University of South Bohemia in České Budějovice

Faculty of Science

Ph.D. Thesis

Ecology and activity of mesic Afrotropic mole-rats

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Annotation:

This Ph.D. thesis focuses on the ecology and activity of mesic Afrotropic mole-rats. In particular, ecological characteristics in habitats of two mole-rat species with different social system, the solitary *Heliophobius argenteocinereus* and social *Fukomys whytei*, were analysed in an area of sympatry and the results are discussed in relation with available ecological data on other species. Two studies bring to light novel data on the ecology and behaviour of the free-living largest social bathyergid, the giant mole-rat *Fukomys mechowii*, especially in relation to ecological characteristics in its natural habitat, burrow system architecture, kin structure and spatial and temporal activity patterns. In the final study, new data on the field metabolism of the silvery mole-rat *H. argenteocinereus* are presented. These new findings are discussed in further detail and expand upon existing explanations for low resting metabolism in subterranean rodents and the differences in field metabolism in relation to seasonality of habitat.
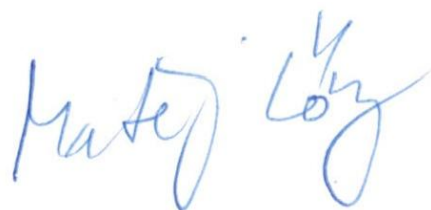
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                                                                              Matěj Lövy

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List of original articles

I. **Lövy M.**, Šklíba J., Burda H., Chitaukali W.N and Šumbera R. Ecological characteristics in habitats of two African mole-rat species with different social systems in an area of sympatry: implications for the evolution of mole-rat sociality.

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Matěj Lövy and Jan Šklíba collected data; M. Lövy performed analyses and significantly contributed to writing of the manuscript

II. Šumbera R., Mazoch V., Patzenhauerová H., **Lövy M.**, Šklíba J., Bryja P. and Burda H. Burrow architecture, family composition and ecological conditions of the largest social African mole-rat; the giant mole-rat constructs really giant burrow system.

(Under minor revision in Acta Theriologica)

Matěj Lövy and Jan Šklíba collected ecological data; Matěj Lövy participated on analysing of GIS data and contributed to writing of the manuscript

III. **Lövy M.**, Šklíba J., Šumbera R. Spatial and temporal activity patterns of the free-living giant mole-rat *Fukomys mechowii*, the largest social bathyergid.

(*Original manuscript*)

Matěj Lövy and Jan Šklíba collected data, Matěj Lövy performed the analysis and did most of the work on the manuscript

IV. Zelová J., Šumbera R., Okrouhlík J., Šklíba J., **Lövy M.**, Burda H. (2011) A seasonal difference of daily energy expenditure in a free-living subterranean rodent, the silvery mole-rat (*Heliophobius argenteocinereus*; Bathyergidae).

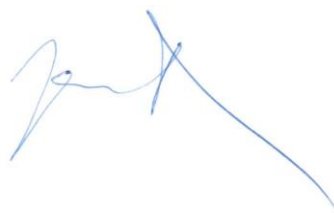*(Comparative Biochemistry and Physiology, Part A 158:17-21)*

Matěj Lövy participated on collecting data and contributed to writing of the manuscript

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Contents (STAG version)

Introduction

African mole-rats as an outstanding group of subterranean mammals

Across the globe more than 300 species of mammals spend most of their lives underground. They belong to 54 genera, 10 families, and 6 orders; most of them are rodents (Nevo 1999, Burda 2003, Begall *et al.* 2007). A new niche for mammals emerged as a result of gradual global cooling and increasing aridity which occurred in several waves from the middle Eocene to the early Oligocene (Savin 1977, Nevo 1999). The subterranean environment provided mammals with shelter from climatic fluctuations and with new food resources in the form of underground storage organs of plants (Nevo 2007). The subterranean ecotope thus benefits from a stable microclimate and safety from predators on the one hand, but highly stressful conditions (permanent darkness, low food productivity, hypoxic and hypercapnic atmospheres in burrows, and energetically demanding digging) on the other. Life underground requires distinct adaptations resulting in one of the most prominent examples of convergent evolution of unrelated taxa in the animal kingdom (Nevo 1999, Lacey *et al.* 2000).

Considering the unique biology of subterranean rodents and their ecosystem function – they are called ecosystem engineers (Reichman & Sealblom 2002) - it is not surprising that many subterranean taxa have become model groups in various studies in zoology, ecology, ecophysiology, animal behaviour etc. Besides, outstanding findings have been recently published in various fields of human medicine, such as aging and senescence (Dammann & Burda 2006, Perez *et al.* 2009, Dammann *et al.* 2011), cancer protection (Nasser *et al.* 2009, Seluanov *et al.* 2009) and tolerance of the brain towards hypoxia (Avivi *et al.* 2006, Larson & Park 2009). Despite the indisputable significance of these studies, most of them are based predominantly on laboratory experiments and basic aspects of the biology and behaviour of most species of subterranean rodents remain almost unknown under free-living conditions (see Begall *et al.* 2007).

