

THE KALAHARI RESEARCH CENTRE



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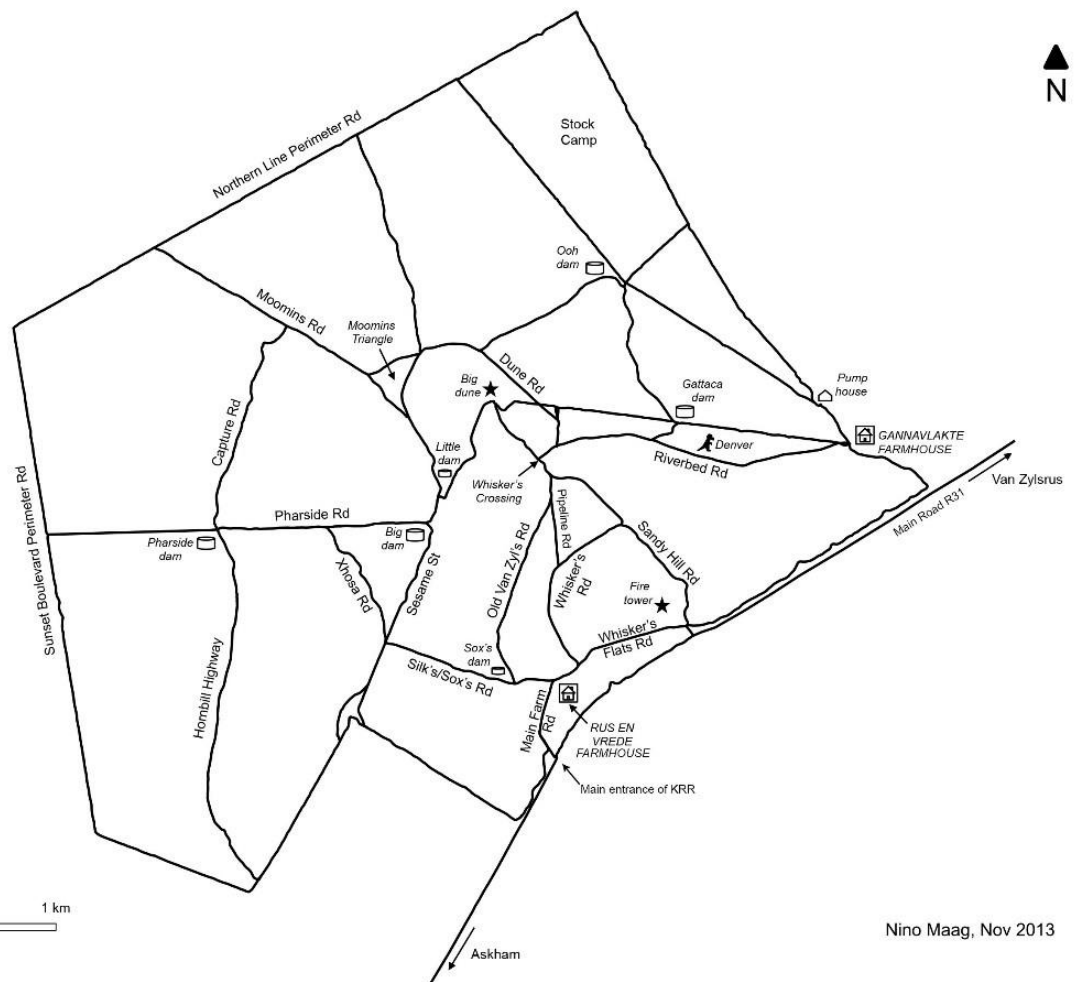
WHERE ARE WE?



Our study site is close to Van Zylsrus in the Northern Cape of South Africa in the southern Kalahari. Unlike the Sahara, the Kalahari is an ancient desert and has probably been arid for at least 20 million years. As a result, many of the species that live there show adaptations to dry, unpredictable conditions where variation in rainfall leads to large fluctuations in food availability.

ORGANISATION OF THE KALAHARI RESEARCH CENTRE

The Kuruman River Reserve (KRR) is an ex-ranch of 3,500Ha purchased in 2001 by the Kalahari Research Trust as a base for scientific research on meerkats, mole-rats and other indigenous species.



