Chapter 1

Introduction

Introduction

The endemic African family, the Bathyergidae, comprises five genera of rodent moles exhibiting the widest range of body mass (35 – 1200 g) and social structure (solitary to eusocial) of any of the seven families or sub-families of subterranean rodents. Representatives are found in a diversity of habitats (mesic to arid) and in a wide variety of soils, altitudes and climates. Although they have a ubiquitous distribution throughout much of Africa, little is known of many of the species and particularly those outside of the borders of South Africa (Jarvis & Bennett 1990, Bennett & Faulkes 2000).
The subterranean habitat imposes very similar constraints on all subterranean mammals (Nevo 1979, 1982). Consequently, considerable convergence occurs worldwide in subterranean mammal species with very diverse evolutionary histories. The Bathyergidae show much convergence with other subterranean rodents but also show noteable exceptions, particularly with respect to sociality.

Fossil record

Hystricomorph families appear to have diverged as early as the mid-Cretaceous period before dinosaur extinction (approximately 109 million years ago) (Bennett & Faulkes 2000). Various fossils resembling extant Bathyergidae have been found in fossil beds of the Miocene era (25 mya). Bathyergids appear to have an ancient African origin with the closest outgroup among fossils being the Eocene Ctenodactyloids (Bennett & Faulkes 2000).

Mitochondrial DNA analyses by Honeycutt *et al.* (1987) show wide genetic distances between bathyergids and related taxa that infer that the bathyergids have an ancient origin or a rapid rate of molecular evolution. Three genera of fossils have been found in beds of the early Miocene in East Africa and Namibia (Lavocat 1978). These are the *Bathyergoides, Proheliophobius* and *Paracryptomys* fossil genera.

Taxonomy

The Bathyergidae are a family of entirely subterranean rodents that are endemic to sub-Saharan Africa. They are a monophyletic group, whose closest relatives are the Rock rats (Petromuridae), Cane rats (Thryonomyidae) and Old World Porcupines (Hystricidae). This was shown by parsimony analysis of sequence differences in the mitochondrial 12S rRNA gene (Nedbal *et al.* 1994). The taxonomy of the Bathyergidae and in particular the genus *Cryptomys* is currently under review. There is considerable genetic variability amongst the *Cryptomys* from Zambia and the province of Gauteng in South Africa, in which several yet undescribed species of *Cryptomys* have been found.

The bathyerid family is classed into two sub-families; the Bathyerginae (consisting monotypically of the *Bathyergus* genus) which are separated from the Georychinae (consisting of *Heterocephalus*, *Heliophobius*, *Georychus* and *Cryptomys*) by the presence of *grooved* extrabuccal incisors (De Graaff 1981, Roberts 1951).

Phylogeny within the Bathyergidae

There are currently15 recognised bathyergid species whose phylogeny to one another has been studied in terms of their sequence differences in the mitochondrial 12S rRNA and cytochrome-b genes (Faulkes *et al.* 1997). The *Cryptomys* genus is essentially composed of two groups or sub-clades that are identified on features of the infraorbital foramen and the analysis of the cytochrome-b percentage differences of the mitochondrial DNA (Faulkes *et al.* 1997). One subclade, containing *Cryptomys damarensis* has a thick walled infraorbital foramena (at least 6 species), whereas the other clade containing *Cryptomys hottentotus*, possesses an elliptically shaped and thin walled infraorbital foramena (at least three species).

Sociality

Bathyergids occupy a wide range of habitats (mesic to arid) and member species show a continuum of sociality; ranging from strictly solitary (*Bathyergus suillus, Bathyergus janetta, Georychus capensis* and *Heliophobius argentiocinereus*) through to two eusocial species (*Heterocephalus glaber* and *Cryptomys damarensis*) (Jarvis 1981, Jarvis & Bennett 1993 and Faulkes *et al.* 1997). In general, solitary and weakly social species occupy mesic areas, whereas the two eusocial species occur in arid regions. Most subterranean mammals are solitary and strongly xenophobic towards conspecifics (Nevo 1979).

Sociality in the Bathyergidae is different from that exhibited by other 'social' subterranean rodents in that colony members remain in the social unit until conditions become optimal for dispersal. Colony growth occurs by offspring retention in their natal colony (Jarvis & Bennett 1990). The Curoro, *Spalacopus cyanus* is the only other social subterranean rodent that shows similar features of sociality (Jarvis & Bennett 1990).

