Damaraland mole-rat (Faulkes *et al*., 2004; Ingram *et al*., 2004). Like the Damaraland mole-rat they breed throughout the year Scharff *et al*., (2001), however, they occur in areas with higher rainfall and thus colony dispersal opportunities may arise frequently (Bennett & Faulkes 2000). Interestingly, in the giant mole-rat, non-reproductive female members of the colony exhibit similar circulating basal concentrations of LH as the reproductive female as well as a similar response to an exogenous GnRH challenge of LH release from the pituitary to the reproductive female Bennett *et al.*, (2000). Thus in the giant mole-rat reproductive inhibition within colonies appears to be due to incest taboos. Phylogeny would suggest that the eusocial giant mole-rat *F. mechowii* and *F. damarensis* are closely related species and are both spontaneous ovulators. This relationship between the two species further elaborates that although there was geographical structuring of halotypes in both species, there was no apparent clinal pattern to their distribution, possibly as a result of weak bootstrap support nodes within the species clade and low levels of sequence divergence Faulkes *et al.*, (2004). In such a case the penis of the male should also lack elaborate ornamentation such as small spines or protrusions. In contrast, rainfall patterns in their habitat would point towards a mode of induced ovulation and penile ornamentation. We evaluate these possibilities in the present

study that phylogeny rather than habitat characteristics alone would determine the mode of ovulation in females and penile morphology in males.

## Materials and methods

Six non-reproductive females of giant mole-rat were captured from 6 different colonies in Kakalo and Mushishima Farm blocks in Chingola, Copperbelt Province, Zambia. Twelve males were also captured in the same Farm blocks but from 6 colonies located 1000m distant from where the females were collected to ensure that they were not closely related. Animals were shipped to Pretoria and experimental details are chronologically explained in Chapter 2.

## Results

Experiment 1 showed the increased urinary progesterone concentrations which commenced after 37 days in captivity and during the last 10 days of an experiment. The highest progesterone concentration (97.7nmolsP/mmols creatinine) was recorded in animal No. 4 on the 49$^{th}$ day of the experiment while animal No. 6 had the lowest concentration (7.2 nmolsP/mmols creatinine) amongst all non-breeding females on the same 49$^{th}$ day of experimental period (Fig. 6.1). Experiment 2 steadily continued with progesterone concentrations in both control and chemical periods with 32.6 and 36.1nmolsP/mmols creatinine recorded highest on 15$^{th}$ and 35$^{th}$ days for control and chemical periods for animal Nos 6 and 2, respectively. Unlike in the first experiment, animal No. 4 was recorded with the lowest progesterone concentration on the 49$^{th}$ day (11.3 nmolsP/mmols creatinine)(Fig. 6.2). In experiment 3, the control period was recorded with alternating progesterone

concentrations per animal which ranged from 15 to 30.3 nmolsP/mmols creatinine. In the second part of experiment 3, females were physically brought into contact with a vasectomised male and mating took place within the first couple of days. In this part of experiment, the range of progesterone was observed highest from 29.9 to 152.7 nmolsP/mmols creatinine suggesting that ovulation appears to be enhanced in non-reproductive females by the presence of a non-related breeding male (Fig. 6.3).

### *Baseline period*

Progesterone values were markedly higher during the second part of Experiment 1 (4.43 ± 2.9 ng /mg Cr, n=6) compared to the first part (1.43 ± 0.5ng Progesterone/mg creatinine, n=6) (Fig. 6.1). Similarly, the progesterone values measured during the first part of Experiment 2 and 3 tended to be higher (Z= -2.201, p=0.028 for both comparisons) than those measured during the first 83 days of Experiment 1. However, this was not significant after Bonferroni correction. The progesterone values were also elevated during the second phase of Experiments 2 and 3 but not significantly so (Experiment 1 vs. 2: Z=-1.782, p=0.075, Experiment 1 vs. 3: Z=-2.201, p=0.028). Thus, chemical or physical stimulation by a male does not appear to be necessary for ovulation in female giant mole-rats (Fig. 6.1).

