CHAPTER 6

SYNTHESIS

African mole-rats (Bathyergidae) are of particular interest as they are widely distributed across Africa and occupy a variety of different habitats and offer a number of interesting, some of which are unique, characteristics in a single family. In this family, a wide range of social behaviour is displayed, some species are strictly solitary whereas other species have highly organised social societies. Social species have a highly skewed reproductive success such that a single female and a few male consorts are responsible for reproduction. Reproduction in subordinate animals can be inhibited by the dominant individuals by various mechanisms. In extreme cases, ovulation is blocked physiologically, but more commonly, behavioural interactions and incest avoidance is sufficient to prevent subordinate animals from reproducing. This family provides the ideal model to glean insight in the mechanisms of reproductive suppression, both seasonally and socially.

This study firstly focused on the endocrine, neuroendocrine and neuroanatomical parameters of wild caught, seasonally breeding Cape mole-rats, and secondly, by using endocrine, neuroendocrine and neuroanatomical parameters, to gain insight into the seasonality of reproduction in the Natal mole-rat and the socially induced fertility of subordinate Natal mole-rats, to identify where this mole-rat fits into the spectrum of the sociality continuum.

Seasonality

All solitary African mole-rats studied to date are seasonal breeders, while the majority of social species are aseasonal (Bennett & Faulkes 2000). The Cape mole-rat has a distinct breeding season (Bennett & Jarvis 1988a) but does not appear to possess the physiological characteristics of a classical seasonal breeder. Typically, reproductive function is down-regulated during the

reproductively quiescent period in seasonally breeding species (Gerlach & Aurich 2000). In females, ovulation occurs only during part of the year, and in males spermatogenesis is reduced or ceased.

In contrast with most seasonally breeding species, female Cape mole-rats do show follicular development during both the breeding and the non-breeding seasons (Oosthuizen & Bennett 2007). In both males and females, circulating steroid hormone concentrations, as well as the pituitary response on exogenous GnRH are not significantly different in winter compared to summer. In the brain of female Cape mole-rats, there is no difference in the number of GnRH neurons or the size of the cell bodies, moreover the amount of GnRH peptide stored in the median eminence is similar in summer and winter.

The findings of this study therefore lead us to believe that the Cape mole-rat is an opportunistic breeder with the physiological ability to produce all year round, but it is prevented from breeding during certain periods of the year by ecological constraints. During the dry season, the soil is hard and burrowing is energetically costly. Therefore the breeding season correlates well with the rainfall pattern. It is possible that unpredictable rainfall patterns due to El Nino southern ocean patterns may have selected against a strictly seasonal reproductive physiology in the Cape mole-rat.

The Natal mole-rat, although phylogenetically closely related to the common mole-rat and the highveld mole-rat (Faulkes *et al*. 1997), does not appear to have a distinct breeding season. Histological results from the gonads in both males and females show no seasonal variation in numbers of follicles or degree of follicular development (Viljoen, 2006) and post-mortem findings reveal embryos during the entire year (M.Oosthuizen *pers obs*.). No seasonal

patterns are observed in steroid sex hormones or the pituitary response to exogenous GnRH, and GnRH neuron size and number are comparable over season. Furthermore there are no seasonal differences observed in the GnRH content of the median eminence.

The Natal mole-rats used for this study occur in a region with a much higher yearly rainfall than the habitats of the common and highveld mole-rats. For these animals, abundant food and dispersal opportunities are available throughout the year, and by utilising an opportunistic breeding strategy, they are able to reproduce when conditions are favourable. It is possible that Natal mole-rats that occur in drier areas may also exhibit seasonal reproductive quiescence if food and dispersal opportunities are restricted.

Thus it appears that a number of mole-rat species that are classified as seasonal breeders, are physiologically able to reproduce throughout the year, but are restricted from doing so by environmental factors. Rainfall seems to be an important determining factor in seasonality of mole-rats.

Sociality

All the members of the genus *Cryptomys* are social. These species occur in most habitat types in sub-Saharan Africa, and the degree of sociality is correlated both with the stringency of reproductive suppression and the aridity of the habitat where the species occur (Figure 6.1).

Neither male nor female non-reproductive Natal mole-rats appear to be physiologically inhibited from reproducing by the breeding animals. In Natal

mole-rats, spermatogenesis takes place in reproductive and non-reproductive males, and likewise, both reproductive and non-reproductive females show follicular development (Viljoen 2006). No significant differences were seen in testosterone concentration between reproductive and non-reproductive males, neither was there a difference in the oestrogen concentrations between reproductive and non-reproductive females. Progesterone concentrations were significantly higher in reproductive females, however, the Natal mole-rat is an induced ovulator, and requires coitus to induce ovulation and follicular development to the stage of corpus luteum. No difference was seen in the response of the pituitary to an exogenous GnRH challenge between reproductive and non-reproductive animals of either sex. In the brain of the Natal mole-rat, the distribution, number and size of GnRH perikarya was similar in reproductive and non-reproductive animals of both sexes, however the GnRH innervation of the median eminence (ME) was much denser in the non-reproductive males and females compared to the reproductive animals. This implies that in non-reproductive animals, GnRH is synthesized in non-reproductive but is retained in the ME. The findings of this research suggest that the reproductive skew in the Natal mole-rat is maintained through incest avoidance and is behaviourally controlled by the dominant animals.

Jarvis *et al.* (1994) proposed the aridity food distribution hypothesis (AFDH) to explain the continuum of sociality seen in the bathyergid rodent moles. This hypothesis relates the costs and risks associated with living in an arid habitat. For mole-rats inhabiting arid areas, burrowing is a significant energetic expenditure, therefore living in large group sizes is advantageous as it reduces burrowing costs while simultaneously increasing the foraging efficiency.