The Kalahari Research Trust (KRT) is a not-for-profit trust, based in South Africa established by Tim Clutton-Brock in 2001 to own the Kuruman River Reserve and maintain the Kalahari Research Centre. The KRT currently has three trustees (Tim Clutton-Brock, Cambridge; Marta Manser, Zurich; Mike Cherry, Stellenbosch).

Tim Clutton-Brock has been its Secretary since its establishment in 2001, while Marta Manser took over this role in March 2017. The KRT is supported by the research fees it charges resident scientists, grants from a Swiss foundation and some income from filming. It employs most of the South African staff working at the site.

The Kalahari Research Centre (KRC)<<http://kalahari-meerkats.com/kmp/>> consists of the KRR and the facilities it provides – including accommodation for up to fifty scientists, students and assistants; the mole-rat colony and associated laboratory; vehicles, radios and computing facilities. The KRT is associated with the Mammal Research Institute of the University of Pretoria.



The Kalahari has an unpredictable climate. Annual rainfall is between 100 and 400ml. Rain falls mostly between December and March. There is a cold dry season between May and August. In dry years the ground has very little vegetation cover while in wet years the grass is waist high.

RESEARCH AT THE KALAHARI RESEARCH CENTRE

Kalahari Meerkat Project

The Kalahari Meerkat Project (KMP) is the longest running project based at the site and has been running since 1993. The principal aim of the project is to investigate the evolution of cooperative breeding and its ecological consequences – though our work has several ancillary aims, including investigation of the mechanisms controlling reproduction and



Photo credit D. Cram

ageing rates; vocal and olfactory communication between group members; the dynamics of groups and their influence on population regulation; the causes and consequences of variation in immune responses; the role of TB in limiting numbers; and the consequences of short and medium-term variation in climate.

The KMP maintains 10-15 habituated groups of meerkats (usually 200-300 animals) all of which are marked and chipped so that they can be recognized as individuals. Most individuals have been genotyped. In the course of the project, we have monitored the life histories from birth to death of over 3000 individual meerkats, providing the most detailed and extensive record of individual variation in development, behaviour and breeding success available for any wild animal. Almost all individuals can be weighed repeatedly and we have built a multi-generational pedigree that can be used to assess the heritability of growth, behaviour, breeding success and ageing rates. Blood and faecal samples are collected from recognizable individuals and are used to provide hormonal profiles for individuals. Our data are stored in a customized SQL database and are accessed by members of the project and by our collaborators based at Cambridge, London, Liverpool, Zurich, Duke, Stellenbosch, Cape Town and Pretoria. A list of recent publication is attached. The KMP is funded by grants to Tim Clutton-Brock from the ERC and to Marta Manser from Swiss National Fonds. The KMP is run jointly by Tim Clutton-Brock and Marta Manser.

Damaraland Mole-rat Project

Since its start in 2012, the Damaraland mole-rat project has investigated the physiological mechanisms controlling reproductive suppression, cooperative behaviour and aging as well as the social organisation of natural colonies. We monitor membership of 20-30 wild groups (approximately 200-250 animals) trapping, marking, measuring and sampling their members each year. In addition we have established a breeding facility on site that houses 50-70 breeding colonies in plastic tube systems, providing opportunities to manipulate growth, breeding experience and group membership, and to explore the consequences of these experiments on breeding success and longevity. The mole-rat project is run by Tim Clutton-Brock, P Vulliod and M Zöttl and is currently supported by Tim Clutton-Brock's ERC grant.



Photo credit K. Finn

Cape Ground Squirrel Project

10 colonies of Cape ground squirrels have been habituated and their members monitored since 2010. As yet, the main focus of the project has been on communication, but we shall shortly begin work on life history variation and population dynamics. The Cape ground squirrel project is run by Marta Manser.



H. Villar/A. González

Pied babbler research project

Pied babblers live in groups whose structure is similar to that of meerkats and mole-rats. Research on their reproductive strategies, development and life histories has been running since 2005, directed by Amanda Ridley (University of Western Australia). It also currently involves Susan Cunningham (UCT).



Photo credit: T. Flower

Ungulate research projects

Work in progress is investigating the effects on variation in physiology, growth, breeding success and survival in the ungulates living on the reserve.



Other research projects

Other projects at the site have investigated vocal mimicry in drongos (T. Flower, Capilano University, Canada), incubation and temperature regulation in hornbills (T van de Ven, Cape Town) and temperature regulation in ungulates (A Fuller, Witwatersrand). In addition, our study site offers opportunities for research of wide range of smaller vertebrates, insects and plants found in arid habitats.



