

African mole-rats (family Bathyergidae): models for studies in animal physiology

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The African mole-rats of the family Bathyergidae are an excellent model group of mammals for undertaking physiological research. The wide spectrum of social organizations, coupled with their underground lifestyles, make this unique family ideal for studies that embrace broad principles in physiology. Here I present an overview of past and ongoing research into the energetics, locomotory activity patterns, pineal melatonin function and reproductive physiology of these fascinating subterranean mammals.

Key words: mole-rats, physiology, energetics, activity patterns, reproduction.

OVERVIEW

The Bathyergidae is a family of subterranean rodents endemic to the continent of Africa that has received far more attention than would appear merited by the actual number of species, and their overall visibility in the wild. Their wide spectrum of social organizations, coupled with an underground lifestyle, make members of this family ideal subjects for a multitude of studies that embrace broad principles in physiology. The subterranean niche has necessitated morphological, physiological and behavioural adaptations to exist in an environment where conditions of light, temperature and gaseous composition of the tunnel system are markedly different to that above ground.

Mole-rats spend their entire lives underground in a burrow system comprising an extensive labyrinth of superficial foraging tunnels and deeper nest chambers. In most species, the tunnel system is sealed from the surface, except briefly during the initial stages of mound formation, or for slightly longer periods in naked mole-rats (*Heterocephalus glaber*) while they dispose of excavated soil from an open volcano-shaped mound. All mole-rat species use soil plugs to thoroughly seal off the completed mound, which reduces the risk of predation, but also limits gaseous exchange between the burrow and the outside world. As such, their burrows have unique microhabitats that necessitate specific physiological adaptations. The burrow system, and most notably the nest chamber(s), are characterized by a potentially hostile gaseous environment with high carbon dioxide (hypercapnic) and low oxygen (hypoxic) concentrations (Kennerly 1964). On the other hand, the burrows are also comparatively

thermostable environments also characterized by high relative humidities (>95%). The greatest range in annual and daily sub-soil temperatures occurs in the foraging burrows 10–40 cm below ground (Bennett *et al.* 1988). This probably explains why mole-rats excavate nest chamber(s) at greater depths where there is thermal stability. Although exhibiting both diurnal and seasonal fluctuations in temperature, the temperature fluctuations in superficial burrows are more muted than those on the soil surface and in the air, but with a lag in the times at which maximal and minimal temperatures occur.

ENERGETICS

Mole-rats exhibit many thermoregulatory and metabolic adaptations to living in burrows. One of these most striking characteristics is a reduced resting metabolic rate (RMR). At thermoneutrality (the temperature range where metabolic heat production is unaffected by an ambient temperature change), all mole-rat species have resting metabolic rates substantially lower than those of surface dwelling rodents of comparative body mass (Lovegrove 1986a,b, 1987; Bennett *et al.* 1992, 1993a,b; Bennett *et al.* 1994). Furthermore, mole-rats typically have core body temperatures that are lower, but a thermal conductance that is higher, than similar-sized surface-dwelling rodents.

McNab (1966) proposed that reduced RMRs and low body temperatures, coupled with a high thermal conductance, may assist in reducing overheating in the confines of a closed burrow system. Within the Bathyergidae, the thermoregulatory abilities of species range from poikilothermy, exhibited by the naked mole-rat, through to

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homeothermy in species such as the Damaraland mole-rat (McNab 1979; Buffenstein & Yahav 1991). Interestingly, while results suggest that the naked mole-rat acts like a poikilotherm, these trends are not reflected in tissue uptake of oxygen, which resembles that of warm-blooded homeotherms (Gesser *et al.* 1977). The Damaraland mole-rat, *Fukomys damarensis*, and the common mole-rat, *Cryptomys hottentotus hottentotus*, as with many of the other haired mole-rats, show a homeothermic response of body temperature to ambient temperature (Bennett *et al.* 1992). Interestingly, the Mashona mole-rat, *Fukomys darlingi*, shows a more typically homeothermic profile with regard to its oxygen consumption, but exhibits heterothermy with respect to its body temperature (Bennett *et al.* 1993a). The broad range of thermal properties exhibited by mole-rats thus makes the family an excellent model for examining the evolution of endothermy.