Among subterranean rodents, African mole-rats (Bathyergidae, Rodentia) are one of the species most adapted to a subterranean environment. The Bathyergidae are endemic to sub-Saharan Africa where they occupy a wide range of divergent habitats (Bennett & Faulkes 2000). Over the last three decades, African mole-rats have received far more scientific attention than would appear merited by one relatively small rodent family. Probably the most interesting feature, drawing the attention of behavioural ecologists, sociobiologists and

evolutionary biologists, is the divergence of social systems encountered within this family. Such divergence is surprising because subterranean mammals tend to solitary, strictly territorial habits (Nevo 1979, Nevo 1999). In African mole-rats, recent taxonomy distinguishes about 22 species in six genera (Kock *et al.* 2006) from which species belonging to the genera *Bathyergus*, *Georychus*, and *Heliophobius* are solitary, whereas mole-rats of the remaining three genera - *Heterocephalus*, *Cryptomys* and *Fukomys* - are social, many of them probably eusocial (Jarvis 1981, Jarvis & Bennett 1990, 1993, Burda & Kawalika 1993, Jarvis *et al.* 1994, Burda 1999). Two species of mole-rats have been denoted as eusocial so far – the naked mole-rat *Heterocephalus glaber* and the Damaraland mole-rat *Fukomys damarensis* (Jarvis *et al.* 1981, Jarvis *et al.* 1994). Mole-rat eusociality is a unique social organisation not found among any other vertebrates (Bennett & Faulkes 2000). It is characterised by monopolisation of reproduction by one or few individuals within the group, division of labour, overlap of generations, cooperative brood care and by lifelong philopatry of most of the offspring (for review see Burda *et al.* 2000).

The phenomenon of eusociality and flaming debates concerning its evolutionary origin has caused general knowledge on the biology of mole-rats to be strongly biased. Most of the scientific interest has been dedicated to two eusocial species, *Heterocephalus glaber* and *Fukomys damarensis*. Furthermore, mole-rats occurring in the South African subregion, i.e. species belonging to both the social genus *Cryptomys* and solitary genera *Bathyergus* and *Georychus*, have always been more frequently studied. However, this situation is one big paradox considering that more than half of all species occur in Central and Eastern tropical Africa (VanDaele *et al.* 2004, 2007). Of these, the vast majority belong to the genus *Fukomys* representing the most derived lineage within the bathyergids (VanDaele *et al.* 2007). Nevertheless, the biologies of those species remain almost unknown. Until recently, a similar scenario referred to another species from the tropical region, the solitary silvery mole-rat *Heliophobius* (monotypic genus with one recognised species the silvery mole-rat *H. argenteocinereus*). Despite the fact that this mole-rat is among the most widely distributed bathyergid species, it has remained the least known taxon among solitary mole-rats. Only recently published studies have brought to light very interesting findings on the biology and behaviour of this species (Šumbera *et al.* 2007a, 2008; Šklíba *et al.* 2007, 2009). Thus, to comprehensively understand the unique biology of African mole-rats and evolutionary processes within the family, future research should also be focused to other species, especially those from Central and Eastern tropical Africa.

Ecological characteristics in habitats of African mole-rats and the implications for the evolution of mole-rat sociality

African mole-rats inhabit climatically and physically divergent habitats and excavate their burrows in various soil types (Bennett & Faulkes 2000). Besides that, they are found over a wide range of altitudes, ranging from coastal to high mountainous areas where they can reach over 3300 m a. s. l. (Bennett & Faulkes 2000, Broekman *et al.* 2006). Thus, it seems that the ecological factor which primarily dictates the distribution of mole-rats is the presence of geophytes as their staple diet. Apart from two species of the genus *Bathyergus* that also consume aerial vegetation, all species of mole-rats feed exclusively on geophytes, the underground storage organs of plants (in form of bulbs, corns, tubers and fleshy roots) (Bennett & Faulkes 2000).

As highlighted above, social evolution within the African mole-rats has been under debate for the last two decades. The most frequently mentioned theory used to explain the evolution of sociality, the aridity food distribution hypothesis (AFDH), emphasises the role of ecological factors in the mole-rats' social evolution (Jarvis *et al.* 1994, Bennett & Faulkes 2000). The most important of which are size and spatial distribution of food resources and the quality of soil, through which an animal burrows in search for resources (Jarvis *et al.* 1994, Jarvis *et al.* 1998, Spinks *et al.* 2000, Faulkes & Bennett 2007). These factors are thought to follow a gradient of aridity (see Fig. 1). The AFDH insists that mole-rat sociality is a derived trait and that eusociality evolved as an adaptive response to a combination of the patterns of rainfall and the distribution of food in harsh arid environments (Jarvis *et al.* 1994, Faulkes *et al.* 1997). The two extant mole-rat species denoted as eusocial live mainly in arid regions, where the soil is hardly workable, because it is either extremely hard (in the case of *Heterocephalus glaber*) or loose (in the case of *Fukomys damarensis*) for most of the year (Bennett & Faulkes 2000) and the food resources are clumped or widely spaced (Brett 1991a, Jarvis *et al.* 1998; Lovegrove & Knight-Eloff 1988). On the contrary, solitary species may inhabit mesic areas, where food resources are evenly spaced and rainfall is higher and its pattern predictable (Jarvis *et al.* 1994, Bennett & Faulkes 2000).

The competing hypothesis of phylogenetic constraints (HPC - Burda *et al.* 2000, Šumbera *et al.* 2007a) considers sociality (cooperative monogamy) to be an ancestral trait and a precondition to occupy harsh environments (Burda *et al.* 2000). Although this hypothesis does not emphasise ecological relations, it basically agrees with the AFDH in the expectation