Photo credit: T. Flower

PI's and STAFF



Prof Tim Clutton-Brock



Prof Marta Manser
Secretary of the Kalahari
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Research manager



Tim Vink
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Database manager



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Jacob Brown
Volunteer manager



Dr Markus Zöttl
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Mole-rat postdoc



Dr Philippe Vullioud
Mole-rat research manager,
Mole-rat Postdoc



Dr Tanja van de Ven
Meerkat postdoc,
Guest reservations

A BRIEF INTRODUCTION TO COOPERATIVE BREEDING

In most animals, all adult females are fertile and either mate promiscuously or have polygynous mating systems (where one male breeds with several females) or monogamous ones (where one male breeds with a single female). However, in a minority of species, a single female monopolizes reproduction in each group, usually breeding with a single male, and other group members are prevented from breeding and spend part or all of their lives rearing young produced by the breeding female in their group. Systems of this kind are common among bees, wasps, ants and termites and are also found in a number of birds (including pied babbblers) and some mammals (including meerkats and mole-rats). Insects that breed in this way are usually referred to as being 'eusocial' while birds and mammals with breeding systems of this kind are referred to as 'singular cooperative breeders'. Both in birds and in mammals, singular cooperative breeders are commonly associated with arid unpredictable environments.

Since the process of natural selection favours traits associated with individual breeding success and survival, the evolution of cooperative breeding systems (where many individuals do not breed themselves and spend their lives assisting in the breeding attempts of others) presents a challenge to evolutionary biologists – as Darwin himself recognised. As a result, cooperative breeders have been a focus of research by zoologists over the last 30 years.

The central question that needs answering is why helpers do not breed themselves and, instead, help other individuals to breed. The general answer here is that helpers are usually prevented from breeding by the most dominant female who commonly suppresses their development, kills their young and evicts them if they repeatedly attempt to breed. Helpers are usually closely related to breeders and the juveniles they are rearing and so can propagate their genes by assisting related breeders. Since the dominant female and the dominant male are the parents of most young born in the group, helpers are usually rearing full sibs ($r = 0.5$) which are as closely related to them as their own offspring.

Both cooperative mammals and eusocial insects have a number of unusual traits including:

- Temporary or permanent sterility in females other than the breeding female or queen
- Extensive and costly forms of cooperation
- In some mammals, flexible patterns of growth and development that are adjusted to variation in social conditions, including the capacity to restart growth in adulthood.
- Longer lifespans in breeding females than in helpers. This has been interpreted as evidence that breeding extends the lifespan of individuals. However a more likely explanation is that dominant breeders only tolerate the presence of helpers that have not yet reached adult size.
- Unusually high variation in breeding success in females, who can rear large number of offspring per year.
- Intense competition for breeding opportunities between females who are more frequently aggressive than males
- Equal levels of testosterone in adults of the two sexes and greater suppression of immune function in breeding females than in breeding males.
- Positive correlations between population density and breeding success/survival as a result of the effects of helper number on productivity.

A BRIEF INTRODUCTION TO MEERKATS



Niche

Meerkats are diurnal, desert-adapted mongooses found in sandy areas of Southern Africa. They live on insects and their larvae and small vertebrates they find in the sand.

Groups

Like other diurnal mongooses, meerkats are social and live in stable groups of 2-50 + that consist of a monogamous breeding pair and a variable number of non-breeding helpers of both sexes. In meerkats, groups defend territories of 3-5km² against neighbouring groups, sleeping in different sites on successive nights. Relationships between neighbouring groups are hostile and intruders can be killed. In addition, groups go on raids into each other's territories and kill their neighbour's pups if they find breeding burrows.

In meerkats, resident females (including breeders) have mostly been born in the same group they breed in. Older female helpers are evicted from breeding groups by resident females when they are 3-4 years old and then either form a new group or die. Breeding females can live for 12 years, producing up to 100 surviving offspring during their lives while breeding males have shorter lifespans. Following the death of a dominant female, resident subordinate females compete intensively for the dominant position and the heaviest individual wins.