The majority of solitary subspecies show a marked seasonal reproduction. The two social species *Cryptomys hottentotus hottentotus* and *Cryptomys hottentotus pretoriae*, which inhabit environments similar to the solitary species, also exhibit marked seasonal reproduction (Spinks 1998, Janse van Rensburg, 2000). In these environments there are marked precipitation and temperature changes and it is believed that these are important to herald reproductive activities.

Cryptomys is by far the most specious genus of the family with all currently recognised species being social. The genus *Cryptomys* is an interesting group that contains a number of species that exhibit a broad spectrum of sociality. *Cryptomys damarensis* is the only species within the genus that has been recognised as being truly eusocial based on data from lifetime reproductive success. It shares this position with the naked mole-rat, *Heterocephalus glaber*. Eusociality has apparently evolved independently in the two genera *Cryptomys* and *Heterocephalus* (Jarvis & Bennett 1993).

A strong correlation exists between aridity/food distribution and the level of sociality exhibited. In general as aridity increases (and food distribution becomes less predictable) the level of sociality increases (Jarvis 1985, Lovegrove & Wissel 1988, Bennett 1988, Lovegrove 1991 and Jarvis *et al.* 1994). As aridity increases, so rainfall decreases. This results in the soil being harder to dig in and for the mole-rats to successfully throw up the characteristic mounds of subsurface excavated soil. Both of these factors make the energetic cost of burrowing greater and the risk of unsuccessful foraging higher (Bennett 1988, Lovegrove 1991 and Jarvis *et al.* 1994). These factors together with a high risk of dispersal (a high chance of predation and a low chance of mating successfully subsequent to dispersal) are thought to select for group living, co-operative foraging and communally caring individuals.

Dispersal risks between habitats are influenced by group size and resource characteristics (Lovegrove 1991). Other factors that are thought to influence dispersal risks are body size, thermoregulation, metabolic rate, soil conditions and caste structure (Lovegrove 1991). A large group size is formed to offset the high foraging and dispersal risks (Lovegrove 1991). Foraging within a habitat also poses certain risks, the most important being the temporal dependence on rainfall (Lovegrove 1991). Dispersal risks in turn affect the preferred mating system (inbreeding or outbreeding). When risks increase, the genetic relatedness amongst colony members is seen to be higher (Lovegrove 1991).

In most co-operatively breeding species, it is proposed that severe ecological constraints imposed on the opportunity to breed underlies the evolution of familial helping and group living (Emlen 1982). There are two situations when offspring will have very low probabilities of successfully reproducing on their own. The first situation arises when ecological requirements are such that suitable breeding locations are restricted and marginal habitats are rare. This results in a shortage of breeding openings (Brown 1974). The second situation arises from inhabiting a changing, unpredictable environment; the erratic changes in carrying capacity creates functional equivalents of breeding openings and closures. Individuals frequently faced with environmentally harsh conditions will have low chances of reproductive success when the costs of breeding independently are high (Brown 1974). In both cases, the energetic costs of independent breeding may be prohibitive and younger, less experienced individuals delay breeding and postpone dispersal (Brown 1974).

The prolonged bonds that are therefore formed in familial groups cause partitioning within the groups, which favours kin selection (Emlen 1982). Social competition exists in any structured social unit where the frequency of interactions and conflicts are high (Emlen 1982). It is expected that each individual in a group (depending on its social position) would behave in such a way as to maximise its inclusive fitness (Emlen 1982).

Dominance

As with any gregarious species, variations in behaviour will inevitably result in certain individuals appearing stronger than others. This "assertiveness" (Bennett & Faulkes 2000) may be evident in the individual being given priority to resources or high quality resources (usually food). These individuals are thought of as being dominant to other individuals in the group. Dominance in a social group of individuals may be linear (A dominates B, B dominates C, A dominates C) or non-linear (A dominates B, B dominates C, C dominates A).

Dominance may come about in several ways specific to the species behavioural repertoire. For example, in social mole-rats, dominance is thought to be achieved by agonistic (aggressive) interactions – the dominant individual performing the agonistic behaviour whilst the less dominant individual accepting the behaviour of the more dominant individual (ie: not challenging the more dominant individual). An individual's position in the dominance hierarchy of the group is thought to be closely linked to its competitive ability and hence the individual's fitness (Dewsbury 1982).

