

Field evidence for colony size and aseasonality of breeding and in Ansell's mole-rat, *Fukomys anselli* (Rodentia: Bathyergidae)

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Ansell's mole-rat, *Fukomys anselli*, is a cooperatively breeding bathyergid endemic to the Lusaka Province of Zambia. During a 12-month field study involving the capture of 33 colonies of mole-rats, the number of occupants, breeding females and sex ratio within colonies were recorded. While thirty of these social groups contained a single breeding queen, three were found to exhibit plural breeding among females, having two queens present simultaneously. Mean \pm S.E.M. colony size was 8.7 ± 2.2 (range 6–16, $n = 33$). The occurrence of plural breeding and small group size is consistent with the predictions of the aridity food distribution hypothesis for social species inhabiting mesic habitats. The sex ratio of the population was skewed towards females at 1.2:1. The mean mass of adult males was 63.0 ± 18.3 g (range 36.7–110.3, $n = 87$) while that for adult females was 52.9 ± 11.8 g (range 35.1–77.8, $n = 86$). Pregnant and lactating females were found throughout the study period from February 2009 to February 2010, indicating an aseasonal pattern of breeding in this species. Autopsy of individuals ($n = 288$) from the 33 colonies revealed a total of 19 pregnant females. Nine of these were in the latter stages of pregnancy and mean litter size was determined as 2.7 pups (range 1–4). Collectively, these new data reveal that *Fukomys anselli* share many similarities in life history and reproductive traits with the phylogenetically closely related giant Zambian mole-rat, *Fukomys mechowii*.

Key words: *Fukomys anselli*, Bathyergidae, reproduction, colony size, seasonality, reproductive skew.

INTRODUCTION

African mole-rats are widely distributed across sub-Saharan Africa and are well known for their range of social behaviours and cooperative breeding strategies (for recent review see: Faulkes & Bennett 2007, 2009). *Fukomys anselli* (Ansell's mole-rat) is one of perhaps 30 or more chromosomally diverse clades/species within the genus, many of which are endemic to Zambia and which form localized populations that may have arisen from changing patterns of drainage of main river systems in the region (Van Daele *et al.* 2004, 2007a,b). Molecular phylogenies place *F. anselli* within a well-supported clade that includes sister taxa *F. micklei* and *F. kafuensis* ('Micklei Clade': Van Daele *et al.* 2004). Limited in its distribution, *F. anselli* occurs in the Miombo woodlands and grasslands of the Lusaka Province of Zambia. Its

presence has been recorded in a variety of soil types ranging from sand to clay, around both Miomba and agricultural land near Chainama Hills Golf Club, Lusaka, Zambia (Burda *et al.* 1999; de Vries *et al.* 2008), areas to the east and west of Lusaka, and around Lusaka International Airport (Cotterill 2002; Van Daele *et al.* 2004). Like other African mole-rats, *F. anselli* is herbivorous, feeding predominantly on geophytes, bulbs and agricultural root crops such as cassava and sweet potatoes that are encountered during burrowing (Burda & Kawalika 1993; Sichilima *et al.* 2002; Barnett *et al.* 2003; Kawalika *et al.* 2007; Sichilima *et al.* 2008a).

Studies mainly based on captive colonies suggest that the social lifestyle of *F. anselli* is similar to that of *F. mechowii*, with a cooperative breeding system and reproduction highly skewed towards a single female and a small number of male consorts (Burda 1989; Bennett & Aguilar 1995; Sichilima

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et al. 2008a). However, little is known about free-living colonies of this species regarding group size, composition, and reproductive biology (Burda 1989, 1992; Arndt & Burda 1992; Burda & Kawalika 1993; Bennett & Aguilar 1995; Scharff *et al.* 1999, 2001). Colony size and reproductive skew in particular are important components in comparative studies of mole-rats that seek to understand the ultimate and proximate factors implicated in the evolution and maintenance of cooperative breeding and sociality. Colony size also provides an indirect measure of the degree of dispersal/philopatry that takes place within a colony (Faulkes *et al.* 1997). Cooperatively breeding mole-rats that inhabit mesic regions, such as those occurring in Zambia, are of especial interest because the aridity food distribution hypothesis (AFDH; Jarvis *et al.* 1994) predicts that colony size and reproductive skew should be reduced, and frequency of dispersal increased, in these habitats where ecological constraints are relaxed. This study aims to investigate life history and reproductive traits fully for the first time in a wild population of *F. anselli*.

