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

By

Alfred Matafwali Sichilima

Submitted in partial fulfillment of the requirements for the degree of

Doctor of Zoology in the Faculty of Natural and Agricultural Sciences

University of Pretoria

Pretoria

September 2008

Study leaders: Professor Nigel C. Bennett

Dr. Chris G. Faulkes

TABLE OF CONTENTS

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

Beyond every suitable word for which one can express thanks, I am greatly indebted to my supervisor, Prof. Nigel C. Bennett for his patience, understanding, generosity, overwhelming foresight, his long hours spent with me on all chapters of my study and the confidence he had in me. Prof. Christian T. Chimimba is mostly appreciated for his constructive criticism and the tangible guidance in the Cranial chapter of my thesis. I express my appreciation to Prof. A. E. (Braam) van Wyk, of the H.G.W.J. Schweickerdt Herbarium, Department of Botany at the University of Pretoria for identifying the geophytes. Dr Kenneth Joubert, BVSc is thanked for performing the vasectomies. I am also grateful to the Director of Mammal Research Institute (MRI), Prof. Elissa Cameron for having been considerate in making my study environment cordial and access-free to ideal study aids. I am thankful to Prof. Philip W. Bateman for encouragement and for providing morale and material support during the period of my study. I also thank James van Sandwyk, the lab technician and Leanne Hart for providing some worthwhile technical insights on some chapters of my study. The IT specialist Human Buirski and the Technical Assistant Babsie Potgieter are mostly acknowledged for having been available to me during my times of need. I am thankful to Dr. Eitimad Rahman for both moral and technical support where it was due. I am further extending my appreciation to Allan Hall of the Microscopy Department for providing the prudent help that I needed to work on my images. There may be no study environment as still as water and that the list may be too long to mention by name but I sincerely thank everybody in the Department of Zoology and Entomology from the Departmental Head, Prof. Sue Nicolson to all technical and administrative staff who may have morally or technically rendered a specific assistance to me during my study period. Finally, I thank the Animal Use and Care Committee of the University of Pretoria for having approved my research on permit number AUCC 060504-011.

Queen Mary University of London, UK

I express my sincere appreciation to Dr. Chris G. Faulkes, my co-supervisor in my study for having been instrumental and creative and for providing invaluable contributions towards my study. Dr. Steve C. Le Comber is mostly thanked for providing a rare and unique skill to my study which unlocked and elaborated important conclusions.

The National Foundation Research (NRF) and University of Pretoria are thanked for providing bursaries towards my study. Again, my appreciation is further extended to the

DST and NRF for providing a "South African Research Chairs Initiative (SARChI)", entitled "Mammal behavioural ecology and Physiology" to Prof. Nigel C. Bennett, without which my studies would not have been accomplished.

I would like to thank my beloved parents for their constant support and care during my basic education and for understanding during my long absence.

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)"

List of figures

List of Tables