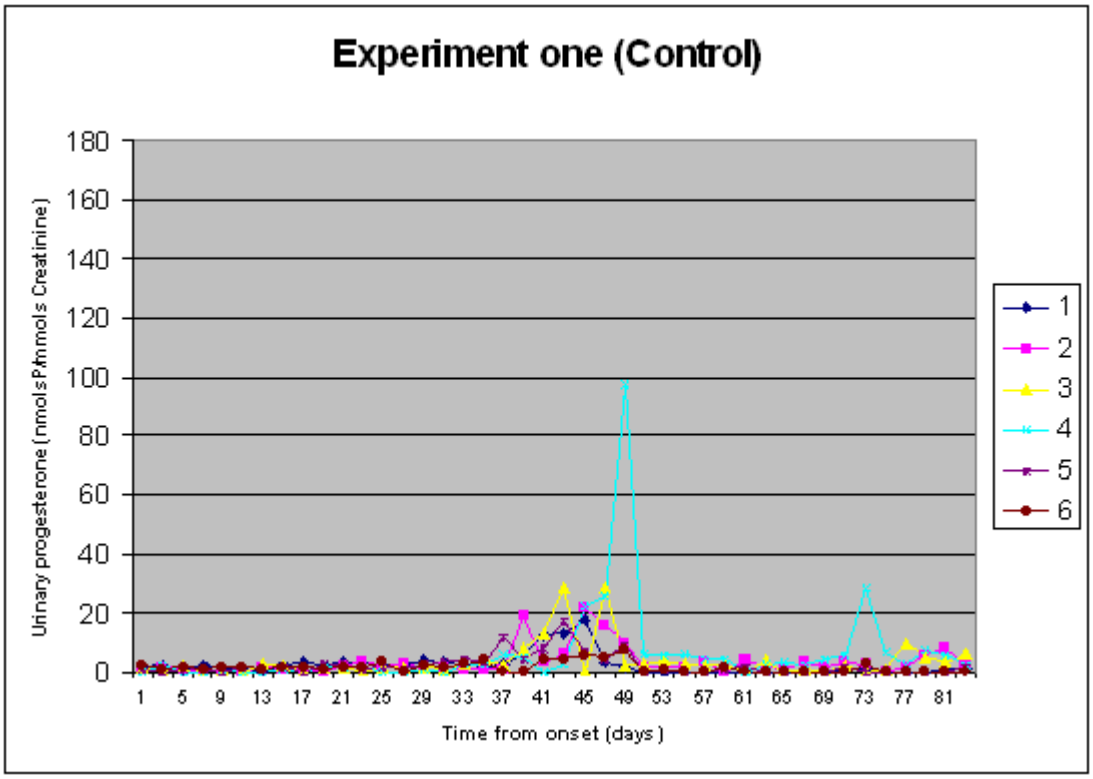


**Figure 6.1.** Mean urinary progesterone profile (nmolsP/mmols creatinine) before experimental manipulation of female (*F. mechowii*) housed singly without any contact with a male.

Progesterone values tended to be higher during the second part of Experiment 1 (4.43 ± 2.9 ng /mg Cr, n=6) compared to the first part (1.43 ± 0.5ng Progesterone/mg creatinine, n=6), however, this was not significant (Wilcoxon, Z=-2.201, p=0.075). Similarly, results of progesterone values measured in the first part for Experiment 2 were not significant (Z= -0.943, p>0.05; 9.57 ± 2.6ng Progesterone /mg Creatinine with n=6) compared to the second part of Experiment: (8.45 ± 2.2ng Progesterone/ mg creatinine) (Fig. 6.2).

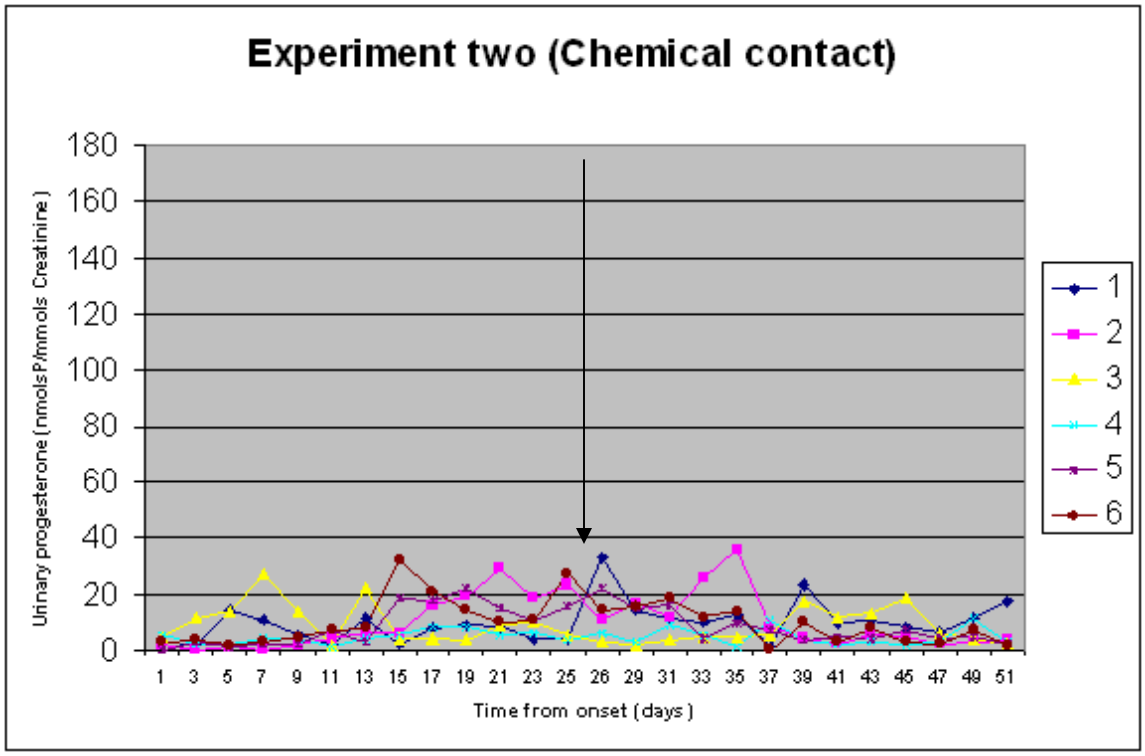


**Figure 6.2.** Mean urinary progesterone profile (nmolsP/mmols creatinine) after experimental manipulation of female (*F. mechowii*) housed in a chemical contact with a male. The middle arrow indicates the first part of experiment to the left and second part of experiment to the right.