Mole-rats also provide excellent models for examining the costs of foraging and the consequent property of risk sensitive metabolism, as found by Lovegrove & Wissel (1988). A simple model was developed to investigate the associated risks of unproductive foraging by these geophytic feeders as a function of i) resource dispersion characteristics and ii) group size. The model predicted that the main benefit of group foraging is the reduction of foraging risk, rather than the securing of food resources. The energetic costs of non-workers and the breeding pair are met in social groups by a reduction of the total energetic expenditure of the colony. Mole-rats achieve this by having a small body size, by huddling in the nest, and having a low metabolism.

High energetic costs are incurred as subterranean mammals excavate their burrow systems and then transport the loosened soil onto the surface. Lovegrove (1989) found that the cost of burrowing, as a function of distance burrowed in two arid-dwelling mole-rat species (the Damaraland mole-rat and rat and the naked mole-rat), is lower in moist compared to dry soils. Per unit energy expended, mole-rats therefore excavate a specific length of tunnel more quickly in moist than in dry soil. However, instantaneous measurements of metabolic rate suggest that burrowing in moist soil may actually be more energetically costly than in dry soil (Lovegrove 1989). These results at first appear contradictory, but show that mole-rats are able to dig more effectively, and with greater speed, in moist soils. This may well explain why

mole-rats engage in massive bouts of excavation following good rains, and restrict their burrowing in the dry season to minor excavations for harvesting geophytes in areas that were previously searched when the soil was moist (Jarvis *et al.* 1998). It has been estimated that burrowing (digging metabolic rate) is five times energetically more expensive than resting metabolic rate. Mole-rats thus mainly burrow when the soil is moist and readily workable.

Locomotor activity patterns

Generally, most subterranean rodents have been reported to exhibit evenly distributed periods of activity that are neither confined to the night or day, for example pocket gophers (Vaughan & Hansen 1961; Anderson & MacMahon 1981; Gettinger 1984) and bathyergids (Jarvis 1973; Hickman 1980). In the past this was intimated to be the result of a lack of a photoperiodic signal penetrating the burrow. African mole-rats are only exposed to external light during mound formation, since they are truly subterranean and rarely, if ever, emerge above ground (Bennett & Faulkes 2000). The small superficial eyes possess a well-developed pupil and well-organized retina. The ganglia of the retina in mole-rats project to all visual structures, which is typical of surface-dwelling sighted rodents (Nemec *et al.* 2008). Interestingly though, the suprachiasmatic nucleus is large and receives bilateral innervation, but all other visual nuclei are reduced in size. Despite this, mole-rats possess well-developed visual subsystems that are involved in photoperiodicity in other mammals (Nemec *et al.* 2008).

Recent studies investigating locomotor activity patterns of subterranean African mole-rats under controlled photoperiodic regimes suggest that while activity is not restricted to a particular phase of the day, mole-rats may be classified as either exhibiting predominantly nocturnal, diurnal or arrhythmic patterns of locomotor activity (Oosthuizen *et al.* 2003; Vasicek *et al.* 2005a,b; Hart *et al.* 2004a; Schottner *et al.* 2006; de Vries *et al.* 2008). These locomotory activity rhythms may be entrained to a light/dark cycle and, moreover, show an endogenous circadian pattern under constant darkness, which is slightly less than the 24-hour solar rhythm. In solitary mole-rat species, activity appears to be more confined to a particular section of the light/dark cycle (Fig. 1). By contrast, the activity of individuals of social species appears to be less restricted to a specific part of the