that social mole-rats would be able to live under harsher conditions than their solitary counterparts. HPC is based on Nevo's (1979) proposition that an intense intraspecific
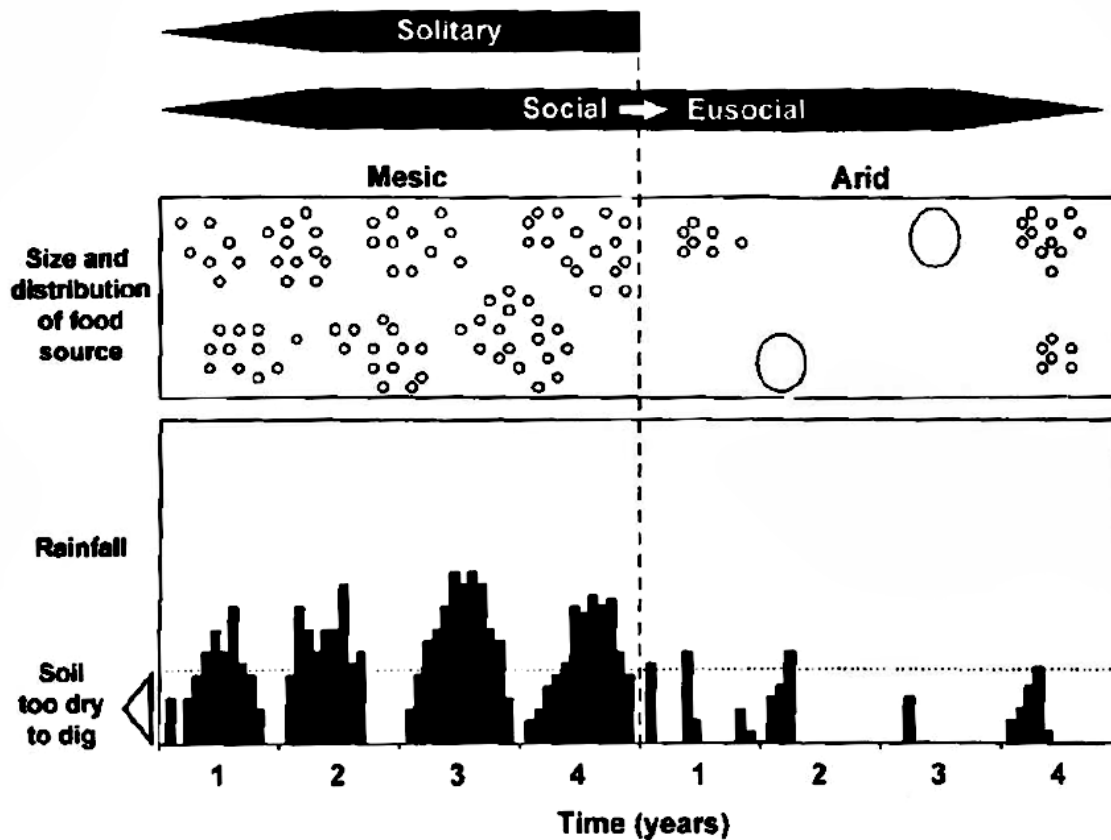
Figure 1. A schematic representation of the ecological conditions in habitats occupied by solitary, social and eusocial species of African mole-rats (from Bennett & Faulkes 2000).

competition for underground food resources lead to solitariness and aggressive territoriality in subterranean mammals. The fact that in two lineages of African mole-rats sociality has been preserved, or even more elaborated is explained by the existence of phylogenetic constraints, such as slow postnatal development (Burda *et al.* 2000).

Despite the fact that the AFDH has been accepted by many authors as the most plausible hypothesis explaining mole-rats sociality, to draw general conclusions from this theory seems to be arguable. The principal demerit of the AFDH lies in the fact that it is based on ecological characteristics of habitats of only two species occupying very harsh arid environments. Unfortunately, empirical data on the ecological conditions in representative habitats of most solitary and other social species of mole-rats are largely missing. It is important to emphasise that other social species of mole-rats, especially those of the genus *Fukomys*, fulfil the preconditions of the eusocial system described in *H. glaber* and *F. damarensis* (Burda *et al.* 2000). Importantly, apart from *F. damarensis* all of them inhabit

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mesic habitats in tropical regions (VanDaele *et al.* 2007). Additionally, ecological characteristics in habitats of some solitary species contradict preconditions of the AFDH. The distribution area of the Namaqua dune mole-rat *B. janetta* is restricted to coastal sand dunes which are ranked among the most arid sites in Africa, with an average annual rainfall of only about 150 mm (Herbst *et al.* 2006). Furthermore, studies on the silvery mole-rat *H. argenteocinereus* found that this afrotropical mole-rat is a generalist surviving in a variety of habitats with markedly different ecological conditions (Šumbera *et al.* 2007a). Šumbera *et al.* (2003) showed that this mole-rat thrives in habitats with an even lower abundance of food than was suggested to preclude solitary existence in subterranean rodents (Lovegrove 1991). Besides, food resources in its natural habitats are clumped (Šumbera *et al.* 2007a, Šklíba *et al.* in press), thus falsifying the precondition of the AFDH that solitary species would avoid such habitats.

In subterranean mammals, interspecific competition results in largely parapatric distributions, where each species is better adapted to, and more efficient in its preferred microhabitat (Nevo 1979, 1999). In African mole-rats, however, distribution of several social species overlaps with that of a solitary species or they can even be found syntopically (Bennett & Faulkes 2000). Analysing the microenvironmental conditions of these species in areas of sympatry can be very helpful to identify the mechanism of niche differentiation and the role of the social system in it.

In conclusion, current knowledge on ecological characteristics in habitats of African mole-rats is heavily biased in favour of two eusocial species, *H. glaber* and *F. damarensis*. It is dispiriting that relevant ecological data, such as food resource and soil parameters, are missing even in the most recent ecological studies on *Bathyergus janetta*, *B. suillus* and *F. mechowii* (Herbst & Bennett 2006, Thomas *et al.* 2009, Sichilima *et al.* 2008). To answer the questions concerning the evolution of mole-rat sociality and what is the role of ecological factors, thoroughly designed studies on ecological characteristics in various species of mole-rats, especially on solitary mole-rats from the South African region and (eu)social *Fukomys* species from mesic Central Africa, are of particular interest.