Progesterone values measured in the first part for Experiment 3 were also not significant (Z= -1.572, p>0.05; 6.61 ± 1.2ng Progesterone /mg creatinine with n=6 compared to the second part of Experiment: 14.59 ± 8.4ng Progesterone /mg creatinine) (Fig. 6.3).

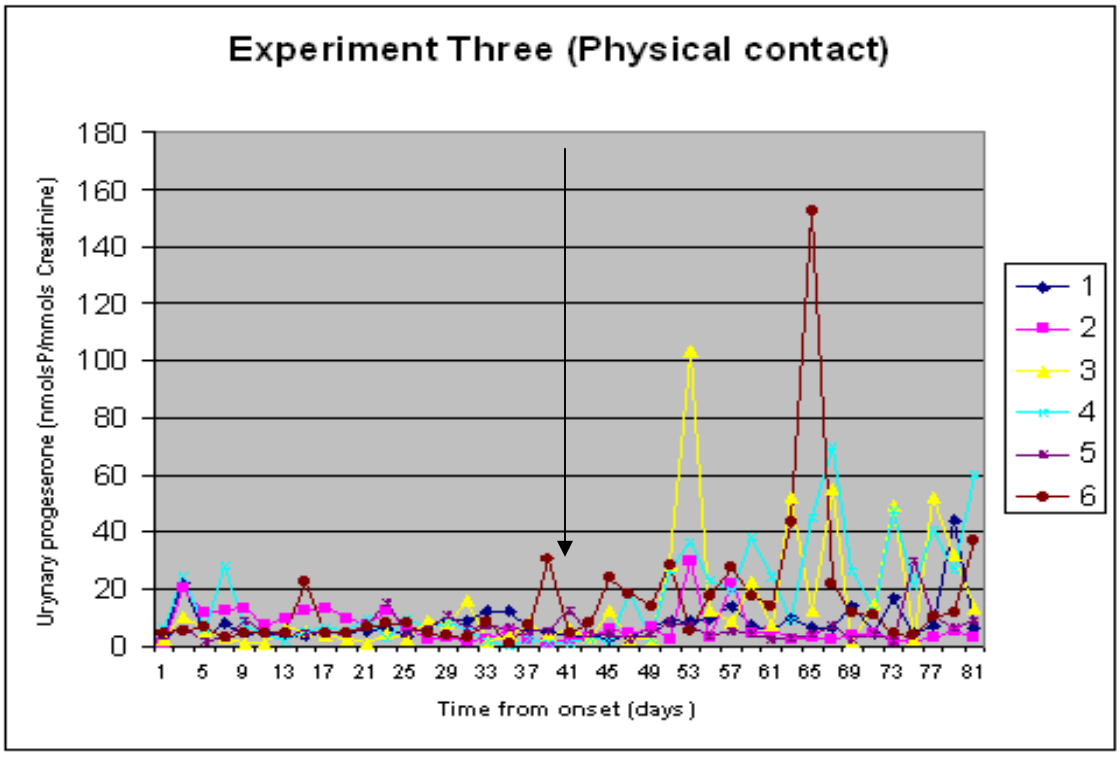


**Figure 6.3.** Mean urinary progesterone profile (nmolsP/mmols creatinine) before and after experimental manipulation for female (*F. mechowii*) housed singly, in physical contact with a vasectomised male. The middle arrow indicates the first part of experiment to the left and second part of experiment to the right.

### *Experimental manipulations*

Pairwise comparisons of progesterone concentrations between the control and experimental manipulation for 3 experiments revealed non significant results between Experiments 1 ($P$ = 0.8707, $F$ = 0.348736) and 2 (P =0.361606, $F$ = 1.25244) but experiment 3 was significant at $P$ = 0.00238, $F$ =9.2374 (Fig 6.4). However, the varying differences noticed in the progesterone concentration of experiments 1-3, for the control period were not significant

i.e. experiment 1, $P$ = 0.939319, with $F$ = 0.205787, experiment 2, $P$ = 0.588757, with $F$ = 0.86161 and experiment 3, $P$ = 0.393088, with $F$ = 1.4964 (Fig 6.4).