MATERIALS & METHODS

The study was undertaken over a period of 12 months from February 2009 to February 2010, on Mukulaikwa Farm Block, located 15 km west of Lusaka (14°65'S, 27°48'E). The Lusaka Province, where the animals were captured, is located at an altitude of 1633 m above sea level and receives a mean (\pm S.D.) annual rainfall of 800 \pm 134 mm/year, with a mean maximum annual temperature of 31.6°C recorded in October, and a mean minimum temperature of 10.1°C in June (Table 1; www.zambiatourism.com/travel/hisgeopeople/geograph.htm; accessed July 2010). The rainy season is mainly from mid-November to mid-April each year with a peak from January to March. In general, 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 from mid-November to April and occasionally, extending to the second week of May.

A total of 33 colonies were investigated. Each burrow system was initially located by the presence of mole hills on the surface and were between 500 and 700 m apart to ensure that only distinct colonies were recorded (Sichilima *et al.* 2008b). The burrow systems were mostly situated in agricultural fields, grassland and dambos (shallow

wetlands) and involved a variety of soil types ranging from clay to sandy loams. The animals were captured by completely digging out the burrows leading to the centrally positioned nest, food stores and toilet chambers. On capture, mole rats were euthanased using chloroform, weighed, sexed and the breeding status of females determined.

The breeding females were identified by elongated teats and a perforate vagina while the putative breeding males were determined by the presence of a characteristic area around the mouth stained by glandular secretions, testes that bulge prominently within inguinal pockets, and a large body size (Bennett & Aguilar 1995; Sichilima *et al.* 2008b). Animals were categorized as juveniles (weighing 3–24 g), subadults (25–34 g) or adults (35 g and above). These age-class categories were based on laboratory observations of growth and development in this species. Body weights were compared using a standard *t*-test.

Animals were humanely treated, following the guidelines of the American Society of Mammalogists (Gannon & Sikes 2007). The project was reviewed and passed by the Ethics Panel of the University of Pretoria (ref. No. EC001-09). Capturing of mole rats was authorized by the Department of Veterinary and Nature Conservation in the Lusaka Province of Zambia.

RESULTS

In total, 288 mole-rats were captured from the 33 colonies, comprising 87 adult males, 86 adult females, 17 subadult males, 41 subadult females, 18 juvenile males and 39 juvenile females. There was a highly significant difference ($t = 4.05$, $P < 0.00007$, d.f. = 171) in body mass between the adult males and females: mean \pm S.E.M. (standard error of the mean) mass of adult males was 63.0 \pm 18.3 g (range 36.7–110.3, $n = 87$) while that for adult females was 52.9 \pm 11.8 g (range 35.1–77.8, $n = 86$). The mean \pm S.E.M. colony size was 8.7 \pm 2.2 (range 6–16, $n = 33$). The sex ratio of the overall population captured was skewed towards females at 1.2:1 (female:male).

Among adult females, the breeding queens were the heaviest with a mean mass of 64.1 g (pregnant: range 52.7–80.5, $n = 19$) and 62.3 g (non-pregnant: range 42.3–83.3, $n = 17$) while the average mass of non-reproductive adult females was 45.0 g (range 35.1–59.5, $n = 50$). Nineteen pregnant females, 17 lactating females and their associated juveniles were found during the study period. Three of the

Table 1. Colony composition (numbers), capture season and the reproductive status of females in Ansell's mole-rats from the Lusaka province of Zambia, captured from February 2009 (Colony 1) to February 2010 (Colony 33). * = Colonies recorded with queens having early pregnancies; Abbreviations: PRF = pregnant reproductive females; NPRF = non-pregnant reproductive females; L = lactating; NRF = non-reproductive females; F = foetuses. Age subdivisions are based on body mass (see Material and Methods).