Architecture of burrow systems and burrowing in African mole-rats

Subterranean mammals spend most of their lives in self-constructed burrow systems that provide them with safety from predation, climatic extremes and ensure access to food

resources (Nevo 1999, Busch *et al.* 2000). Thus, on the one hand the burrow systems of all mole-rats have a similar architecture – they consist of a superficial network of foraging tunnels interconnected with a system of more deeply located chambers used for nesting, food storage and sanitation (Hickman 1979, Brett 1991a, Nevo 1999, Spinks *et al.* 2000). On the other hand, the level of social organisation, group size, habitat characteristics and individual variability are relevant factors influencing the architecture of mole-rat burrow systems (Hickman 1990, Nevo 1999, Bennett & Faulkes 2000, Šumbera *et al.* 2008).

The burrow systems are mainly changed as mole-rats search for new sources of food (Bennett & Faulkes 2000). According to the principal assumptions of the AFDH, parameters of food resources are just those which discriminate between habitats occupied by social and solitary mole-rats (for citations see above). Therefore, it is expected that burrow architecture would be different in arid and mesic environments, for solitary and social species (LeComber *et al.* 2002). Accordingly, in arid habitats, where geophytes are patchily distributed and inter-patches distances are relatively long, burrow systems may be large and linear, whereas in mesic habitats burrow systems are expected to be more branched and not so extensive. Besides, in social species burrow systems may be larger and more complicated than for solitary ones due to cooperative digging.

The burrow system characteristics among various species of mole-rats are summarised in Table 1. The largest completely excavated burrow system so far is that of the naked mole-rat from Kenya (Jarvis 1985). But it should be noted, that Brett (1991a) estimated (on the basis of radio-telemetry) that a naked mole-rat family may inhabit more than 3 km of tunnels. In social *C. h. hottentotus*, longer and more linear burrow systems were found in arid areas compared to more reticulate and interwoven systems from mesic habitats (Spinks *et al.* 2000). In solitary species, mole-rats from the genera *Bathyergus* and *Georychus* from the South African sub-region construct relatively simple burrow systems (Davies & Jarvis 1986, Herbst & Bennett 2006, Thomas *et al.* 2009) and the largest were found in the largest solitary bathyergid, *B. Suillus* (Davies & Jarvis 1986). In the solitary Afrotropic silvery mole-rat, burrow system architecture show a great variability and the shape of burrow system mainly reflects the habitat type and availability of food resources - the burrow systems were rather linear in grasslands with a low abundance of food, but more branched in miombo woodland where the abundance of geophytes is higher (Šumbera *et al.* 2003, 2008). Furthermore,

Table 1. Parameters of burrow systems characteristics in various species of African mole-rats (M – males, F – females, NA – not available, mean values are presented if available).

Species	Degree of Sociality	Habitat	Locality	Length (m)	Fractal dimension[1]	Source
H. glaber	Eusocial	Arid	Mtito Andei, Kenya	595	1.34	Jarvis 1985
			Lerata, Kenya	> 3000[2]	1.47	Brett 1991a
C. h. hottentotus	Social	Arid	Stienkopf, South Africa	313	1.33	Spinks *et al.* 2000
		Mesic	Sir Lowry's Pass, South Africa	127	1.37	Spinks *et al.* 2000
		Mesic	Darling, South Africa	NA	1.51	Cited in LeComber *et al.* 2002
F. mechowii	Social	Mesic	Chingola, Zambia	NA	1.23	Cited in LeComber *et al.* 2002
		Mesic, dry season	Chingola, Zambia	239	1.24	Sichilima *et al.* 2008
		Mesic, rainy season	Chingola, Zambia	259	1.30	Sichilima *et al.* 2008
F. darlingi	Social	Mesic	Goromonzi, Zimbabwe	NA	1.33	Cited in LeComber *et al.* 2002
B. suillus	Solitary	Mesic	Pella, South Africa	400	1.36	Davies & Jarvis 1986
			Darling, South Africa	100[M], 38[F]	NA	Thomas *et al.* 2009
B. janneta	Solitary	Arid	Northern Cape, South Africa	128	NA	Herbst & Bennett 2006
G. capensis	Solitary	Mesic	Darling, South Africa	NA	1.26	Cited in LeComber *et al.* 2002
			Darling, South Africa	130	1.41	Du Toit *et al.* 1985
H. argenteocineresus	Solitary	Mesic	Athi Plains, Kenya	43[3]	1.32	Jarvis & Sale 1971
		Mesic, dry and cold season	Blantyre, Malawi	47	1.19	Šumbera *et al.* 2003
		Mesic, dry and hot season	Blantyre, Malawi	99	1.33	Šumbera *et al.* 2003
		Mesic, dry and cold season	Mpalaganga, Malawi	202	1.46	Šumbera *et al.* 2008