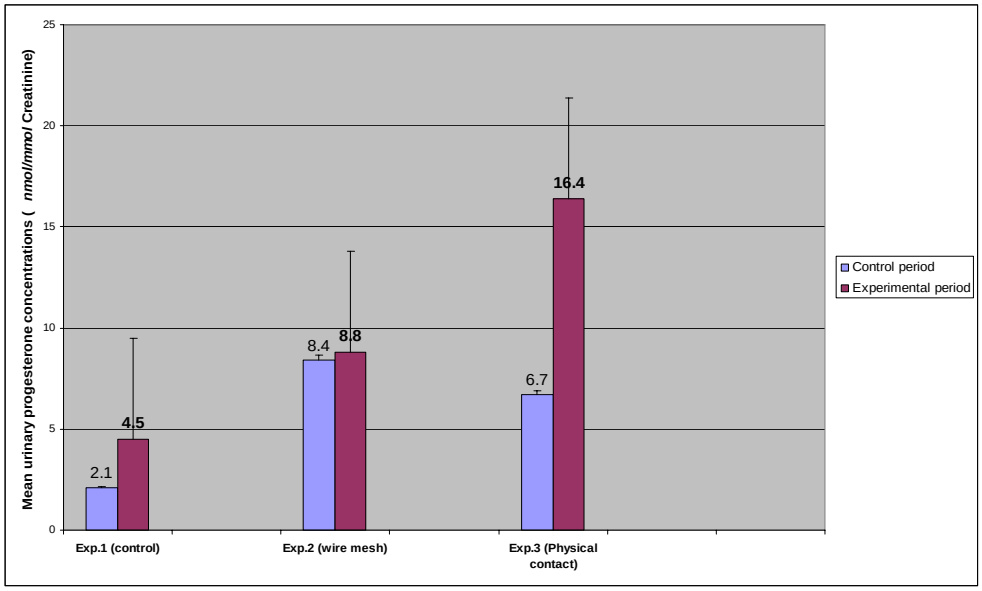


**Figure 6.4.** Mean urinary progesterone concentrations (nmolsP/mmol/ creatinine) before and after experimental manipulation for female (*F. mechowii*) housed singly, in a chemical contact with a male and physical contact with a vasectomised male.

### *Penile structure of the giant mole-rat*

Electrone micrograph of the penis of the giant mole-rat, revealed it to possess a number of slightly raised longitudinal ridges with a distinct lack of obvious spines or rounded protrusions as similar to that of *Fukomys damarensis* and the naked mole-rat (*Hetercephalus glaber*) which also exhibit spontaneous ovulators Parag *et al.*, (2006) (Fig. 6.5 a, b).

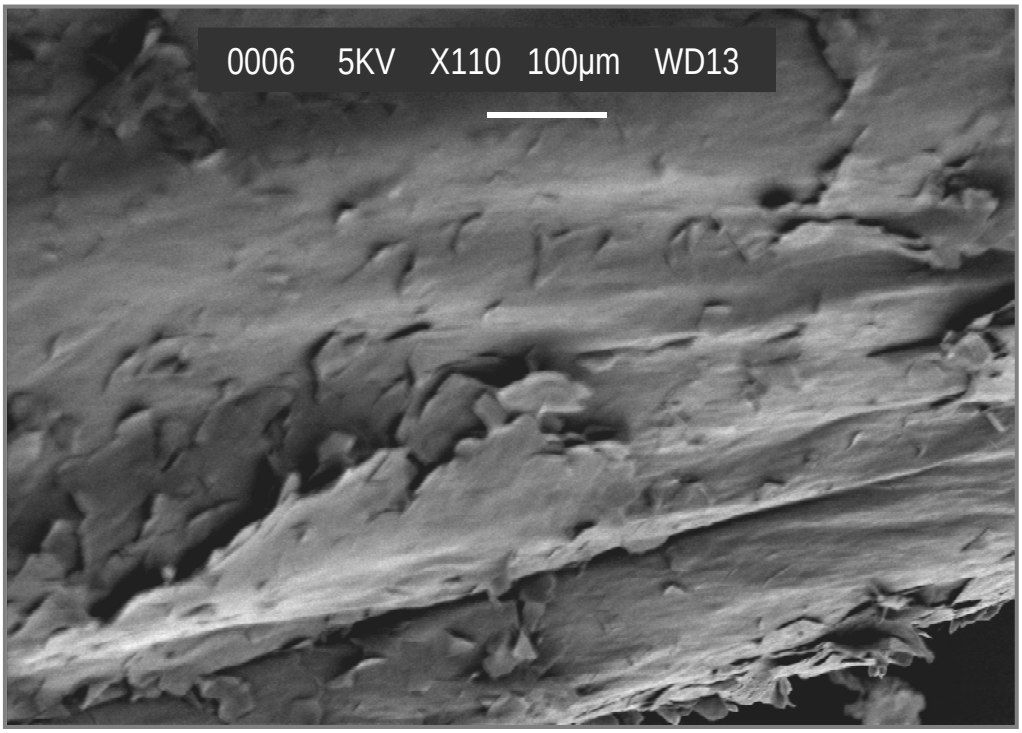


**Figure. 6.5a.** Electrone micrograph of penis of male *F. mechowii* showing smooth glans and shallow longitudinal ridges on the surface of penis.