In highly social or eusocial mole-rat species (naked mole-rat and Damaraland mole-rat), reproductive control of subordinate animals is very stringent. They occur in arid areas and dispersal opportunities are infrequent. As a result, dispersal is delayed in subordinate animals and necessitate drastic measures on the part of reproductive animals to remain dominant. Non-reproductive animals in these species are frequently physiologically suppressed from reproducing (Faulkes *et al.* 1990a, Faulkes *et al.* 1991, Bennett *et al*. 1993, Bennett *et al.* 1996).

In social mole-rat species occupying more mesic habitats (Mashona mole-rat, common mole-rat, Zambian mole-rat, higveld mole-rat) reproductive control of subordinate animals tends to be enforced through behavioural mechanisms and incest avoidance. Dispersal opportunities are more predictable and regular, concequently the survival of the colony does not rely on large numbers of individuals to locate food patches. Subordinate animals have the option to leave the natal colony and set up an independent colony. The reproductive physiology of the Natal mole-rat compares well with that of representatives of this latter category (Figure 6.1). It fits in at the lower end of the continuum of socially induced fertility as proposed by Bennett *et al*. (2000) where subordinate non-reproductive males and females show a similar basal circulating LH concentration and subsequent elevation in response to a pharmacological overdose of GnRH as the dominant reproductive animals.

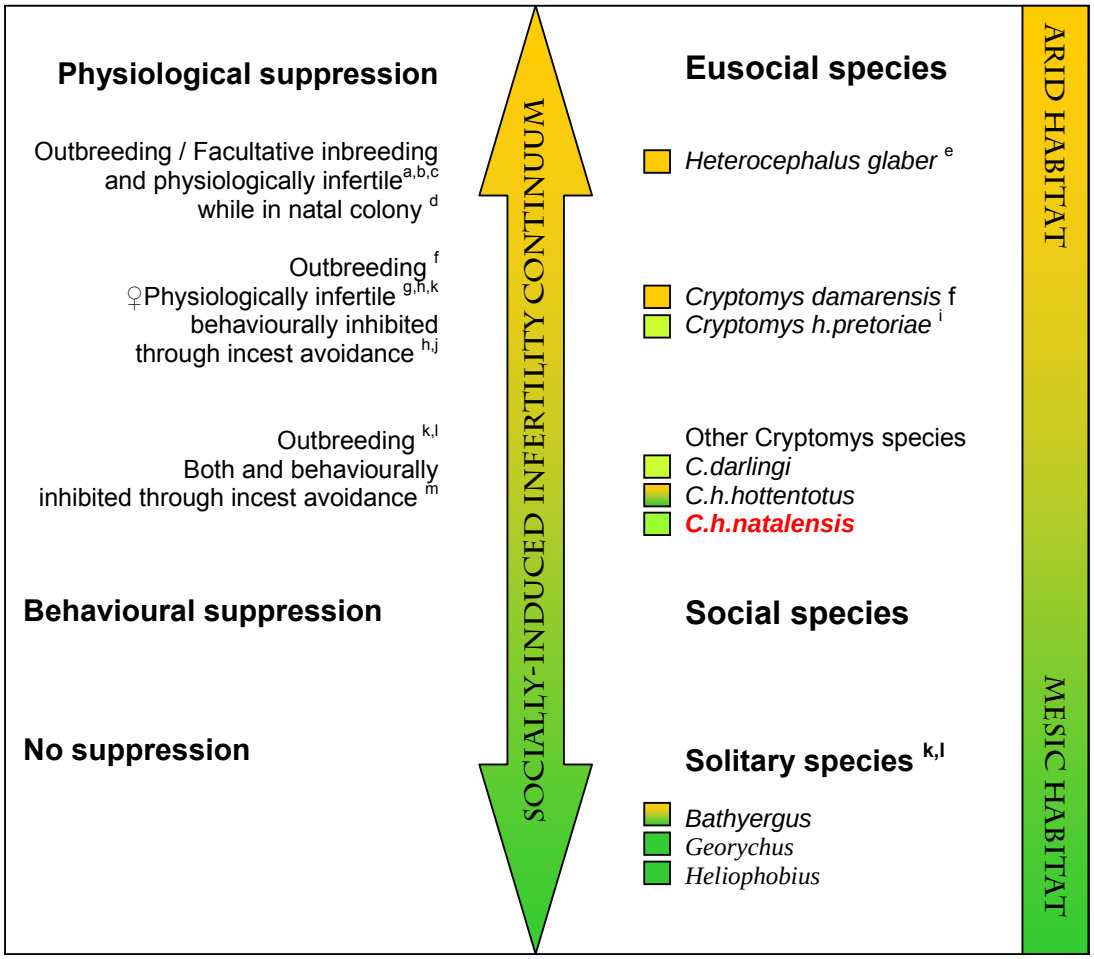

Figure 6.1: Species of the family Bathyergidae assembled according to the degree of sociality displayed and type of habitat in which they occur, with the Natal mole-rat (***C.h.natalensis***) grouped with other behaviourally suppressed species. (Modified from L. van der Walt 2003).

[a] Reeve *et al*. 1990; [b] Braude 2000; [c] Clarke & Faulkes 1999 [d] Faulkes *et al*. 1990, 1991; [e] Jarvis 1981; [f] Jarvis & Bennett 1993; [g] Bennett *et al*. 1996; [h] Bennett 1994; [i] Moolman *et al*. 1998; [j] Van der Walt *et al*. 2001; [k] Jarvis & Bennett 1991; [l] Bennett & Faulkes 2000; [m] Spinks *et al*. 1997, 1999, 2000; ♀ - female; ♂ - male.