1) Fractal dimension (FD) has been proposed as an appropriate approximation of burrow system complexity. Simple, non-branched burrow systems exploring relatively little surrounding area have a FD close to 1.0, whereas systems exploring area more thoroughly have a FD closer to 2.0 (see LeComber *et al.* 2002 for details).
2) Not completely excavated (see Brett 1991a)
3) Subadult individuals

burrow systems from the latter habitat belong to the most complicated found in mole-rats, regardless of social organisation. The most striking findings are on the giant mole-rat *F. mechowii*, the largest social bathyergids inhabiting the same habitat as the silvery mole-rat. The burrow systems of this species were smaller than expected and very simply branched (Sichilima *et al.* 2008, for an example see Fig. 2). Surprisingly, although giant mole-rat
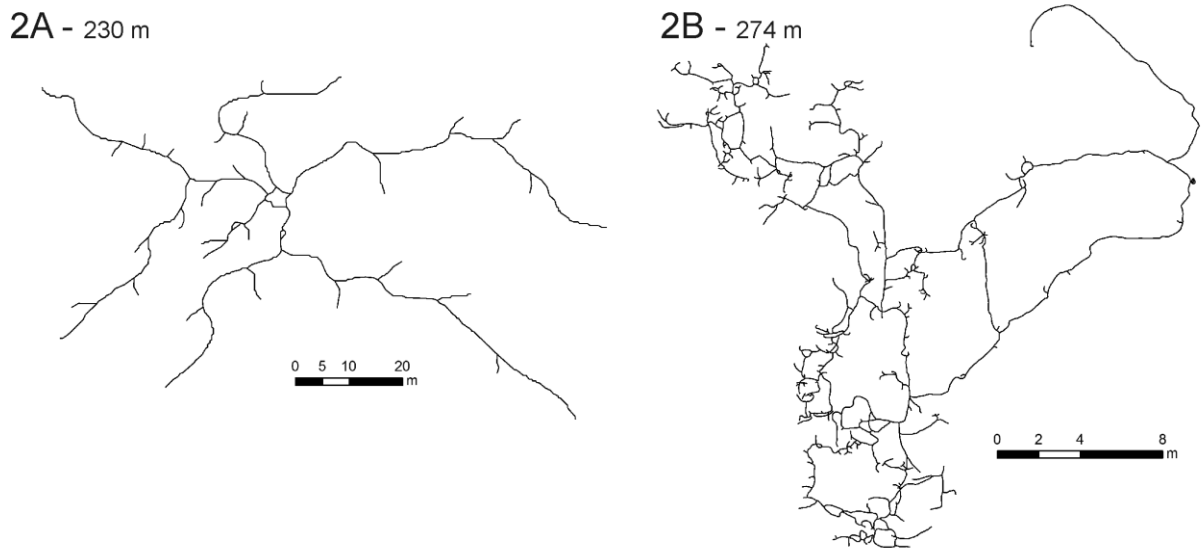
2A - 230 m   **2B** - 274 m

Fig. 2 Examples of burrow systems of *F. mechowii* (2A) and *H. argenteocine*reus (2B) mapped during the dry season (lengths of all tunnels comprising burrow systems are given; redrawn from Sichilima *et al.* 2008 and Šumbera *et al.* 2008).

systems were larger than those of the silvery mole-rat, the total length of tunnels was comparable between these species (Table 1; Fig. 2). Such findings could probably be explained by the fact that this study was carried out in semi-natural habitats and minor tunnels were probably neglected.

Besides the general pattern reflecting the interspecific and interhabitat differences, burrow systems are dynamic structures changing throughout the year (Šklíba *et al.* 2009). It has been suggested that burrowing activity probably occurs mainly during and just after rains when the soil is softened and hence easily workable (Brett 1991a, Jarvis *et al.* 1994). The hardness of soil is considered to be a limiting factor especially in arid habitats (Jarvis *et al.* 1998, Spinks *et al.* 2000) and cooperative burrowing in social mole-rats seems to be advantageous under such conditions (Bennett & Faulkes 2000). However, Burda *et al.* (2000) argue that the soil in generally mesic Afrotropic regions may become as hard as that in arid habitats of the naked mole-rat during the dry season. Interestingly, in the mesic solitary silvery mole-rat overall digging activity did not cease even during the advanced dry season

(Šumbera *et al.* 2003). Nevertheless, all these assumptions are based on monitoring of new mounds or mapping of burrow systems and the burrowing activity itself has rarely been examined. A significant increase in daily energy expenditure (it most likely indicate increase in burrowing activity) during the rainy season has only been documented in *F. damarensis* using the double labelled water (DLW) method (Scantlebury *et al.* 2006), and it is unclear whether the rain serves as a trigger for activity in other species, especially those from mesic regions.

During the rainy season, social mole-rats extend the main tunnels linearly into new unharvested areas (Lovegrove & Painting 1987) and probably only a little harvesting of food occurs (Jarvis *et al.* 1998). As the soil dries out, tunnels are revisited by the mole-rats and short side, highly branched tunnels, are dug from the main tunnels in search of food (Lovegrove & Painting 1987). A similar burrowing pattern has also been documented in the solitary silvery mole-rat occurring in grasslands (Šumbera *et al.* 2003). Moreover, during the dry periods of the year, mole-rats preferably deposit soil underground (Jarvis *et al.* 1998, Šklíba *et al.* 2009) because mound construction is probably energetically very costly in hard soil as suggested by Šumbera *et al.* (2003). Additionally, in the sandy habitats of *F. damarensis*, the loose sandy soil precludes the permanent existence of superficial burrows during the dry season (Lovegrove & Painting 1987, Jarvis *et al.* 1998). Thus, it seems that the pattern of burrowing and burrow system architecture follows the optimal foraging strategy, i.e. mole-rats adjust their burrowing activity to the most favourable ecological conditions to maximise foraging effort.

Spatial and temporal activity in African mole-rats: what determines mole-rat activity?

The life of almost every animal is divided into two basically different behavioural states: activity and rest (Halle & Stenseth 2000). Subterranean rodents predominantly rest inside the nest and a variety of vital tasks, such as foraging, maintenance of the burrow system, exploration and patrolling, are performed within the area of the home-range. Adjusting the activity to periodically changing environmental conditions has an adaptive significance in all living organisms (Enright 1970) and choosing the right time for activity and rest results in their better survival and/or increased reproductive success (Halle & Stenseth 2000).