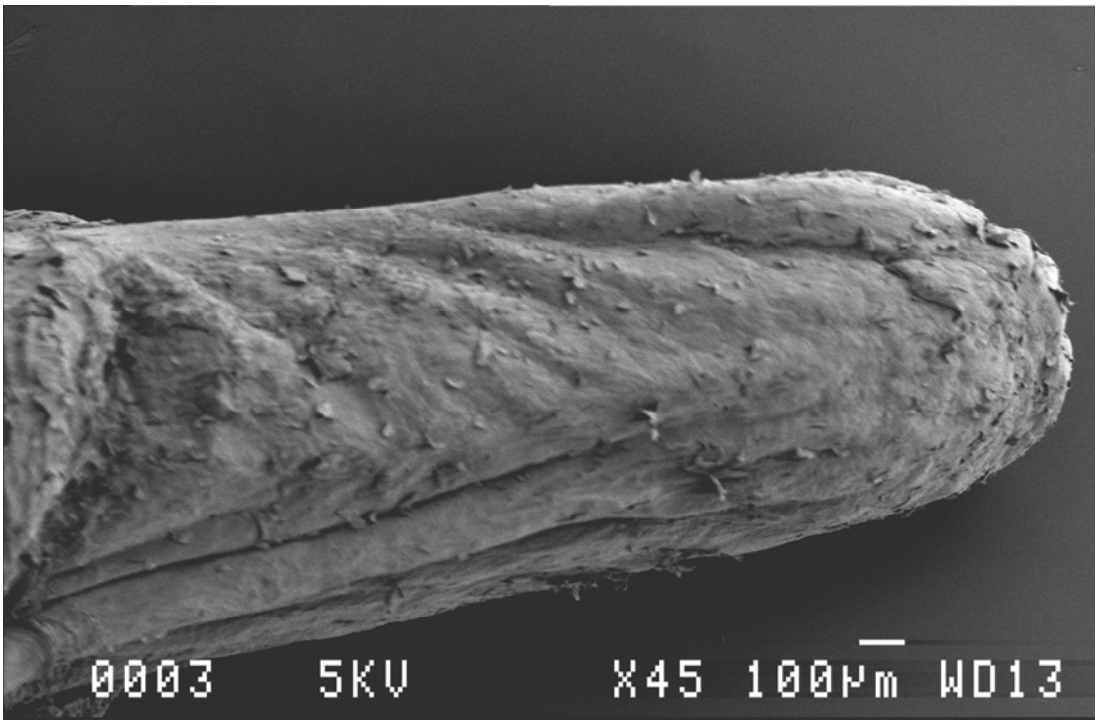


**Figure. 6.5b.** Electrone micrograph of penis of male *F. mechowii* showing smooth glans and shaft with shallow longitudinal ridges.

All results in this study have indicated that the giant mole-rat can be considered a spontaneous ovulator since in all control portions of experiment 1, 2 and 3 as well as the experimental section of experiment 1, there are cycles of progesterone observed in non-reproductive females which are housed singly. When non-reproductive females are housed with or placed in the presence of a vasectomised but not allowed physical contact or physically in contact, the intensity of the progesterone concentrations are enhanced showing that males do have some component. The spontaneous ovulation of the giant mole-rat is also confirmed with the lack of penile ornamentation on the males as one of the hypothesis in the social mole-rats.

## Discussion

African mole-rats are the only truly subterranean rodent group that exhibits a wide range of sociality and reproductive tactics (Jarvis & Bennett, 1990). Currently, most other families of subterranean rodents have representatives that are entirely solitary and in the majority of cases the females exhibit induced ovulation (Zarrow & Clark, 1968). Solitary subterranean species rely heavily on brief periods of interaction with opposite sexed conspecifics. In the solitary Ctenomyidae, the tuco tuco, *Ctenomys talarum* ovulation is found to be induced Weir, (1974) as is predicted by the hypothesis that solitary species of fossorial rodents are induced ovulators, whereas the solitary Mediterranean mole-rat Spalacidae, *Spalax ehrenbergi* exhibits spontaneous ovulation Shanas *et al*., (1995). Our hypothesis distinctly elaborates that induced ovulation requires the mechanical stimulation of the cervix and vaginal walls to initiate follicular development and subsequent ovulation Milligan, (1972). Within the family Bathyergidae, the solitary Cape mole-rat, *Georychus capensis* is an

induced ovulator (van Sandwyk & Bennett, 2005). Examination of the penis of the higveld mole-rat, *Cryptomys hottentotus pretoriae* has shown that the glans and the shaft of the penis to be covered with small spinose protrusions. It is thus surprising that within the two species of social African mole-rat, *Cryptomys hottentotus natalensis* and the high veld mole-rat *Cryptomys hottentotus pretoriae,* exhibit seasonal breeding yet their ovulation pattern is induced (Malherbe *et al*., 2004b; Jackson & Bennett, 2005). Studies on the highveld mole-rat, *Cryptomys h. pretoriae* and the Natal mole-rat, *Cryptomys natalensis* have shown that the males of these species have small protrusions emanating from the glans and shaft of the penis Parag *et al*., (2006).

In contrast, the two eusocial species of mole-rat, the naked mole-rat, *Heterocephalus glaber* and the Damaraland mole-rat, *Fukomys damarensis* are both reportedly spontaneous ovulators (Faulkes *et al*., 1990; Snyman *et al*., 2006). These two species are found in arid habitats where rainfall is sporadic and unpredictable, furthermore rains may fail in some years and hence dispersal is impossible due to unfavourable soil conditions for burrowing. Spontaneous ovulation may have arisen or persisted in these two species because colony turnover is less frequent. As a consequence of extreme natal philopatry and more prolonged mating opportunities, there may be no selective advantage to induced ovulation and hence elaborate ornamentation to the penis in these two species Parag *et al*., (2006). We predicted that based on the sociality and phylogenetic relationship between the *F. mechowii* and *F. damarensis* where both species were found with geographical structuring of halotypes and low levels of sequence divergence within the species clade Faulkes *et al*., (2004), the giant mole-rat should also be a spontaneous ovulator. This is borne out in the endocrine profiles

where in the control phase of the study there are raised concentrations of progesterone indicative of an ovulation event in non-reproductive females removed from the colony and isolated on their own. The longitudinally ribbed characteristic of the penis and shaft further reflects the lack of mechanical stimulation required in a species where follicular development and subsequent ovulation is spontaneous and does not require the mechanical stimulation of the cervix and vagina. In solitary and social species exhibiting induced ovulation, the male is characterized by possessing spines or blunt spinose ornamentation along the glans and shaft of the penis Parag *et al*., (2006). However, as in the Damaraland mole-rat and naked mole-rats (Faulkes *et al.,* 1990; Snyman *et al*., 2006), the progesterone concentrations of the giant mole-rat acquires elevated progesterone concentrations only when females are in direct physical contact with males. Ovulation also appears to be enhanced in presence of non-related male (Fig. 6.3.)