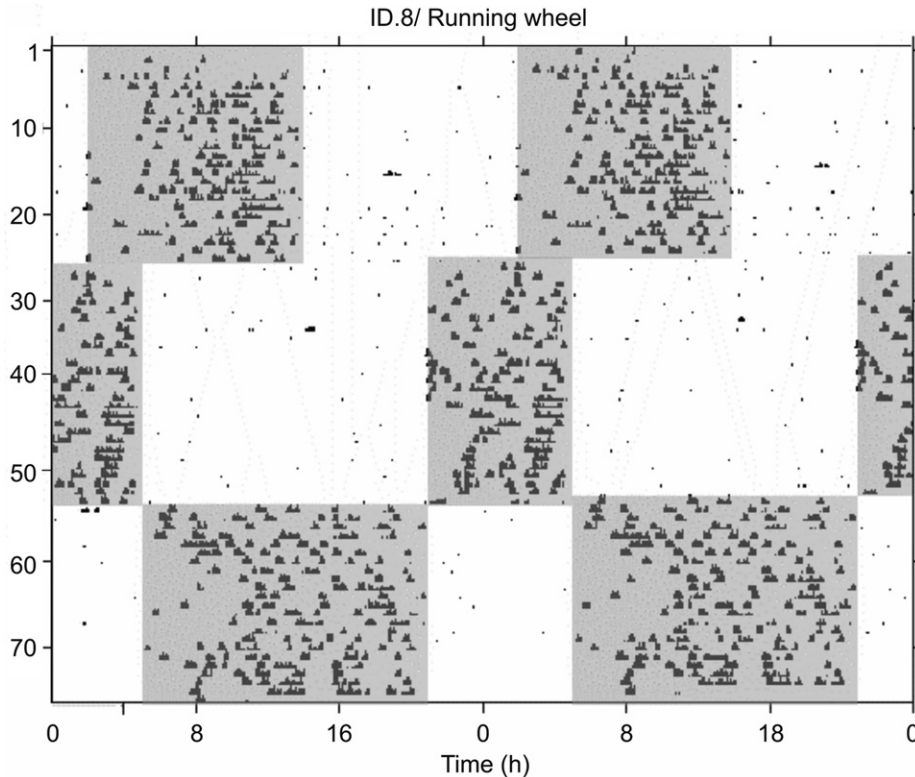


Fig 1. Actogram of the Cape mole-rat, *Georychus capensis* showing immediate entrainment of activity when the lighting regime is switched. The grey shading indicates the dark phase of the light cycle. (Modified from Oosthuizen *et al.* 2003.)

light/dark cycle and their activity is more uniformly distributed throughout the 24-hour day, although they still display more activity during either the dark or light phase (Fig. 2). What is truly fascinating is that within a single colony of the social species (e.g. the Damaraland mole-rat), some individuals may display most of their activity at night (nocturnal), some display the predominant activity in the day (diurnal), whereas others can be completely arrhythmic. The reason why some animals display a predominantly nocturnal or diurnal activity pattern in an underground burrow system is to date unknown. Regardless of the physiological basis for such variation in activity patterns, this ensures that the extensive burrow systems of social species may be patrolled throughout the 24-hour period, which could benefit colonies from predation or invasion by conspecifics.

PINEAL MELATONIN SECRETION

The underground habitat deprives subterranean mammals of one of the most ubiquitous *zeitgebers*

that is involved in the measurement of daily and seasonal changes in the environment – light. In four species of African mole-rats, melatonin secretion has been found to be both diurnal and circadian, but relatively insensitive to acute exposure to light and dark (Richter *et al.* 2003; Gutjahr *et al.* 2004; Hart *et al.* 2004; Vasicek *et al.* 2005a,b). The diurnal pattern of melatonin secretion is similar to that of above ground mammalian species in which a 24-h rhythm of melatonin has been described. Interestingly, ocular regression is not associated with an accompanied loss of circadian melatonin secretion. Indeed, melatonin secretion has been reported in the completely blind Mediterranean mole-rat (Pevet *et al.* 1984).

In addition to possessing a circadian rhythm of melatonin secretion, mole-rats are able to alter this rhythm when they are exposed to different photoperiods (i.e. from 14L:10D to 10L:14D) suggesting that they can measure day-length. These findings support the notion that even brief exposure to light during mound formation has the potential to function as a *zeitgeber*, despite the

