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).

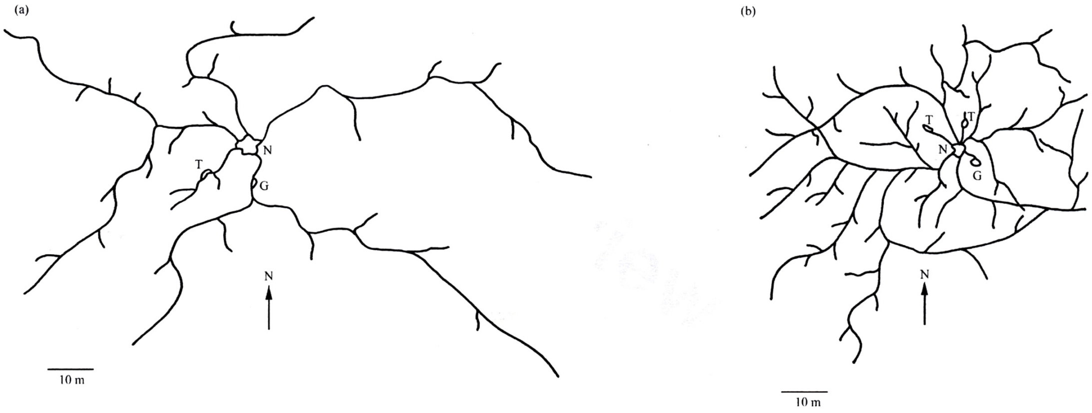

Figure 3.1. Two burrows representing the observed differences in fractal dimension, from (a) the dry season (colony 24, fractal dimension =1.194) and (b) the rain season (colony 15, fractal dimension = 1.422). G = granary; N = nest; T = toilet chamber.

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		Sub-adult		Juveniles		Borrow Length (m)	Fractal dimennsio	Food Mass (g)	Rain/Dry	Captured
			M	F	M	F	M	F					
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).

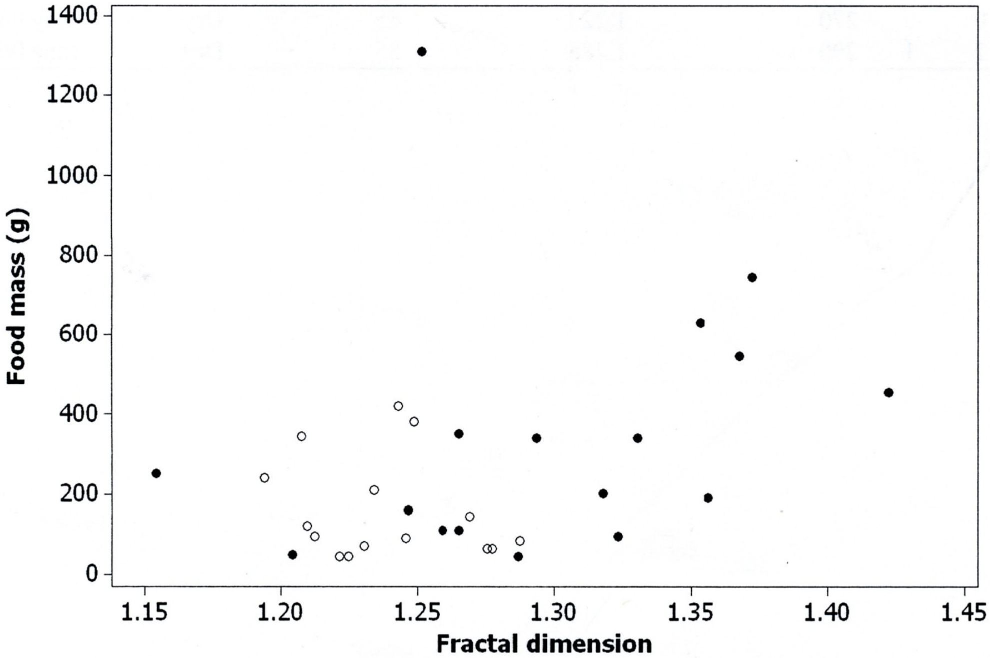

Figure 3.2. The mass of food in the burrow as a function of burrow fractal dimension. Open circles: dry season, Filled circles: rainy season. Note the anomalous data point for colony 23, with 1310g of food.

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.