Unlike breeding females, dominant breeding males are almost always immigrants from other groups. When they are 3-4 years old, natal males start visiting other groups and searching for evicted females. When they find a breeding group whose

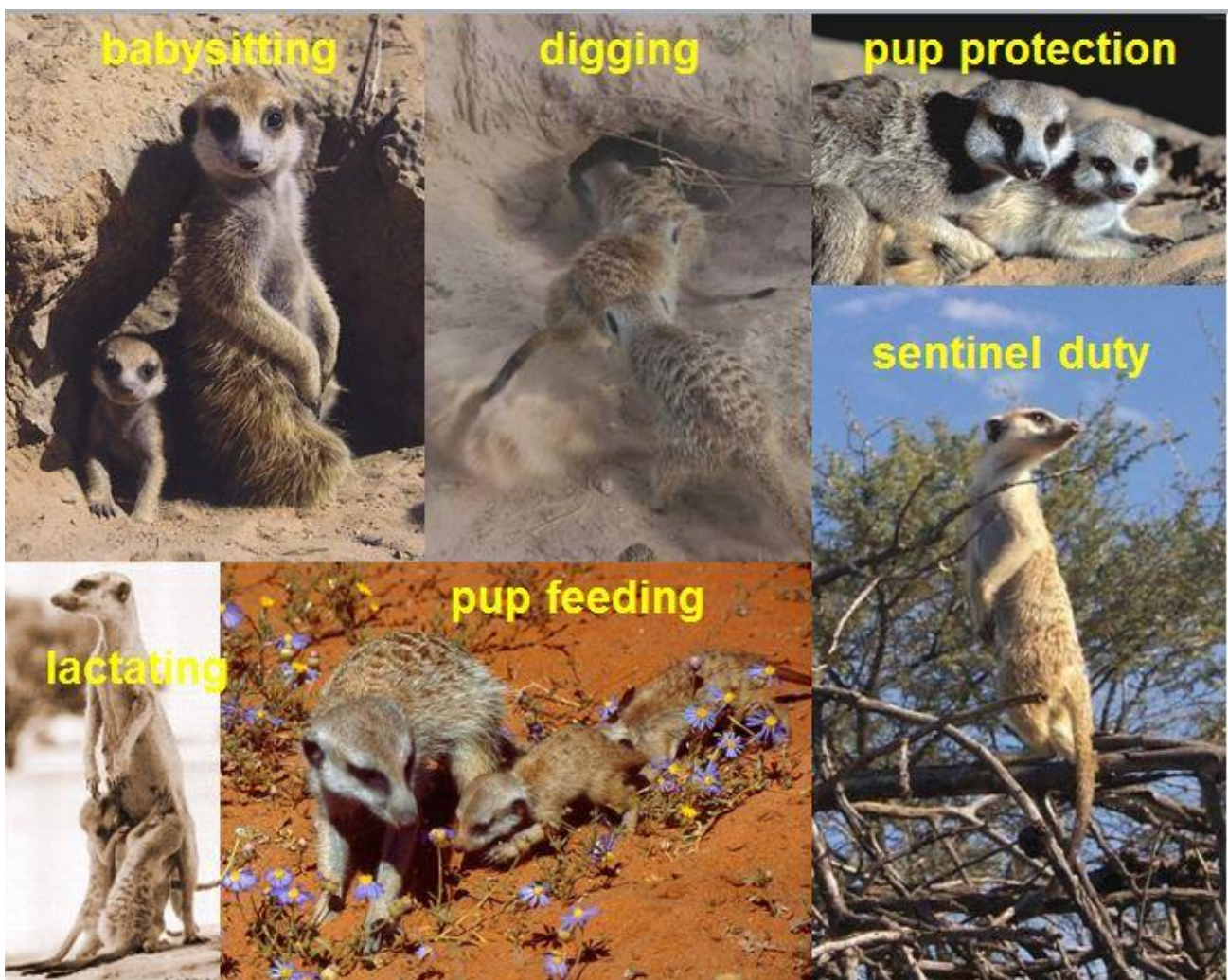
breeding males have died or several evicted breeding females they commonly join them. However the failure rate of new groups is high.

Predators and parasites

Approximately one in four adults die each year. Meerkats are regularly taken by raptors (especial martial eagles), jackals, wildcats and snakes. In addition dispersing individuals are often killed by resident groups. They also suffer from a meerkat specific TB.

Reproduction and longevity

A single dominant female and a single dominant male are the parents of most juveniles born in each group. As in many other social mammals, breeding females avoid mating with related males. Dominant females commonly rear 3 litters of two to seven pups during each breeding season (Aug to April). In natural populations, both sexes can live up to 12 years though many die before this. Dominant females retard the sexual development of subordinate females and often kill their pups if they attempt to breed. They usually evict subordinate females once they are over three years old. Less than 25% of females that reach adolescence ever breed successfully.