Periods of activity follow circadian periodicity in most mammals (Bartness & Albers 2000). The circadian periodicity may be related to light, temperature, predation risk, and food

availability (Halle & Stenseth 2000). However, the underground niche is permanently dark, thermally buffered and neither food availability nor predation risk is thought to change much during the course of a 24-h cycle (Nevo 1999; Bennett & Faulkes 2000, Burda 2003; Begall *et al.* 2007). That raises the question whether activity in African mole-rats has a circadian character and if so what factor/factors may serve as zeitgebers of the circadian activity rhythms.

In mammals, the most important environmental zeitgeber is light (Bartness & Albers 2000, Favreau 2009). Despite a regressed visual system, both solitary and social mole-rats exhibit light entrained circadian rhythms under laboratory conditions (reviewed by Němec *et al.* 2007). However, there is an important question whether the photoperiod may serve as principal zeitgeber under natural conditions where mole-rats are not likely to be exposed to light, except for the short and sporadic occasions when they open a tunnel to the surface (Brett 1991b). This is probably too rarely to reset their circadian clock.

In African mole-rats, an important environmental determinant of their activity could be soil temperature. An association between soil temperature and activity has been found in other subterranean rodents occurring in temperate climate zones, the Middle East blind mole rat *Spalax ehrenbergi* and the plain pocket gopher *Geomys bursarius* (Rado *et al.* 1993, Benedix 1994). However, daily and seasonal changes in temperature are lower in habitats occupied by African mole-rats (Bennett *et al.* 1988). Among them, one of the highest temperature fluctuations are known from arid regions occupied by eusocial *F. damarensis* (Lovegrove & Knight-Eloff 1988, Roper *et al.* 2001). There, mean winter and summer temperatures at the depth of primary burrows are physiologically stressful for *F. damarensis* because they are above and below the upper and lower limits of thremoneutrality for this species (Lovegrove 1986). Hence, during the hottest period of the year, Damaraland mole-rats have to engage in frequent but short bouts of activity probably to avoid hyperthermia during burrowing (Lovegrove 1988).

On the contrary, the mesic Afrotropic region is characterised by relatively lower daily and seasonal changes in soil temperature (Šumbera *et al.* 2004). Despite that, an association between activity and burrow temperature has been found in the Afrotropical solitary silvery mole-rat whose activity pattern was closely related to slight below ground temperature fluctuations, mostly less then 3°C (Šklíba *et al.* 2007). Silvery mole-rats increased their activity with rising temperatures during the coldest part of the year but at the beginning of the hot and dry season the period of enhanced activity was earlier in the day and there was a drop

in activity during the warmest hours of the day (Šklíba *et al.* 2007). Unfortunately, activity and its determinants under natural conditions have never been studied in any social species of the genus *Fukomys* occurring in a similar habitat to the solitary silvery mole-rat. Such comparisons are very intriguing, especially since laboratory data indicate different adaptations to cope with temperature between the silvery mole-rat and *Fukomys* species (Šumbera *et al.* 2007b).

The spatial activity of subterranean rodents belongs to the most intriguing aspects of their biology. Underground locomotion involves extensive burrowing which results in a great impact on the landscape. The animals redistribute soils between different horizons and contribute to aeration, irrigation, and fertilisation of soils. Consequently, these processes promote diversity and maintain disturbance-dependent components of plant communities (Reichman & Seablom 2002). Therefore, subterranean rodents are considered to be a major physical force in their native ecosystems (Huntly *et al.* 1988) and are denoted as a classic example of ecosystem engineers (Cameron 2000, Reichman & Seablom 2002, Zhang *et al.* 2003).

Only little is known about the spatial activity of Bathyergidae. Since they feed on the underground storage organs of plants whose short-term renewability is low, their burrow system must be dynamic, contrary to some subterranean insectivores whose burrows may act as pitfall traps for prey (Macdonald *et al.* 1997). In the solitary *H. argenteocinereus* it has been found that the whole burrow system is a very dynamic structure with remarkable shifts of activity of inhabitants in space (Šklíba *et al.* 2009). According this study, silvery mole-rats continually rebuild their burrow systems and excavate approximately 0.7 m of new tunnels per day and backfill on average 64% of all tunnels. On the contrary, stable home-ranges are expected in social bathyergids having large burrow systems (Bennett & Faulkes 2000). Large colonies of *H. glaber* and *F. damarensis* remain in the same home-range for many years (Brett 1991a, Jarvis *et al.* 1998). Nevertheless, continual excavation of new burrows must also occur in social species in order to locate new food resources.

In socially living species, the behaviour of other conspecifics could be a relevant stimulus influencing individual activity (Favreau 2009). Mole-rat societies are hierarchically organised multigenerational family groups in which division of labour between family members is supposed to occur (Bennett & Jarvis 1988, Jarvis *et al.* 1994). According this scenario, high-cost tasks such as labour is restricted mainly to the smallest non-breeding individuals, the frequent workers (Bennett & Jarvis 1988, O´Riain *et al.* 1996). Hence,

differences in spatial activity between individuals are presumable. To date only three field studies have dealt with activity in social mole-rats. Unfortunately, radio-telemetry studies on *F. damarensis* and *H. glaber* have not provided comparisons between individual mole-rats within studied families (Lovegrove 1988, Brett 1991a). Only the study on *F. damarensis* using the DLW method has proved that non-breeders were the most active individuals within their families (Scantlebury *et al.* 2006). Although this study showed that the DLW method could be an excellent way to assess activity in subterranean mammals, some fundamental aspects of activity cannot be examined this way. Thus, whether the activity of individual mole-rats is synchronised within a family and how different individuals utilise the family home-range are questions which still need to be answered.