Colony	Total animals	Adults		Subadults		Juveniles		PRF	NPRF	NRF	F	Season	Month
		Female	Male	Female	Male	Female	Male						
1	8	1	1	2	1	3	0	0	1 (L)	0	0	Rainy	February
2	7	1	3	0	1	1	1	0	1 (L)	0	0	Rainy	February
3	7	3	2	0	0	1	1	0	1 (L)	2	0	Rainy	February
4	9	3	2	2	1	1	0	0	1 (L)	2	0	Rainy	March
5	6	1	3	1	0	1	0	0	1 (L)	0	0	Rainy	March
6	8	3	3	1	1	0	0	1	0	2	*	Rainy	March
7	7	3	2	1	0	1	0	1	0	2	*	Rainy	April
8	10	2	2	1	1	2	2	0	1 (L)	1	0	Rainy	April
9	9	4	2	0	0	2	1	1	0	3	*	Dry	April
10	14	3	3	4	1	1	2	0	1 (L)	2	0	Dry	May
11	8	3	2	0	0	2	1	1	1 (L)	1	2	Dry	May
12	10	3	3	1	1	1	1	1	1 (L)	1	3	Dry	June
13	13	4	2	3	0	2	2	1	1 (L)	2	2	Dry	June
14	8	2	3	0	1	2	0	0	1 (L)	1	0	Dry	June
15	8	4	2	1	0	1	0	1	0	3	*	Dry	July
16	16	3	3	7	1	1	1	1	0	2	*	Dry	July
17	8	3	3	1	1	0	0	1	0	2	3	Dry	August
18	9	2	3	0	2	2	0	0	1 (L)	1	0	Dry	August
19	8	2	3	1	0	0	2	1	0	1	*	Dry	September
20	10	3	4	0	0	3	0	0	1 (L)	2	0	Dry	September
21	10	5	3	0	0	2	0	1	0	4	4	Dry	October
22	8	2	3	1	0	2	0	1	0	1	2	Dry	October
23	7	3	3	1	0	0	0	1	0	2	1	Dry	November
24	8	1	3	2	1	1	0	1	0	0	*	Rainy	November
25	9	2	5	1	1	0	0	1	0	1	*	Rainy	December
26	8	1	4	1	1	1	0	0	1 (L)	0	0	Rainy	December
27	11	4	3	2	0	2	0	1	0	3	*	Rainy	December
28	7	3	2	1	0	1	0	1	0	2	3	Rainy	January
29	7	2	2	1	1	1	0	0	1 (L)	1	0	Rainy	January
30	7	1	3	1	0	0	2	0	1 (L)	0	0	Rainy	January
31	8	3	1	2	1	0	1	1	0	2	4	Rainy	February
32	7	4	1	0	0	1	1	0	1 (L)	3	0	Rainy	February
33	8	2	3	2	0	1	0	1	0	1	*	Rainy	February
Total	288	86	87	41	17	39	18	19	17	50			

33 colonies (Colonies 11, 12 & 13; Table 1) were found to contain two breeding females, in each with one pregnant queen whereas the other one was lactating.

It was difficult to identify individual foetuses from 10 of the pregnant queens dissected in the field because these females were in the early stages of pregnancy. However, the average litter size determined from the nine queens where the foetuses could be counted was 2.7 pups (range 1–4).

DISCUSSION

This study represents the first extensive field-based assessment of colony size and reproduction in *F. anselii*. The mean social group size of 8.7 animals is similar to that reported for another Zambian mole-rat, *F. mechowii*, where a mean of 10 animals (range 6–16) was reported from a study of 32 colonies (Sichilima *et al.* 2008a). The colony sizes of *F. anselii* from this study, and those for *F. mechowii* reported by Sichilima *et al.* (2008a), do not support the suggestion that social groups of *Fukomys* in Zambia may reach large sizes (e.g. 40–60 animals for *F. mechowii*; Burda & Kawalika 1993).