The release from the inhibition of ovarian cyclicity in the non-breeding females of giant mole-rat is longer than in other social mole-rat species. The urinary progesterone concentrations of the naked mole-rats in captivity showed ovarian cyclicity within 7 days Faulkes *et al.,* (1990) while the first elevation of progesterone for the giant mole-rats were only observed on the 79th day in captivity following removal from the colony. Nevertheless, the giant mole-rat is a spontaneous ovulator. Both the hormone profiles (Fig. 6.2 and 6.3) and the findings from the structure of the penis of the male support the general reasoning that ovulation is a spontaneous affair in the giant mole-rat.

In species that are obligate outbreeders such as the giant mole-rat there is incest avoidance between father and daughters, as well as between brothers and sisters, but the incest avoidance between mother and sons seems to be weaker. Experiments and observations to date (Burda 1995; H. Burda unpublished) suggest that behavioural control (mate guarding) by the dominant male (the father) may also play an important role in inhibition of male reproduction. This fact may have represented a selective pressure leading to significant increase in the body mass (and sexual dimorphism) of breeding males in this species.

Bennett *et al.*, (2000) demonstrated that non-reproductive female giant mole-rats are not physiologically suppressed at the level of the pituitary and furthermore that the response of the pituitary to an exogenous overdose of GnRH is similar to that exhibited in reproductive female giant mole-rats. All of this evidence points to the fact that non-reproductive female giant mole-rats are capable of reproduction but do not because of strict incest taboos.

# CHAPTER 7

# Synthesis

## The giant mole-rat

Considerable efforts have been made in the studies of reproductive biology, burrow system and colony size of the giant Zambian mole-rat (Bennett & Aguilar, 1995; Scharff *et al.*, 2001; Burda & Kawalika 1993). Other separate studies include the pituitary sensitivity to exogenous GnRH Bennett *et al.*, (2000). Until recently however, the existing published information on the reproduction of the giant mole-rat was derived from laboratory studies (Bennett & Aguilar, 1995; Scharff *et al.*, 1999) with a small field study Scharff *et al.*, (2001) in which aseasonal reproduction was suggested to take place in the giant mole-rat. Other anecdotal reports were from Ansell (1978) who captured young animals throughout the year. Mostly, the speculation on the larger group sizes of captured animals which varied from 40+ animals Scharff *et al.*, (2001) to 60+ animals (Burda & Kawalika, 1993), either involved two or more colonies or was gleaned from local hunters. With the low sample sizes, colonies involved and the period of sample collection in these studies, reliable and conclusive results could not be attained.

This study is the most extensive to date and is mainly focused on the description of the general burrow architecture of the giant mole-rat from 32 burrow systems, excavated in their entirety, throughout the year. It was imperative to employ the burrow fractal dimensions analysis on the burrows of the giant mole-rat, in order to compare its effects on the burrow structure, length and its relationship to foraging success Le Comber *et al.*, (2006) in both rainy and dry seasons (Fig. 3.1). Furthermore, the fractal dimension provides a good indication of the extent to which a burrow explores the surrounding area and also offers a more useful burrow metric than burrow length Le Comber *et al.*, (2006). It was also

predicted that formidable indicators emanating from the burrow fractal dimensions can explain and relate the importance of the Aridity Food Distribution Hypothesis (AFDH) (Jarvis *et al.*, 1994; 1998), in the giant mole-rat.

The fractal analysis component was then employed on the mapped burrow systems to answer three general questions relating specifically to the assumptions of the AFDH: (1) Is burrow fractal dimension higher in the rainy season, as might be predicted if either or both the energetic costs of digging, or differences in patterns of food distribution, vary between seasons? (2) Do larger colonies have burrows with higher fractal dimensions? This might be the case if, as the AFDH suggests, foraging is more efficient in larger, cooperatively foraging colonies. (3) Is higher fractal dimension associated with a greater mass of food in the burrow? (Le Comber *et al.*, 2006) showed, using computer simulations, that burrows with high fractal dimension located more food; here, this study tests whether this is reflected in larger food stores in a natural situation.

Furthermore, there was need in this study to address the uncertainties involved in colony composition of the colonies of giant mole-rats captured. The cranial morphometric analyses and the structure of age classes, based on tooth-wear and eruption patterns were carried out to ascertain whether (i) the species is sexually dimorphic and (ii) if sexual dimorphism is evident does it arise early in the life history or following maturation and the attainment of adulthood. There was also need in this study to investigate whether the giant mole-rat is an aseasonal or seasonal breeder. The final component of the study investigated if ovulation in

non-reproductive females removed from the confines of the colony is of a spontaneous or induced nature.

## Burrow Systems

The general burrow architecture of 32 burrow systems was described, including the burrow structure, length and diameter of tunnels, location and depths of nests, food stores and toilets. Foods found in food stores, including stored tuber crops and geophytes were identified and weighed for each colony.

The length of burrow system did not differ between seasons but increased with the number of animals in the colony. The range of burrow lengths of the giant mole-rat fell within the category of solitary species *Barthyergus suillus* (Davies & Jarvis, 1986), *Bathyergus janetta* (Herbst & Bennett, 2006) and *H. argenteocinereus* (Šumbera *et al.*, 2003c). The food store had a higher mass during the rainy season than in dry season (Fig. 3.2).