Cooperation

Pups born to dominant breeders are guarded and fed by non-breeding helpers of both sexes as well as by the breeding pair. Non-breeding subordinate females also commonly suckle pups. Helpers also teach pups how to handle dangerous prey, like scorpions and contribute to acting as sentinels when the group is foraging and to digging sleeping burrows and boltholes.

Sex differences

Males and females are of similar weight and size. This is partly because they are older but when they acquire breeding roles, they show a 2-3 month period of accelerated growth that helps to establish them as the heaviest animals in their group. In contrast to most other animals, breeding females have testosterone levels similar to those of males and are usually more aggressive than males and dominant to them.

A BRIEF INTRODUCTION TO MOLE-RATS

Niche

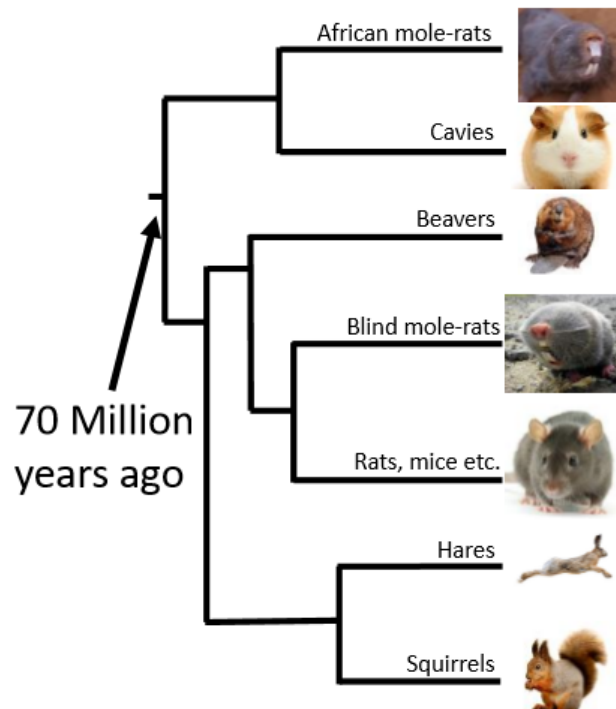
Mole-rats are burrow living-rodents that live and feed underground on the nutritious tubers of plants. They are almost entirely blind and rely on acute olfactory and auditory senses. They are active throughout the 24 hours.



Taxonomy

The African mole-rats (which include the naked mole-rat and the Damaraland mole-rat) are related to the porcupines and cavies.

There are 33 known species of African mole-rats (and probably more undiscovered species). There are three groups of solitary species and two groups of social species: the “common mole-rats”, including the Damaraland mole-rats of the Kalahari, and the naked mole-rat (a single species) which is more distantly related and is found in the horn of Africa.



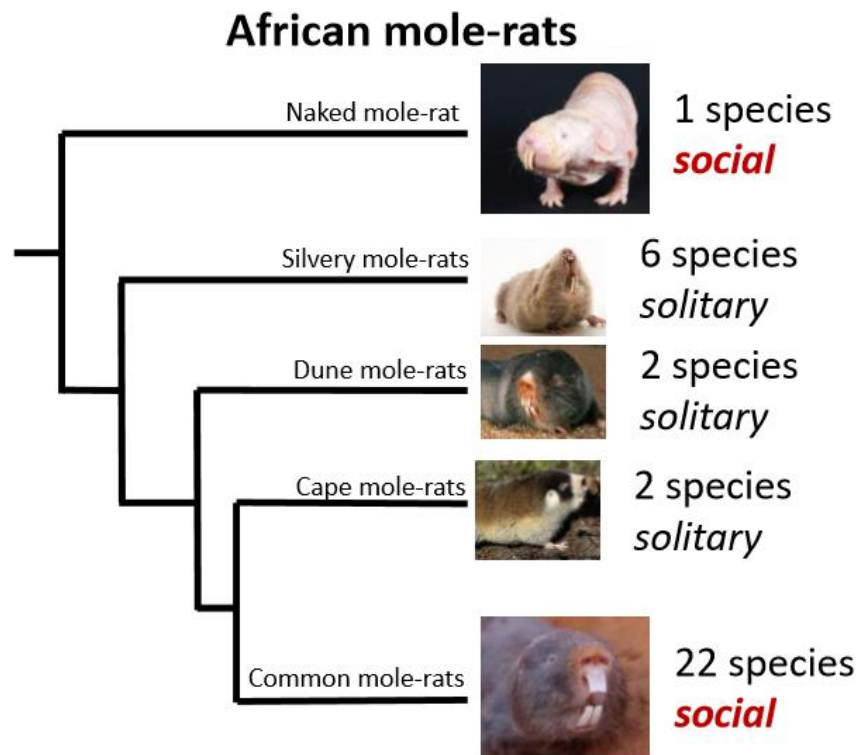
The African mole-rats are most closely related to the South American cavies and are only very distantly related to blind mole-rats (Spalax), sharing an ancestor with them 70 million years ago.