Many previous studies on *Fukomys* species from Zambia have either been based on small sample sizes of free-living colonies, or from colonies maintained in the laboratory (Burda & Kawalika 1993; Bennett & Aguilar 1995; Scharff *et al.* 1999, 2001). Our field data supports laboratory findings that *Fukomys* species studied to date (*F. anselii* (Burda 1989); *F. damarensis* (Bennett & Jarvis 1988; Bennett & Faulkes 2000); *F. darling* (Bennett *et al.* 1994)) are aseasonal breeders with pups being born throughout the year. It is, however, noteworthy that within the more southerly occurring genus of *Cryptomys*, reproduction appears to be strictly seasonal, e.g. *Cryptomys h. hottentotus* (Spinks *et al.* 1997, 1999) and *Cryptomys h. pretoriae* (Janse van Rensburg *et al.* 2002).

The small litter sizes (2–4 pups) produced by *F. anselii* are similar to those reported by other species of Afrotropical *Fukomys* (Bennett & Jarvis 1988; Burda 1989; Bennett *et al.* 1994; Bennett & Aguilar 1995; Scharff *et al.* 2001), as well as southern African *Cryptomys* (Bennett 1989; Malherbe *et al.* 2004; Oosthuizen *et al.* 2007). These litter sizes tend to be smaller than the solitary species of South African mole-rats, e.g. *Bathyergus janetta* and *Georychus capensis* in which the litter size ranges from, 1–7, and 4–10, respectively (Bennett *et al.* 1991; Bennett & Faulkes 2000).

The skew of sex ratio towards females in the

colonies of *F. anselii* in this study is also similar to that reported for *F. mechowii* (Scharff *et al.* 2001; Sichilima *et al.* 2008a), but differs from those of *F. damarensis*, *C. h. hottentotus* populations in mesic habitats and the divergent naked mole-rat (*Heterocephalus glaber*), in which adult sex ratios are skewed towards males (Bennett & Faulkes 2000).

In all the social bathyergid genera (*Cryptomys*, *Fukomys* and *Heterocephalus*) there is a marked reproductive skew where breeding is almost always restricted to a single reproductive female and one or a few male consorts (Bennett & Jarvis 1988; Burda 1989; Braude 1991; Bennett *et al.* 1994; Bennett & Aguilar 1995; Bennett & Faulkes 2000; Scharff *et al.* 2001). The findings of this study are similar to that on *F. mechowii* (Sichilima *et al.* 2008a) in identifying examples of plural breeding among females in wild – three of the 33 *F. anselii* colonies had evidence of two queens actively breeding compared with four out of 32 for *F. mechowii*. This observation is not common in the social bathyergid species studied to date. In an extensive four-year mark–release–recapture study of *C. h. hottentotus*, 49 colonies surveyed at two geographic locations were found to always contain a single reproductive female (Spinks *et al.* 2000). Many other small studies have also not yielded more than one reproductive female per colony (e.g. Bennett 1989). However, there has been one case of plural breeding recorded out of 30 colonies of *C. h. hottentotus* captured at Somerset West, South Africa, over a two-year period (N.C. Bennett, unpubl. data). Plural breeding in naked mole-rats was recorded in two instances by Braude (1991), out of a total of 2051 naked mole-rats from 23 colonies in Meru National Park, Kenya.

The small colony sizes and presence of plural breeding in both *F. anselii* and *F. mechowii* is consistent with the predictions of the aridity food distribution hypothesis for social species inhabiting mesic habitats, and suggests reduced philopatry and higher colony turnover than in species inhabiting more arid regions, e.g. the Damaraland mole-rat, *F. damarensis* (Jarvis & Bennett 1993). In mesic habitats, the constraints on successful dispersal are reduced because dampened soil is easier to dig. Furthermore, food resources (in the form of underground roots and tubers) are more easily located by single individuals or small groups due to a more uniform distribution (Jarvis & Bennett 1993; Jarvis *et al.* 1994). These factors facilitate the movement of individuals among social groups to occur, and the possibility of unre-