## Burrow fractal dimensions

A number of studies on the Bathyergidae have examined burrow architecture although not necessarily fractal dimensions (Hickman, 1977; Davies and Jarvis, 1986; Zuri & Terkel, 1996; Rosi *et al.*, 2000; Spinks *et al.*, 2000a; Šumbera *et al.* 2003c and Herbst & Bennett, 2006) but the majority of these have concentrated on solitary species that only have plural occupancy during the breeding season or when mother has young. There have been relatively few studies reporting the burrow fractal dimensions and architecture of social dwelling mole-rats (Spinks *et al.*, 2000a) but usually, the sample sizes were very small.

Fractal dimensions increased with both the length of the burrow and the number of animals, but especially adults in the colony and was higher during the rainy season than the dry. Similarly, the mass of food in the burrow also tended to increase with fractal dimensions and was higher during the rainy season than in the dry season (Fig. 3.2). An interesting point to note was that while fractal dimensions were greater in rainy season, there was no overall difference in total burrow length. This might be due to the point that burrows in rainy season had more of the short side tunnels than those in dry season and resulted into substantial increase in fractal dimensions in the rainy season without necessarily increasing the total burrow length (Fig. 3.1). During periods when soil was softened by rainfall, geophytes began to proliferate and mole-rats took this advantage to forage and store sufficient food to last them through the dry season. Thus, the limiting factor for burrow excavation in mole-rats mainly depends on (i) amount and periodicity of rainfall and (ii) number of animals in the burrow system available for digging. These results provide evidence in support of each of these factors.

During the rainy season, foraging was found to be more efficient and colony size increased, prompting higher fractal dimensions and more food mass in burrows. These results concur with foraging models of (Lovegrove & Wissel, 1988) and (Spinks & Planganyi (1999) which suggested that colony size is important in foraging risk, especially for mole-rat species occurring in arid environments.

These results are in line with previous data in which Jarvis *et al.*, (1998) indicated that larger colonies of social mole-rats have greater survival and make for the first time the link between colony size, burrow architecture and foraging success (Table 3.1). To summarize, these results are important because they link for the first time rainfall, colony size, burrow architecture and foraging success in a single social mole-rat species, and thus support the critical assumptions that underlies the aridity food distribution hypothesis.

## Aseasonality and Colony size

Colony size and reproductive biology are important factors to African mole-rats because colony size particularly is a crucial comparative parameter and component which plays an important role in sociality and is an indirect measure of the degree of dispersal/philopatry. Until recently, previous studies have shown uncertainties on the colony size in free living colonies of giant mole-rat. The first study by Burda & Kawalika, (1993) revealed that the social group size of giant mole-rat to be over 60 animals per colony. Unfortunately, this information was sourced from local hunters without any distinct colony surveying knowledge. Another small study done by Scharff *et al.*, (2001) only compared six complete colonies, five of which ranged from 3-12 in group size, but the sixth possibly totalling 40 animals or more. However, it is speculated that the animals from the latter colony may have been caught from neighbouring burrows, as the area in question was difficult to survey. Both studies were based on small sample sizes with very little time by workers devoted to extensive field work. Information pertaining as to whether the giant mole-rat is aseasonally or seasonally breeding has also been wanting. Anecdotal reports by Ansell (1978) were merely based on capturing young animals throughout the year. A lack of information on

maximum colony size as well as data on whether free living giant mole-rats are aseasonal or seasonal breeders remained uncertain. Much of the information pertaining to the reproductive biology of giant mole-rats was from laboratory studies, which may be mostly limited to litter size and gestation periods of the species.

From the 32 carefully surveyed and excavated free living colonies, the mean colony size of the giant mole-rat is now clarified to be around 10, being closer but below that of *F. damarensis*, an extensively studied species which has the colony size of 12 (Bennett & Faulkes, 2000). Throughout the entire period of 10 months which included both rainy and dry seasons, one or occasionally two pregnant females and juveniles were recorded in the burrows of the giant mole-rat (Tables 4.1). Sex ratio in the wild is skewed towards females, with males being larger than females. This concurs with earlier reports by Scharff *et al.* (2001), from the 5 colonies where it was reported that colonies range from 3-12 animals. Results of this an extensive field data collection complements the findings of earlier laboratory studies that the giant mole-rat is without doubt an aseasonal breeder.

## Relative age classes

The use of tooth-wear on its own has been shown to be a poor ageing method in mammals (Hall *et al.* 1957; Keiss, 1969; Morris, 1972 and Gilbert & Stolt, 1990). This study suggests that in the absence of data on the absolute ageing, the estimation of age based on molar eruption and tooth-wear may be an appropriate method for relative ageing in the giant mole-rat. In studies on single geographically related species where the diet is fairly uniform,

application of tooth-wear on the cusps of the molariform teeth may be used as a relative rather than absolute variable for ageing a population.

The time of tooth-wear and eruption is less variable and can serve as a valuable marker of relative age. This method can in conjunction with skull morphometrics be used to investigate potential sexual dimorphism with age in populations of mammals. Indeed, Bennett *et al*., (1990) successfully used this method to investigate sexual dimorphism in two species of social mole-rat, they found that within colonies, it was absent in the common mole-rat, *C. h. hottentotus* but distinctly marked in the Damaraland mole-rat, *F. damarensis*. Similarly, sexual dimorphism and relative age variation in nine age classes estimated from the degree of molar tooth-row eruption and wear in the giant mole-rat were assessed using traditional cranial morphometric data and a range of univariate and multivariate analyses.