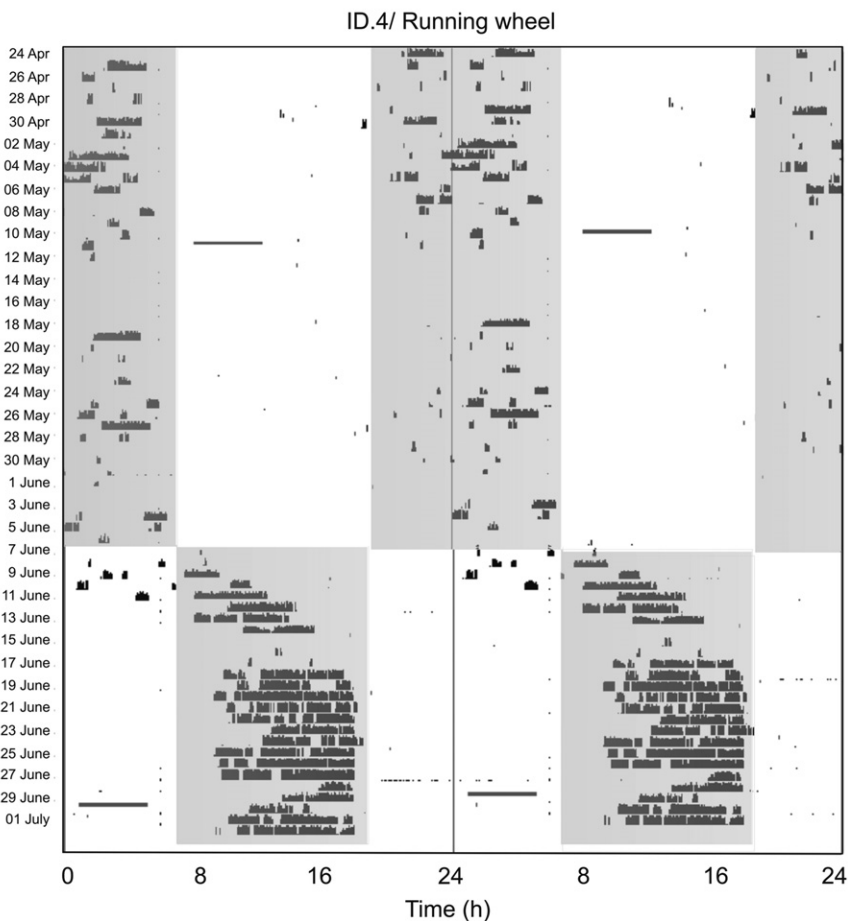


Fig. 2. Actogram of the common mole-rat, *Cryptomys h. hottentotus* showing gradual entrainment of activity when the lighting regime is switched. The grey shading indicates the dark phase of the light cycle. (Modified from Oosthuizen *et al.* 2003.)

mole-rats living a subterranean existence (Richter *et al.* 2003; Gutjahr *et al.* 2004; Vasicek *et al.* 2005b).

REPRODUCTIVE PHYSIOLOGY

The African mole-rats provide an unparalleled opportunity with which to examine the correlates of social evolution, and moreover, the development of reproductive repression in social species. The solitary species of southern African mole-rats (in the genera *Georychus* and *Bathyergus*) breed seasonally and generally inhabit mesic habitats that have a distinct seasonality with respect to photoperiod, temperature and rainfall pattern (Bennett & Jarvis 1988a; Jarvis & Bennett 1990; Jarvis & Bennett 1991; Bennett *et al.* 1999; Bennett & Faulkes 2000). The solitary eastern African mole-rat species of the genus *Heliophobius* inhabit mesic regions where temperatures and photoperiod are more equable,

but rainfall is still seasonal and the animals breed throughout the year (Sumbera *et al.* 2003). A number of species with some degree of social organization (e.g. the common mole-rat, *Cryptomys h. hottentotus*) may also occur in these mesic areas, but they also are able to colonize drier ecotopes (Spinks *et al.* 1999; Janse van Rensburg *et al.* 2002). Finally, the species generally regarded as the most social, the eusocial mole-rats (e.g. the Damaraland mole-rat and the naked mole-rat) tend to occur in semi-arid to arid habitats, or areas where rainfall, although seasonal, is highly unpredictable or sporadic (Jarvis & Bennett 1990; Jarvis & Bennett 1991; Jarvis *et al.* 1998).

Herbst *et al.* (2004) found a strong correlation between rainfall pattern and raised sex steroid profiles in wild male and female Namaqua dune (*Bathyergus janetta*) mole-rats, implying that rain-

fall may be an important environmental cue for timing reproduction. This finding is also supported from a study on sex steroid profiles of the sister species, the Cape dune mole-rat, *Bathyergus suillus* from the Western Cape, in which the onset of the rains correlates with the initiation of the breeding season (Hart *et al.* 2006).

The genera *Cryptomys*, *Fukomys* and *Heterocephalus* contain both social and eusocial species that occur in familial groups. The family units comprise the dominant reproductive parents and a number of litters of philopatric, non-reproductive offspring (Jarvis & Bennett 1993; Faulkes *et al.* 1997; Bennett & Jarvis 1988b; Burda *et al.* 2000; Burland *et al.* 2002; Burland *et al.* 2004). Unrelated immigrants of either sex, but more often males, may also be present within, or pass through, colonies in both *F. damarensis* (Burland *et al.* 2002, 2004) and *C. h. hottentotus* (Bishop *et al.* 2004).

