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

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**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.**

**Key words:** ***Fukomys mechowii,*** **Bathyergidae,** ***Cryptomys,*** **colony size, seasonality, reproductive skew.**

## INTRODUCTION

The giant mole-rat *Fukomys mechowii* (Peters, 1881; formerly *Cryptomys mechowi*) is an Afrotropical subterranean rodent that occurs in the Miombo woodland and savannas of Zambia, Democratic Republic of 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-repro-

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ductive 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 & METHODS

The study was conducted over a 10 month period (September 2005 – June 2006 inclusive) on two farms, Kakalo and Mushishima, located 25 km South from Chingola in the Copper Belt Province of Zambia (10°40′S, 20°85′E).

The Copper Belt Province of Zambia (where the animals were collected) receives an annual precipitation of around 2000 mm. Zambia has three 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 to 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 was collected following complete excavation of the burrow systems. Mole-rat burrows were located by the presence of mole-hills on the surface. To ensure that distinct colonies were captured, excavated burrow systems were a minimum of 1000 m apart. The burrow systems occurred in agricultural fields, grasslands and dambos (a class of complex shallow wetlands) within a variety of soil types ranging from clay to sandy loams. 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. 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.

On capture, mole-rats were weighed, sexed and the breeding status of females was determined. Breeding females within the colony were characterized by having a perforate vagina, possessing elongated axillary and inguinal teats, and/or by being pregnant. Breeding males were not identified on capture. Animals were categorized into three age classes based on laboratory studies of growth (Bennett & Aguilar, 1995) as follows: (i) juveniles (weighing 1–100 g, aged approximately 100–150 days); (ii) subadults (101–200 g, aged approximately 1 year); or (iii) adults (201 g and above, aged approximately 1 year and above). Body masses of adults were compared statistically using a $t$-test. Animals were euthanased following the guidelines of the American Society of Mammalogists (1998), using an overdose of halothane anaesthetic. The project was cleared by the ethics committee of the University of Pretoria (Ethics number AUCC 060504-011). Capture of mole-rats was authorized by the Department of Veterinary and Nature Conservation in the Copper Belt Province of Zambia.

## RESULTS

In total, 317 mole-rats from 32 colonies comprising 131 males and 186 females, categorized into 125 juveniles (21.0% of population), 37 subadults (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 ± 20.7 g (range 220–995, $n$ = 79) whilst that of adult females was 391.8 ± 11.7 g (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 424.7 g (pregnant: range 235–650, $n$ = 18) and 400.8 g (non-pregnant: range 250–600, $n$ = 18), while the average mass of non-reproductive adult females was 381.5 g (range 240–600, $n$ = 58). The sex ratio of the population captured was skewed towards females at 1.46:1 (female:male).

Despite large variation in the prevailing environmental and ecological conditions, pregnant females were found throughout the study period (Table 1). Modal litter size was two (10/18 pregnancies), with seven cases of triplets and a single example of a female carrying four foetuses (Table 1). Mean litter size was thus 2.5 pups. The majority of colonies in which the breeding female

**Table 1**. Date of capture and site location of colonies of *Fukomys 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 |
|---|---|---|---|---|---|---|
| 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 | |

was identified as being pregnant (14/18) had a single reproductive female, but four 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 10 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 16 animals in *F. mechowii* reported here is substantially less than two colonies of 41 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.* were 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* (Sumbera *et al.* 2003; 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 1988a,b; Bennett & Faulkes 2000), *F. darlingi* (Bennett *et al.* 1994) and *F. anselli* (Burda 1989) By 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 1988a; Burda, 1989; Bennett *et al.* 1994; Bennett & Aguilar 1995; Scharff *et al.* 2001) and *Cryptomys* (Bennett 1989; Malherbe *et al.* 2004, Oosthuizen *et al.* 2007). Among the social bathyergid genera *Fukomys* and *Cryptomys,* the species so far investigated all have relatively small litters (2–6 pups; Bennett *et al.* 1991), compared to solitary species, e.g. *Bathyergus suillus, B. janetta* and *Georychus capensis*, in which 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 1988a; 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 of 30 colonies caught at Somerset West, South Africa over a two-year period (N.C. Bennett, unpubl. 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, unpubl. 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 1991). 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.

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