Groups

Colonies of social mole-rats (like those of meerkats) usually include a single breeding female, one or more breeding males that are usually immigrants and a variable number of non-breeders that help to maintain the extensive burrow systems necessary to get access to the tubers they feed on. The largest colonies are found in naked mole-rats and can number over 100 group members. While Damaraland mole-rats usually live in colonies of 5 to 30. In naked mole-rats the presence of the “queen” appears to be sufficient to prevent breeding in subordinates in both sexes.

Predators and parasites

Since they feed underground the African mole-rats are relatively safe from predators which probably explains why they are relatively long-lived. They are not known to suffer from TB and both naked mole-rats and Damaraland mole-rats seldom appear to get cancer. Though cancer has now been reported in both species.



African mole-rats include several closely related social and solitary species.

Reproduction and longevity

Dominant female naked mole-rats (queens) can produce 3 to 4 litters of up to 15 pups per year. While female Damaraland mole-rats also produce 3-4 litters a year but litter size is substantially smaller (2 to 6 pups).

Little is known about the breeding success of males in natural populations of mole-rats. In captive groups of naked mole-rats, a single male may monopolize breeding while in Damaraland mole-rats several males may breed.

In naked mole-rats it was initially thought that individuals frequently bred with close individuals and immigration was uncommon. However, this is now uncertain and there is evidence that both sexes preferentially breed with non-relatives. In Damaraland mole-rats, females avoid breeding with related males and the arrival of a new male generates competition between resident females.

Little is known of longevity in adults in natural populations in any species. In captivity, breeding female naked mole-rats can live up to 30 years and possibly longer while males have shorter lifespans. Damaraland mole-rats are also relatively long-lived but individuals have not yet been kept for as long as naked mole-rats. Naked mole-rats have rarely been observed to get cancers though relatively few older individuals have been monitored. They also show a number of unusual characteristics, including resistance to hypoxia and unusually stable cell wall structure and composition. The extent to which other mole-rats show the same traits is still uncertain.

An important limitation of all studies of captive mole-rats to date is that they have been carried out on the descendants of three original groups. As a result, all existing naked mole-rat groups are heavily inbred – which may have important consequences for their biology, breeding success and longevity.

Cooperation

Both in naked mole-rats and Damaraland mole-rats, all groups members contribute to the maintenance of the tunnel system and defense of colonies. Non-breeding subordinates also groom and retrieve young but do not feed them. It was previously thought that different castes of subordinates are responsible for different tasks but recent analyses show that this is not the case - though the contribution of different individuals to all cooperative activities varies with age.

Sex differences

In naked mole-rats, dominant breeding females are larger than all other members including breeding males. In contrast, in Damaraland mole-rats, the dominant male is usually the largest animal in the group. Like meerkats, mole-rats have unusually flexible growth and adults that attain dominant status may show a period of rapid growth. These changes in weight and size are associated with an elongation of body shape which is thought to increase the capacity of adult females to gestate large litters. As in meerkats, dominant breeding females have unusually high levels of testosterone.

Helpers retrieve and groom pups but do not show the same complexity of cooperative behaviour as meerkats. Non-breeders (especially older females) are commonly evicted from breeding groups but it is not clear who is usually responsible for this.