A number of studies investigating the circulating luteinizing hormone concentrations in reproductive and non-reproductive individuals of either sex, as well as the response of the pituitary to an exogenous gonadotrophin-releasing hormone challenge, have revealed that in some species (e.g. *Fukomys darlingi*) there is a purely behavioural repression of reproductive inhibition though incest avoidance and incest taboos, whereas in other social species (e.g. *Fukomys damarensis*) there is a very definite reproductive suppression operational on non-reproductive females. This is mediated through behavioural interactions between the reproductive and non-reproductive colony members, but results in physiological changes.

In non-reproductive male and female Mashona mole-rats, individuals appear to refrain from sexual activity by being subordinate to their parents, the reproductive pair, and through incest avoidance (Gabathuler *et al.* 1996). Socially-induced infertility in Mashona mole-rats does not result from impaired pituitary function.

Circulating LH concentrations and the response of the pituitary to an exogenous GnRH challenge is comparable between reproductive and non-reproductive individuals of either sex (Bennett *et al.* 1997). In the Damaraland mole-rat, the pituitary of non-breeding females exhibits a reduced sensitivity to exogenous GnRH, compared to breeding females, yet the reproductive and non-reproductive males have comparable concentrations of circulating LH and a similar response of the pituitary to an exogenous GnRH challenge (Bennett *et al.* 1993; Bennett *et al.* 1996). In this

species it would therefore appear that incest avoidance is operative in the males, but that other factors are also operative in the females. Interestingly, in the eusocial naked mole-rat socially-induced suppression of reproductive physiology is found in the non-reproductive animals of both sexes. The non-reproductive animals not only show reduced circulating LH but a depressed response of the pituitary to an exogenous GnRH challenge when compared to their reproductive counterparts (Faulkes *et al.* 1990, 1991, 1994). Incest avoidance is not shown by this species as a new breeder comes from within the same colony upon the death of a previous breeder. Thus, in the social species of African mole-rat there is a continuum of socially induced infertility operational within the family (Bennett *et al.* 1997). The mechanisms that suppress reproduction in the non breeders are varied. Thus, 1) both sexes may be repressed from reproducing through strictly behavioural means (incest avoidance); or 2) only females show suppression; or 3) complete reproductive suppression occurs where there is physiological suppression to reproduction in both sexes.

In both female naked and Damaraland mole-rats, the block to ovulatory activity appears to be due to a disruption of the gonadotrophin releasing hormone GnRH secreting cells in the hypothalamus. Anatomically, there is no difference in the numbers of cells, the morphology, or the size of the cell bodies of the GnRH neurosecretory perikarya between reproductive and non-reproductive female Damaraland mole-rats (Moltano *et al.* 2004). But, there is a distinct difference in the concentrations of GnRH that are retained in the hypothalamic neurosecretory cells of these two groups.

The GnRH concentrations in the median eminence and proximal pituitary stalk are much greater in non-reproductive females compared to reproductive females. By contrast, in the Damaraland mole-rat the mean concentration of GnRH in the hypothalamus of reproductive and non-reproductive males is not significantly different. This implies that the GnRH release is inhibited in non-reproductive females and accumulates in the cells, resulting in an observed increase in GnRH concentrations and greater immunohistochemical staining for GnRH.

Endogenous opioid peptides (β -endorphin) have been implicated in the modulation of GnRH secretion in several mammal species, and their role in the suppression of GnRH/LH secretion in

mole-rats has been investigated. Neither single, nor multiple injections of the opioid antagonist naloxone appears to have any effect on LH secretion, in intact or hysterio-ovariectomized females, indicating that endogenous opioids are unlikely to be involved in socially induced reproductive suppression (Molteno & Bennett 2002).

In conclusion, bathyergid mole-rats lend themselves to further research in many aspects of physiology and physiological ecology because of the unusual lifestyle and varied social structure of the representative species. The varying complexity of the burrow system with increased sociality makes these animals an ideal model for investigating hippocampal size and studies on aspects of neurogenesis in this region. Furthermore the wide diversity of social structure and reproductive strategies also promotes research avenues that venture into neuroendocrinology and such studies are currently under way.

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