The social mole-rats, especially *C. h. hottentotus* and *C. h. pretoriae*, show a wide variety of behavioural activities which could be involved in dominance hierarchy formation and maintenance within their colonies. Behaviours of both an aggressive and submissive nature are exhibited by all individuals in the colony. The eusocial naked mole-rat has been shown to have a distinct dominance hierarchy, with the largest and heaviest individuals possessing the premium rank in the colony (Clarke & Faulkes 1997).

Ecology

All members of the Bathyergidae are herbivorous; feeding on the underground storage organs of geophytic plants (Bennett & Faulkes 2000). African mole-rats rely on these storage organs for all of their nutritional requirements, including hydration requirements, as no free water is consumed. Using geophytic storage organs as a food resource has many advantages. There is little competition in the subterranean niche for these food resources that happen to be available for most of the year (except when the plant is flowering) (Bennett & Faulkes 2000). More importantly, geophytes have a higher concentration of nutrients contained within their storage organs when they are not flowering (Bennett & Faulkes 2000). Although geophytes seem to be relatively unpalatable and even toxic to other mammals, as they contain cardiac glycosides, mole-rats seem to be immune to these factors (Bennett & Faulkes 2000).

It is increasingly apparent that different strategies are employed while feeding. Thus in the Bathyergidae the size of the geophyte determines how it will be handled and harvested (Bennett & Faulkes 2000). Two components are very important in any species feeding strategy (here foraging strategy being excluded); handling time and consumption time. Handling time is especially important in the Bathyergidae as the outer husks of geophytes are usually completely removed prior to consumption. This activity represents an energy loss to the animal as no energy is gained during this process. Only when consumption occurs is energy actually being gained by the individual. It is therefore expected that larger geophytes would be preferred over smaller geophytes as more energy would be gained relative to the cost of dehusking. Larger geophytes have been shown to have a greater amount of total energy content than smaller geophytes (Jarvis *et al.* 1998). Studies on the eusocial Damaraland mole-rat *Cryptomys damarensis* have shown that handling time decreases as the size of the geophyte increases (Barnett 1991), although in Barnett's (1991) study it was found that small geophytes were consumed relative to the geophytes of a larger mass.

In terms of foraging strategy, there appears to be no definite trend evident regarding patch profitability and choices made by individuals. According to the Marginal Value Theorem (Charnov 1976), high quality patches should be exploited in preference to poorer areas. Studies on the social common mole-rat (*Cryptomys hottentotus hottentotus*) and the eusocial Damaraland mole-rat (*Cryptomys damarensis*) have shown that empty patches are still worked by the mole-rats but are exploited less than patches containing geophytes (Bennett & Faulkes 2000).

Reproduction and Development

In non-gregarious mammals, induced ovulation seems to be the norm (Zarrow & Clarke 1968). Also, many social subterranean rodents such as *Ctenomys talarum* (Weir 1974) are induced ovulators. The method of ovulation used by solitary bathyergids is as yet unknown (Bennett & Faulkes 2000) but these species are expected to be induced ovulators. Social bathyergids are intruiging since within the *Cryptomys* genus both spontaneous and induced ovulation takes place. The common mole-rat (*Cryptomys hottentotus hottentotus*) is an induced ovulator (Spinks *et al.* 1999) whereas the Damaraland mole-rat (*Cryptomys damarensis*) appears to be spontaneous (A.J. Molteno & N.C. Bennett unpubl.).

Hystricomorph rodents appear to have relatively long gestation periods (Weir 1974), this is also evident in the Bathyergidae. Solitary bathyergids have shorter gestation periods (44 - 52 days) when compared to that of social species (56 – 110days) (Bennett 1989, Bennett *et al.* 1994 and Bennett & Aguilar 1995).

Bathyergid pups are nidicolous and altricial (Bennett & Faulkes 2000) and are therefore reminiscent of other subterranean rodents (Bennett *et al.* 1994). Bathyergid pups tend to develop slowly, similar to that of other rodent species living in a thermally stable (subterranean) environment (Bennett *et al.* 1991).

Postnatal growth rates in bathyergid pups seems to be dependent of the species level of sociality; pups of eusocial species growing the slowest. Bathyergid pup maximum growth rate ranges from 0.207 gday^{-1} (*Heterocephalus glaber*) to 3.340 gday^{-1} (*Bathyergus suillus*) (Brett 1991 and Bennett *et al.* 1991 respectively).