Unusual characteristics

- Fertility in non-breeding female helpers appears to be more deeply suppressed than in meerkats.
- As in meerkats, growth is unusually flexible and can be resumed when individuals acquire breeding positions.
- In Damaraland mole-rats, males are larger than females while in naked mole-rats the dominant breeding female (the queen) is usually the largest animal in the group.
- Breeding females have unusually high levels of testosterone and are dominant to all other group members.
- In naked mole-rats, breeding females can live for 30 plus years in captivity. It has recently been claimed that they can live indefinitely but the evidence for this is dubious. Little is known of their longevity in natural populations. Breeding females in Damaraland mole-rats also have protracted lifespans but individuals have not yet been maintained for such long periods in captivity so that their longevity is uncertain.
- Naked mole-rats have rarely been observed to get cancers - though relatively few older individuals have been monitored. They also show a number of unusual characteristics, including resistance to hypoxia and unusually stable cell wall structure and composition. The extent to which other mole-rats show the same traits is still uncertain.



At the KRC we have established a breeding facility for Damaraland mole-rats that houses 50 to 60 colonies in pvc tube systems. In addition we monitor membership of 60 wild colonies.

A BRIEF INTRODUCTION TO THE EVOLUTION OF LONGEVITY

Animals are vehicles 'designed' by natural selection to maximize the replication of the genes they carry. Their bodies, lives and behaviour are adjusted to maximising the total number of surviving progeny that individuals produce in their lives under the conditions that the species encounters. They are not adapted to maximising the survival of their species or its overall productivity – though in some cases their attributes may affect this.

To maximise their lifetime breeding success, individuals need to survive and to breed as rapidly as possible and for as long as possible. However, breeding typically has costs which reduce survival and longevity while the development of bodies capable of lasting several decades usually requires an extended period of development and so delays age at first breeding and reduces the rate at which individuals can produce offspring. As a result, natural selection can either lead to the selection of animals with high rates of reproduction and short lifespans or to those of low rates of reproduction and long lifespans.

Contrasts in longevity between species are associated with the risk of dying from things that individuals cannot control – such as the risk of starvation caused by fluctuations in climate, or the risk of being predated, or of dying of epidemic disease. Where species live in unpredictable environments or are exposed to high levels of predation, an individual's chances of dying each year are high and very few individuals will live for more than a few years. Conversely, where individuals live in relatively stable environments and can protect themselves against predators (think giant tortoises) relatively large numbers of individuals may live for 20+ years, producing large numbers of offspring in the course of their lives. Since building a long-lasting body involves costs that delay breeding, individuals living in conditions where their daily risk of dying for reasons that they can't control is high maximise their lifetime reproductive success by building rapidly-developing 'disposable' bodies. In contrast, where individuals have access to stable food supplies and are safe from predators, they may be able to increase their lifetime breeding success by building slow-developing bodies that are designed to last, even if this reduces the number of offspring they can produce per unit time.

A common analogy is made with the purchase of glassware: if you run a pub and your clients break 50% of your glasses each year, there is little point in buying expensive glasses that can last for 100 years, since very few will reach this age. Conversely if your clients break 1% per year, it may be worth your while buying glasses that will last for 100 years even if the initial outlay is higher.

OUTREACH

School Groups and field courses

We maintain links with local schools and our study area has been used for several university field courses.

Filming

We regularly host film teams and almost all recent films/programmes on live meerkats (including *Meerkat Manor*) have been filmed on our study groups.



Friends Of The Kalahari Meerkat Project

Following the television programmes of meerkats, we attracted a number of people who wished to follow the history of meerkat groups and individuals (the Friends of the Kalahari Meerkat Project). We now produce a monthly report for them: "The Meerkatter." (see below)

Tropical Biology Association

We believe that the future of African conservation will depend on training and equipping a new generation of African biologists and conservation specialists. In 1990, Tim Clutton-Brock helped to found a consortium of European and African universities (the *Tropical Biology Association*) that organises courses in ecology, conservation biology and evolutionary biology for students from tropical and subtropical countries. The *TBA* runs two to four month-long courses annually for around 30 students (50% from across Europe and 50% from across Africa) which are taught at field sites in Uganda, Tanzania, Kenya, Madagascar and South-East Asia. The courses are run by outstanding teachers and scientists from across the world. In addition, TBA runs specialized field courses in Africa for teachers, managers, scientists and economists involved in sustainable environmental management. It has now trained more than two thousand students and a substantial proportion of the staff of African conservation NGO's are among its alumni. In addition, it has helped to establish alumni networks throughout Africa and Europe

PUBLICATIONS FROM THE KALAHARI RESEARCH CENTRE SINCE 2007

MEERKATS

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