lated individuals with which to mate. Plural breeding is not likely to occur in a monogamous family unit with overlapping generations as *F. anelli*, like others of the genus *Fukomys*, avoid incestuous matings (Burda 1995; however, incestuous mating has been observed in a single captive colony of *F. mechowii* (J.U.M. Jarvis, pers. comm.)). In terms of reproductive skew among male *F. anelli*, the incidence of multi-male matings and extra-colony copulations are at present unknown but seem likely to occur, given the precedence in both *Fukomys* and *Cryptomys*. For example, a genetic study of *C. h. hottentotus* by Bishop *et al.* (2004) has shown that not only are several males achieving intra- and extra-colony paternities, but that non-breeding females may often be in contact with unrelated males. Similarly, Burland *et al.* (2004), found that multiple and unidentified paternity was widespread within arid dwelling *F. damarensis* colonies and immigrants of both sexes were regularly identified. Opposite-sex non-breeding animals were also present at the same time in some colonies.

Further research using mark-recapture studies and molecular genetic techniques on long-term marked populations of *F. anelli* is now required to further unlock the life history and social habits of this little studied central African mole-rat.

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REFERENCES

- ARNDT, H. & BURDA, H. 1992. Maintenance of the social structure in mole-rats, *Cryptomys* sp., from Zambia (Bathyergidae: Rodentia). *Zeitschrift für Säugetierkunde Supplement* 57: S. 6.
- BARNETT, M., BENNETT, N.C., TELFORD, S.R. & JARVIS, J.U.M. 2003. Foraging in the subterranean social Damaraland mole-rat, *Cryptomys damarensis*: an investigation into size dependent geophyte utilization and foraging patterns. *Canadian Journal of Zoology* 81: 743–752.
- BENNETT, N.C. 1989. The social structure and reproductive biology of the common mole-rat, *Cryptomys hottentotus* and remarks on the trends in reproduction and sociality in the family Bathyergidae. *Journal of Zoology, London* 219: 45–59.
- BENNETT, N.C. & AGUILAR, G.H. 1995. The reproductive biology of the giant Zambian mole-rat, *Cryptomys mechowii* (Rodentia, Bathyergidae). *South African Journal of Zoology* 30: 1–4.
- BENNETT, N.C. & JARVIS, J.U.M. 1988. The social structure and reproductive biology of colonies of the mole-rat *Cryptomys damarensis* (Rodentia: Bathyergidae). *Journal of Mammalogy* 69: 293–302.
- BENNETT, N.C., JARVIS, J.U.M. & McDAID, E.J. 1991. Growth and development in six species of African mole-rats (Rodentia; Bathyergidae). *Journal of Zoology, London* 225: 13–26.
- BENNETT, N.C. & FAULKES, C.G. 2000. *African Mole-rats: Ecology and Eusociality*. Cambridge University Press, Cambridge, U.K.
- BENNETT, N.C., JARVIS, J.U.M. & COTTERILL, F.P.D. 1994. The colony structure and reproductive biology of the Afrotropical Mashona mole-rat, *Cryptomys darlingi*. *Journal of Zoology, London* 234: 477–487.
- BISHOP, J.M., JARVIS, J.U.M., SPINKS, A.C., BENNETT, N.C. & O'RYAN, C. 2004. Molecular insight into patterns of colony composition and paternity in the common mole-rat *Cryptomys hottentotus hottentotus*. *Molecular Ecology* 13: 1217–1229.
- BURDA, H. 1989. Relationships among rodent taxa as indicated by reproductive biology. *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 27: 49–57.
- BURDA, H. 1992. Evolution of sociality in African mole-rats (Bathyergidae). *Zeitschrift für Säugetierkunde Supplement* 57: S. 10–11.
- BURDA, H. & KAWALIKA, M. 1993. Evolution of eusociality in the Bathyergidae: the case of the giant mole-rats (*Cryptomys mechowii*). *Naturwissenschaften* 80: 235–237.
- BURDA, H., ZIMA, J., SCHARFF, A., MACHOLAN, M. & KAWALIKA, M. 1999. The karyotypes of *Cryptomys anelli* sp. nova and *Cryptomys kafuensis* sp. nova: new species of the common mole-rat from Zambia (Rodentia: Bathyergidae). *Zeitschrift für Säugetierkunde* 64: 36–50.
- BURDA, H. 1995. Individual recognition and incest avoidance in eusocial common mole-rats rather than reproductive suppression by parents. *Experientia* 51: 411–413.
- BURLAND, T.M., BENNETT, N.C., JARVIS, J.U.M. & FAULKES, C.G. 2004. Colony structure and parentage in wild colonies of co-operatively breeding Damaraland mole-rats suggests a role for reproductive suppression. *Molecular Ecology* 13: 2371–2379.
- BRAUDE, S. 1991. The behaviour and demographics of the naked mole-rat, *Heterocephalus glaber*. Ph.D. thesis, University of Michigan, Ann Arbor, U.S.A.
- COTTERILL, F.P.D. 2002. Notes on mammal collections and biodiversity conservation in the Ikelenge Pedicle, Mwinilunga district, northwest Zambia. *Occasional Publications in Biodiversity* 10.
- DE VRIES, L., OOSTHUIZEN, M.K., SICHILIMA, A.M. & BENNETT, N.C. 2008. Circadian rhythms of locomotor activity in Ansell's mole-rat: are mole-rats' clocks ticking? *Journal of Zoology, London* 276: 343–349.
- FAULKES, C.G., BENNETT, N.C., BRUFORD, M.,