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The aim and summary of the Ph.D. thesis

The aim of this dissertation thesis is to study the biology of African mole-rats from mesic Afrotropic regions using different methodological approaches. I studied three bathyergid species with different social systems. The solitary silvery mole-rat (*Heliophobius argenteocinereus*) is the most widespread solitary bathyergid representing the second most basal phylogenetic lineage within the family. The other two species, the giant mole-rat *Fukomys mechowii* and Whytei's mole-rat *Fukomys whytei*, are social and belong to the genus which is the youngest lineage among bathyergids. This genus is the most speciose genera within African mole-rats and underwent extensive radiation in the Zambezian region. Some *Fukomys* species, such as *F. mechowii*, are denoted as eusocial by some authors. The giant mole-rat is the largest social bathyergid and is frequently studied in captivity but studies from free-living conditions are scarce. The Whytei's mole-rat is a relatively small species belonging to the least known African mole-rats.

All three bathyergids occupy a similar habitat type - miombo woodland - and areas of their distribution partially overlap. Thus, they face similar macro and microenvironmental conditions and selection pressures in their habitats. Taking into account their opposing lifestyles and similar living conditions, this makes them useful subjects for studying ecological and behavioural adaptations to a subterranean lifestyle in a broader concept. The significance of the studies presented here also consists of the fact that they contribute ecological and behavioural data that have been largely missing in mesic living mole-rats and that are necessary for further rigorous testing of the theories on the evolution of mole-rat sociality.

The main aim of **study I** was to identify ecological parameters which discriminate habitats occupied by the solitary *H. argenteocinereus* and social *F. whytei* in an area of sympatry. Our findings show that the two species of mole-rats occupied habitats that differed markedly in food supply and soil parameters. We suggest that the niche segregation of the two species at the study locality may consist of an inability for the solitary species to survive under harsh ecological conditions, i.e. low food supply and hard soil. We also speculate that absence of the social species in habitats occupied by *H. argenteocinereus* may be due to less effective thermoregulation of *Fukomys* or competitive exclusion. Our results have to be considered as preliminary, because they are limited to only one locality per one species in an area of sympatry. More localities and more transects will be necessary to definitely establish

the pattern of niche segregation among bathyergids. In addition, we used our ecological data together with all available published information on food supply and precipitation for localities inhabited by different species of mole-rats, to elucidate if mole-rat food conditions reflect patterns of rainfall and whether these conditions are clearly separate between localities occupied by solitary and social mole-rats as it is expected from the AFDH.

The principal objective of **study II** was to collect the first ecological data on the giant mole-rat from its natural habitat, miombo woodland. It is a paradox that this information on a mole-rat species so intensively studied in captivity was missing. We also collected data on family size and revealed the family structure and parentage in two of the families studied. Importantly, we provide information on the characteristics of the food supply and soil around giant mole-rats' burrow systems. Our findings rank giant mole-rat burrow systems as the largest ever mapped in any subterranean mammal. Moreover, our findings indicate that giant mole-rats occur in habitats characterised by very hospitable ecological conditions.

The objective of **study III** was to determine spatial and temporal activity patterns in one family of free-living giant mole-rats. In particular, we analysed the home-range size of the whole family and individual animals to see if there is difference in spatial activity between family members. We also specified daily patterns of outside-nest activity and evaluated the association of the outside-nest activity to environmental factors. We found considerable differences in activity between family members; our findings are the first from mole-rats in free-living conditions and support the hypothesis that breeding animals are the least active individuals in mole-rat families.

In **study IV** we used an ecophysiological approach to study mole-rat activity. To test if daily energy expenditure (DEE) in the free-living silvery mole-rat increases after rains (it is expected that this reflects higher mole-rat activity, mainly burrowing) in better workable soils in order to re-established their burrow system and get more food we used the DLW method. We also measured resting metabolic rate (RMR) to determine sustained metabolic scope (SusMS) and examine whether it varies between seasons and what the physiological sustainable level of activity in the silvery mole-rat is. Our findings suggest that rainfall is an important environmental factor responsible for higher energy expenditure in mole-rats.

Study I

Lövy M., Šklíba J., Burda H., Chitaukali W.N and Šumbera R. Ecological characteristics in habitats of two African mole-rat species with different social systems in an area of sympatry: implications for the evolution of mole-rat sociality. *(Accepted in Journal of Zoology)*

Abstract

African mole-rats (Bathyergidae) are subterranean rodents with diverse social systems which range from solitary to highly cooperative. We examined ecological characteristics in habitats occupied by two mole-rat species with different social systems in an area of sympatry in the Nyika Plateau, Malawi. Whereas the solitary silvery mole-rat *Heliophobius argenteocinereus* occurs there in high-elevated afromontane grasslands, the social Whyte's mole-rat *Fukomys whytei* is bound to lower Miombo woodlands. The habitat of *F. whytei* was characterized by a lower food supply and harder soil. We suppose that the niche segregation of the two species in the Nyika Plateau is due to the inability of the solitary species to survive under harsh ecological conditions. Absence of *F. whytei* in higher altitudes may be because of its less effective thermoregulation, competitive exclusion by *H. argenteocinereu*s, or other unknown factors. Analysis of available data on food supply and precipitation from different mole-rat localities revealed that there is no clear separation of the localities inhabited by solitary, social, and so-called eusocial species. We therefore conclude that the distribution of mole-rat species with different social systems may be determined to a great extent historically.