Genetic Relatedness

The two main factors that are thought to influence the genetic structure of mole-rat populations are i) the subterranean niche which the mole-rats have become adapted to and ii) the social structure of individual populations, especially in co-operative breeders (Bennett & Faulkes 2000). These two factors, along with genetic drift and fluctuating population sizes, are stochastic processes associated with the genetic patterns evident in subterranean mammals.

The subterranean niche has a limited capacity for gene flow, especially for those subterranean species that are gregarious in nature. With few dispersal events ever being recorded for bathyergids, it is unlikely that gene flow among populations is prevalent to any large degree. Studies on *Spalax*, a solitary and subterranean myomorph rodent, have shown that limited gene flow can lead to the evolution of several local forms that are morphologically very similar due to convergent evolution and subterranean adaptation (Bennett & Faulkes 2000). It appears that there may be similar forces acting on bathyergids.

The social structure of co-operative breeders can also potentially influence the genetic structure of their populations (Bennett & Faulkes 2000). In bathyergid rodents that have varying degrees of sociality and reproductive skew, one would expect varying patterns of relatedness in the different species.

Although not favoured by several authors (e.g. Sage *et al.* 1986), the 'niche width genetic variation' hypothesis was proposed by Nevo *et al.* (1990) in order to explain genetic patterns in subterranean mammals. This hypothesis, unlike the stochastic processes outlined above, explains the reduced genetic variation in subterranean mammals (when compared to small above-ground mammals) in terms of the subterranean environment that is stable and predictable.

The genetic relatedness of individuals within colonies of social bathyergids has only recently begun to be explored. It is imperative, in order to understand how social systems in bathyergid species evolve and are maintained, that the genetic structure of populations and the genetic relatedness within social groups is understood. With the assistance of genetic markers such as microsatellites as well as relevant software for analysis, parentage (especially paternity) analysis can be routinely undertaken in order to determine genetic relatedness of colony members.

The naked mole-rat (*Heterocephalus glaber*) has been shown to have the highest mean coefficient of inbreeding that has been reported for any natural mammal population (Reeve *et al.* 1990). Other bathyergids have been shown to be obligate outbreeders (for example *Cryptomys damarensis*, Bennett & Faulkes 2000) and a lower mean relatedness is expected, although not yet investigated.

The study species

The highveld mole-rat, *Cryptomys hottentotus pretoriae* is a group living bathyergid. Mean body mass ranges from 88g (females) to 106 g (males) (Jarvis & Bennett 1991). The species inhabits regions with seasonal precipitation patterns (Janse van Rensburg 2000) enabling sufficient burrow excavation during the wet season. The aridity food distribution hypothesis (Jarvis *et al.*1994) predicts that in such an environment, the mole-rats should be solitary or weakly social, only coming together during the breeding season. However, colonies of the highveld mole-rat can exceed 12 animals (G.P. Malherbe and L. van der Walt, pers. obs.).

Knowledge pertaining to the general ecology, reproductive biology and genetic relatedness within colonies is unknown. A study by Faulkes *et al*. (1997) showed that the highveld mole-rat is indeed a sub-species of *Cryptomys hottentotus*. Janse van Rensburg (2000) has demonstrated that the highveld mole-rat is a seasonal breeder that cues its reproduction to seasonal rainfall. Moolman *et al*. (1998) has shown the highveld mole-rat to be social with a non linear ordinal dominance hierarchy.

Aims of the thesis

The primary aim of this thesis was to increase the dearth of knowledge currently known about this social subterranean rodent mole. In chapter 2 I investigated the cardinal dominance hierarchy of the highveld mole-rat. Cardinal dominance determination is the most appropriate measure that can be used on the mole-rat social system. In chapter 3, the handling and consumption time of the geophyte *Ornithogalum secundum* of varying size was investigated. Foraging in terms of size– and density-dependent utilisation and foraging patterns was investigated in light of optimal foraging theory. In chapter 4 the general reproductive biology of the highveld mole-rat was discerned with particular attention to the method of ovulation and growth rates of the offspring. Finally, in chapter 5, the genetic relatedness of colonies of the highveld mole-rat was investigated in order to elucidate the composition of colonies in terms of parentage and relatedness as well as possible mating systems employed in order to be social. Before this could be investigated, it was necessary to determine whether microsatellite primers developed for use on other bathyergid species as well as a universal mammal species could be employed in the study species.

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