- AGUILAR, G.H., O'BRIEN, H. & JARVIS, J.U.M. 1997. Ecological constraints drive social evolution in the African mole-rats. *Proceedings of the Royal Society Series B* **264**: 1619–1627.
- FAULKES, C.G. & BENNETT, N.C. 2007. African mole-rats: behavioral and ecological diversity. In: *Rodent Societies: An Ecological and Evolutionary Perspective*, eds J. Wolff & P.W. Sherman, pp. 427–437. University of Chicago Press, Chicago.
- FAULKES, C.G. & BENNETT, N.C. 2009. Reproductive skew in African mole-rats: behavioural and physiological mechanisms to maintain high skew. In: *Reproductive Skew in Vertebrates: Proximate and Ultimate Causes*, (eds) R. Hager & C.B. Jones, pp. 369–396. Cambridge University Press, Cambridge.
- GANNON, W.L. & SIKES, R.S. & ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* **88**: 809–823.
- JANSE VAN RENSBURG, L., BENNETT, N.C., VAN DER MERWE, M. & SCHOEMAN, A.S. 2002. Seasonal reproduction in the highveld mole-rat, *Cryptomys hottentotus pretoriae* (Rodentia: Bathyergidae). *Canadian Journal of Zoology* **80**: 810–820.
- JARVIS, J.U.M. & BENNETT, N.C. 1993. Eusociality has evolved independently in two genera of bathyergid mole-rats – but occurs in no other subterranean mammal. *Behavioral Ecology and Sociobiology* **33**: 353–360.
- JARVIS, J.U.M., O'RIAIN, M.J., BENNETT, N.C. & SHERMAN, P.W. 1994. Mammalian eusociality: a family affair. *Trends in Ecology and Evolution* **9**: 47–51.
- KAWALIKA, M. & BURDA, H. 2007. Giant mole-rats, *Fukomys mechowii*, thirteen years on the stage. In: *Subterranean Rodents – News from Underground*, (eds) S. Begall, H. Burda & C. Schleich, pp. 205–219. Springer, Heidelberg.
- KAWALIKA, M., BURDA, H. & BRUGGERT, D. 2001. Was Zambia a cradle of the genus *Cryptomys* (Bathyergidae: Rodentia)? A further new ancestral species of *Cryptomys* from Zambia. In: *African Small Mammals*, (eds) C. Denys, L. Granjon & A. Poulet, pp. 253–261. IRD Editions, Collections Colloques et séminaires, Paris.
- MALHERBE, G., BENNETT, N.C. & SCHOEMAN, A.S. 2004. The reproductive biology and postnatal development of the highveld mole-rat, *Cryptomys hottentotus pretoriae* (Rodentia: Bathyergidae). *African Zoology* **38**: 161–167.
- OOSTHUIZEN, M.K. & BENNETT, N.C. 2007. LH responses to single doses of exogenous GnRH in the Cape mole-rat, *Georychus capensis*: the pituitary potential for opportunistic breeding. *Journal of Zoology, London* **271**: 196–202.
- SCHARFE, A., BEGALL, S., GRUTJEN, O. & BURDA, H. 1999. Reproductive characteristics and growth of Zambian giant mole-rats, *Cryptomys mechowii* (Rodentia: Bathyergidae). *Mammalia* **63**: 217–230.