Study II

Šumbera R., Mazoch V., Patzenhauerová H., **Lövy M.**, Šklíba J., Bryja P. and Burda H.
Burrow architecture, family composition and ecological conditions of the largest social
African mole-rat; the giant mole-rat constructs really giant burrow system. *(Under minor
revision in Acta Theriologica)*

Abstract

Among African mole-rats, the giant mole-rat *Fukomys mechowii* is the largest social species.
Despite several attempts to study a free living population, information on its biology from
natural habitats is very scarce. We mapped two neighbouring burrow systems of the giant
mole-rat in miombo woodland in Zambia. We provide information on size and kin structure of
the respective mole-rat families, architecture of their burrow systems, and characteristics of
the food supply and soil around two excavated and additional ten burrow systems. Both
uncovered burrow systems were very large (total length 2,245 and 743 m), making them the
largest burrow systems ever mapped. Food resources around the additional ten burrow system
had a clumped distribution (standardized Morisita index of dispersion = 0.526), but a
relatively high biomass (298 ± 455 g m^{-2}). This, together with favourable soil conditions even
in the advanced dry season (cone resistance 328 ± 50 N m^{-2} and soil density 1.36 ± 0.06 g cm^{-3}) indicates relatively hospitable ecological conditions. Both food supply and soil conditions
were comparable with the conditions found in miombo habitat of the solitary silvery mole-rat
in Malawi. This suggests that there are no ecological constraints which would preclude
solitary life of a subterranean herbivore from the examined habitat. Microsatellite analysis
supported the assumption that giant mole-rats live in monogamous multigenerational families
with only one breeding pair of non-related animals and their offspring. The mean family size
is consistent with previous findings on this species and comparable to that found in other
Fukomys species studied thus far.

Study III

Lövy M., Šklíba J., Šumbera R. Spatial and temporal activity patterns of the free-living giant mole-rat *Fukomys mechowii*, the largest social bathyergid. (*Original manuscript*)

Abstract

Despite the considerable attention devoted to the social species of African mole-rats (Bathyergidae, Rodentia), knowledge is lacking for their behaviour under natural conditions. We studied the activity of the largest social bathyergid, the giant mole-rat *Fukomys mechowii*, in its natural habitat in Zambia using radio-tracking. Our study is based on nine 24 h radio-tracking periods of five individuals within one family and one isolated adult female from another family. Within the family, the breeding male utilised a smaller home-range compared to the nonbreeders. Non-breeding mole-rats overlapped the most in their areas of activity, but some of these (about 17%) were exclusively used. The activity pattern of the breeding male had no distinct peak, whereas non-breeding individuals were more active during the night, when the temperature at the depth of deeper burrows was also the highest. In contrast, the isolated female was active during daylight. We suppose that this female was a dispersing individual that had temporarily adopted solitary habits. Our findings, the first obtained from natural conditions, directly support the scenario that breeding animals are the least active individuals in mole-rat families and that high-cost activities are primarily performed by non-breeders.

Study IV

Abstract

In seasonal climatic regimes, animals have to deal with changing environmental conditions. It is reasonable to expect that seasonal changes are reflected in animal overall energetics. The relation between daily energy expenditure (DEE) and seasonally variable ecological determinants has been studied in many free-living small mammals; however with inconsistent results. Subterranean mammals, i.e. fossorial (burrowing) mammals which live and forage underground, live in a seasonally and diurnally thermally stable environment and represent a suitable model to test seasonality in DEE in respect to seasonal changes, particularly those in soil characteristics and access to food supply. Both factors are affected by seasonal rainfall and are supposed to fundamentally determine activity of belowground dwellers. These ecological constraints are pronounced in some tropical regions, where two distinct periods, dry and rainy seasons, regularly alternate. To explore how a tropical mammal responds to an abrupt environmental change, we determined DEE, resting metabolic rate (RMR) and sustained metabolic scope (SusMS) in a solitary subterranean rodent, the silvery mole-rat, at the end of dry season and the onset of rainy season. Whereas RMR did not differ between both periods, mole-rats had 1.4 times higher DEE and SusMS after the first heavy rains. These findings suggest that rainfall is an important environmental factor responsible for higher energy expenditure in mole-rats, probably due to increased burrowing activity. SusMS in the silvery mole-rat is comparable to values in other bathyergids and all bathyergid values rank among the lowest SusMS found in endothermic vertebrates.

Figure 1 The North Rumphi valley. On the Nyika Plateau, the solitary silvery mole-rat *Heliophobius argenteocinereus* occupies the highest parts of the plateau covered mainly with afromontane grassland.

Figure 2 A view from Jallawe peak. At lower altitudes, the predominant vegetation on the Nyika Plateau is open canopy Miombo woodland, the habitat occupied by the social Whytei's mole-rat *Fukomys whytei*.

Figure 3 Study locality at the Ndola Hill Forest Reserve, Copperbelt Province, Zambia. Miombo woodland shortly after the end of the rainy season (April 2009). Natural habitat of the largest social bathyergid, the giant mole-rat *Fukomys mechowii*.

Figure 4 Excavating the burrow system of the giant mole-rat *Fukomys mechowii*. Deep, tens of meter long tunnels probably serve for fast relocation of mole-rats between remote parts of the burrow system.

Figure 5 Radio-tracked breeding male of the giant mole-rat, shortly after release into the burrow system.

Figure 6 Locating a giant mole-rat after the end of radio-tracking. This animal escaped into the tunnel at a depth of more than 2.5 m.

Figure 7 Miombo woodland during the dry and hot season, Mpalaganga, Malawi 2008.

Figure 8 The same locality after the onset of the rainy season.

Figure 9 Daily energy expenditure of silvery mole-rats was measured using the double labelled water method. Here, we are taking a blood sample from the dorsal hindfoot vein to estimate isotope elimination rates.