In addition, the use of body mass to estimate absolute age in mammals has also been considered to be inappropriate. However, as has been found in the solitary Cape dune mole-rat (Hart *et al*., 2007), body mass which has previously been used to assess the extent of sexual dimorphism and age variation in other social species such as the highveld mole–rat, (*Cryptomys hottentotus pretoriae*) Janse van Rensburg *et al*., (2004) was also used in the current study for comparative purposes.

All the analyses conducted on the giant mole-rat revealed craniometric differences between individuals of age classes 1–3 and those of age classes 5–9, with those of age class 4 being intermediate between these two age class groupings, suggesting that age class 4 is at a point

on a hypothetical growth curve where it begins to stabilize. In contrast, the analyses revealed the absence of sexual dimorphism in the younger individuals of the giant mole-rat of age classes 1–4 and its presence in older age classes 5–9 (Figs. 5.3 & 5.4), and these results were supported by the analysis of the data on body mass, which was non-significant in younger age classes 1-5 and significant in older age classes 6-9 (Fig. 5.5).

## Ovulation

African mole-rats are the only truly subterranean rodent group that exhibits a wide range of sociality and reproductive tactics (Jarvis & Bennett, 1990). Currently, most other families of subterranean rodents have representatives that are entirely solitary and in the majority of cases, females undergo induced ovulation (Zarrow & Clark, 1968). To date, numerous studies have classified these species of mole-rats into ( i ) Solitary and seasonal species where animals live singly in burrows, except at the time of mating or when the mother has pulps Hart *et al.,* (2007) and ( ii ) Social, seasonal or aseasonal species where the natal colony restricts reproduction to a single reproductive female and one or potential two reproductive males allow control of the recruitment of pups into the colony, with most members exhibiting socially induced-sterility and being monogamous (Bennett *et al.* 1993; Bennett, 1994; Bennett *et al.,* 1994; Bennett *et al.,* 1996; Jarvis & Bennett 1991).

The patterns of ovulation for the African mole-rats may be induced where the male counterpart shows elaborate penile ornamentation or spontaneous where a decrease of penis ornamentation results Parag *et al.,* (2006). The common underlying hypothesis distinctly elaborates that induced ovulation requires the mechanical stimulation of the cervix and

vaginal walls to initiate follicular development and subsequent ovulation Milligan, (1972) while apart from the two social and seasonal species, *Cryptomys h. natalensis* and *Cryptomys h. pretoriae* which exhibit induced ovulation (Jackson & Bennet, 2005; Malherbe *et al*., 2004a), most studied eusocial and aseasonal species *F. damarensis* and *H. glaber* exhibit spontaneous ovulation (Faulkes *et al*., 1990; Snyman *et al*., 2006).

In solitary and social species exhibiting induced ovulation, the male is characterized by possessing spines or blunt spinose ornamentation along the glans and shaft of the penis Parag *et al*., (2006). This condition is different in the eusocial species exhibiting spontaneous ovulation like the *F. damarensis* and *H. glaber* which have ridges on the shaft of penis. In this study, it was predicted that based on the sociality and phylogenetic relationship between the *F. mechowii* and *F. damarensis* where both species were found with geographical structuring of halotypes and low levels of sequence divergence within the species clade Faulkes *et al.,* (2004), the giant mole-rat should also be a spontaneous ovulator.

The males of the eusocial and aseasonal giant mole-rat had longitudinally ridged characteristic of the penis and shaft like those of *H. glaber* and *F. damarensis,* which was the first indication of the species being a spontaneous ovulator (Figs 6.5 a, b). Cyclicity in the non-breeding females of the giant mole-rat in captivity was longer than other social mole-rat species like the naked mole-rat, with the first elevation of progesterone only observed on the 79$^{th}$ day in captivity (Fig. 6.1). Nevertheless, the giant mole-rat is a spontaneous ovulator with both the hormone profiles (Fig. 6.2 and 6.3) and the findings

from the penis structure of the male supporting the general reasoning that ovulation is a spontaneous affair. As in the Damaraland mole-rat and naked mole-rats (Faulkes *et al.*, 1990; Snyman *et al.*, 2006), the progesterone concentrations of the giant mole-rat are elevated only when females are in direct physical contact with males. Ovulation also appears to be enhanced in the presence of a non-related male (Fig. 6.3).

## Summary

In this thesis, I have demonstrated that the mean colony size of the giant mole-rat occurring in the mesic Copperbelt of Zambia is lower than that of its more arid adapted counterpart the Damaraland mole-rat. Furthermore, a detailed analysis of the burrow structures excavated throughout the year revealed that with an increase in precipitation, there is a concomitant complexity of the burrow system but the burrow system retains a mean maximal length irrespective of the season. As with other members of the genus *Fukomys* so far studied to date, breeding by the dominant female(s) occurs throughout the year, yet unlike the Damaraland mole-rat, in the giant mole-rat, there may be plural breeding in colonies. The pattern of ovulation is spontaneous as is that of the Damaraland mole-rat and may be phylogenetically constrained. Giant mole-rats exhibit sexual dimorphism that appears to become more apparent with the advancing age of the animals. There is a definite age structure in colonies with the breeding animals being the oldest. This study has furthered our understanding of this little studied central African mole-rat species.

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