- SCHARFE, A., LOCKER-GRUTJEN, O., KAWALIKA, M. & BURDA, H. 2001. Natural history of the giant mole-rat, *Cryptomys mechowii* (Rodentia: Bathyergidae), from Zambia. *Journal of Mammalogy* **82**: 1003–1005.
- SICHILIMA, A.M., ZULU, M.S. & LEIRS, H. 2002. The effects of *Tephrosia vogelii* and land preparation methods on mole-rat activity in cassava fields. In: *Rats, Mice and People: Rodent Biology and Management*, (ed.) J.S.M. Krebs, pp. 254–255. Australian Centre for International Agricultural Research, Canberra.
- SICHILIMA, A.M., FAULKES, C.G. & BENNETT, N.C. 2008a. Field evidence for aseasonality of reproduction and colony size in the Afrotropical giant mole-rat *Fukomys mechowii* (Rodentia: Bathyergidae). *African Zoology* **43**: 144–149.
- SICHILIMA, A.M., BENNETT, N.C., FAULKES, C.G. & LE COMBER, S.C. 2008b. Evolution of African mole-rat sociality: burrow architecture, rainfall and foraging in colonies of the cooperatively breeding *Fukomys mechowii*. *Journal of Zoology, London* **275**: 276–282.
- SPINKS, A.C., VAN DER HORST, G. & BENNETT, N.C. 1997. Influence of breeding season and reproductive status on male reproductive characteristics in the common mole-rat, *Cryptomys hottentotus hottentotus*. *Journal of Reproduction and Fertility* **109**: 78–86.
- SPINKS, A.C., BENNETT, N.C. & JARVIS, J.U.M. 1999. Regulation of reproduction in female common mole-rats, *Cryptomys hottentotus hottentotus*, the effects of breeding season and reproductive status. *Journal of Zoology, London* **248**: 161–168.
- SPINKS, A.C., BENNETT, N.C. & JARVIS, J.U.M. 2000. A comparison of the ecology of two populations of the common mole-rat, *Cryptomys hottentotus hottentotus*: the effect of aridity on food, foraging and body mass. *Oecologia* **125**: 341–349.
- VAN DAELE, P.A.A.G., DAMMANN, P., MEIER, J.L., KAWALIKA, M., VAN DE WOESTIJNE, C., BURDA, H. 2004. Chromosomal diversity in mole-rats of the genus *Cryptomys* (Rodentia: Bathyergidae) from the Zambezi region: with descriptions of new karyotypes. *Journal of Zoology, London* **264**: 317–326.
- VAN DAELE, P.A.A.G., VERHEYEN, E., BRUNAIN, M., ADRIAENS, D. 2007a. Cytochrome *b* sequence analysis reveals differential molecular evolution in African mole rats of the chromosomally hyperdiverse genus *Fukomys* (Bathyergidae, Rodentia) from the Zambezi region. *Molecular Phylogenetics and Evolution* **45**: 142–157.
- VAN DAELE, P.A.A.G., FAULKES, C.G., VERHEYEN, E., ADRIAENS, D. 2007b. African mole-rats (Bathyergidae): a complex radiation in Afrotropical soils. In: *Subterranean Rodents – News from Underground*, (eds) S. Begall, H. Burda & C. Schleich, pp. 357–373. Springer, Heidelberg.