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# Thermal biology of a strictly subterranean mammalian family, the African mole-rats (Bathyergidae, Rodentia) - a review

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ABSTRACT

African mole-rats are subterranean rodents, which rarely if ever leave the safety of their burrow systems. The environment of the burrows is humid, with relatively stable temperatures, and may have a hypoxic and hypercapnic atmosphere. One of crucial problems related to the subterranean way of life in mammals is avoidance of overheating, because traditional mammalian cooling mechanisms are not effective under high humidity. In African mole-rats, a variety of adaptations have evolved in response to this and other challenges of the underground ecotope. Traditionally, attention has been devoted mainly to the naked mole-rat *Heterocephalus glaber*, which became popular as a result of its eusociality and absence of fur, both being unique phenomena in small mammals. Despite more recent research, information on other species is still relatively limited and patchy. I review the results of studies on African mole-rats that are relevant for the understanding of their energetics and thermal biology. Attention is paid to the parameters of the burrow environment, which represent the main selection pressures shaping their physiology. In addition, an overview is given of the morphological, physiological and behavioural adaptations helping mole-rats to face temperature extremes, mechanisms by which they deal with a surplus of metabolic heat and how changes in ambient temperature influence their daily activity. The naked mole-rat is compared to its furred relatives to determine whether this species is really exceptional from the point of thermal biology. An ordination analysis was conducted using published data on mole-rat body temperature, thermoneutral zone, resting metabolic rate and thermal conductance. Most of the variability in these characteristics was found to be explained by body mass, followed by temperature characteristics of climate, but not precipitation, of the species distributional ranges. This analysis shows that the naked mole-rat is comparable to the other mole-rat species in these physiological characteristics.

## 1. Why study African mole-rats and their thermal biology?

Many mammals have evolved morphological, behavioural and physiological adaptations to cope with diverse ecological conditions that are considered as adverse from a human point of view. Physiological adaptations of mammals inhabiting challenging environments such as the Arctic zone, high altitudes, and arid deserts, as well as aquatic and aerial environments, have been intensively studied. Nevertheless, there is one group of mammals living in a very challenging, though less spectacular and less known environment; they live just a few centimetres below our feet. Across the globe more than 300 species of unrelated lineages of mammals have independently colonized the subterranean niche (Nevo, 1999). Despite advantages such as microclimatic stability, relatively low temporal variability in the availability of food resources and low risk of predation, it is a stressful environment. It is dark, deprived of most of the sensory cues available aboveground, and hypoxic (low in $O_2$ concentration) and hypercapnic (high in $CO_2$) in some situations. Mammals inhabiting this niche pay high energy costs to find food, because they have to dig through mechanically resistant soils to reach it. When burrowing, they also face a high risk of overheating, as the humid burrow atmosphere makes evaporative cooling ineffective. Some of these mammals have consequently modified their morphology, behaviour, sensory biology, and physiology to cope with these conditions (cf. Begall et al., 2007; Lacey et al., 2000; Nevo, 1999; Nevo and Reig, 1990).

The terms "subterranean" and "fossorial" are interchangeable and quite loosely used for different types of burrowing mammals. Actually, the term fossorial means *adapted to digging* (*fossor* = digger). Unfortunately, both are frequently applied to species with very different levels of adaptation to digging and subterranean life in general. Therefore, the terms should not be used as synonyms and types of fossoriality are better specifically defined. The classification, which I follow in this review, recognises (strictly) subterranean mammals, fossorial mammals and mammals with no remarkable adaptations for

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**Box 1**
Diversity and distribution of African mole-rats

African mole-rats (Bathyergidae) include 22 described species in six genera (Fig. 1) (Bennett and Faulkes, 2000; Kock et al., 2006), but according to recent estimates the species number could exceed 30 (Faulkes and Bennett, 2013). This is an ancient group of hystricognathous rodents, with fossils dating back to the early Miocene, while molecular dating indicates old intrafamilal divergence (the first split within the family - *Heterocephalus* - was estimated to occur between 33 and 48 Mya, Faulkes et al., 2004; Ingram et al., 2004). The newer phylogenetic study suggests a divergence leading to *Heterocephalus* around 31 Mya and divergence of the remaining genera starting around 18 Mya (Patterson and Upham, 2014). Very recently, Bryja et al. (2018) showed an even more recent first diversification in all bathyergid genera (22 Mya).

Bathyergids are endemic to Africa with a distribution extending south of the Sahara. The most speciose genus, *Fukomys,* is found mainly in savannah habitats in tropical Africa, whereas another social genus, *Cryptomys,* has a distribution limited to the subtropics and Mediterranean Southern African region. The monotypic genus *Heterocephalus* is represented by the naked mole-rat, *Heterocephalus glaber,* and occurs in the Horn of Africa. The another monotypic genus *Heliophobius*, represented by the silvery mole-rat, *H. argenteocinereus*, occurs mainly in Eastern Africa and is the only Afrotropical solitary genus, whereas the remaining solitary genera, *Georychus* and *Bathyergus*, are found exclusively in Southern Africa.

digging and subterranean life (non-fossorial or surface-dwelling). Fossorial mammals (sensu Begall et al., 2007) are animals that spend most of their time within their burrow systems, but regularly forage aboveground usually not far from a burrow opening (for example, tuco-tucos *Ctenomys* or the giant root rat *Tachyoryctes macrocephalus*). These mammals possess some adaptations for burrowing and life underground such as shortened ear lobes and tail, and enlarged claws or incisors, but they are more similar in the physiological and sensory traits to surface dwelling mammals. Mammals that live and forage below ground, such as the blind mole rats of the genus *Spalax*, African mole-rats and some talpids, are denoted as subterranean (chthonic). These mammals are adapted exclusively for life in the underground environment and their morphology, physiology and sensory biology are modified accordingly. They share a variety of physiological specializations not found in surface dwelling taxa (Buffenstein, 2000). This review deals with the African mole-rats, which belong to mammals best adapted for whole-life existence in burrow systems.

African mole-rats (Box 1) have attracted a great deal of attention in many biological disciplines such as behavioural ecology, physiology and sensory biology, with some of the species ranking among the best known of all mammals. Although mole-rats have been studied for more than three decades, the majority of researchers have focused their attention mainly on the naked mole-rat *Heterocephalus glaber*, one of the most peculiar mammals of all. The reason for this is the combination of unique traits in this species, such as the absence of fur, and the associated poor thermoregulatory capability, as well as its eusociality (Box 2). Recently, the naked mole-rat became a model for biomedical research, due to its longevity, pain insensitivity and purported cancer resistance (see Buffenstein, 2005; Fang et al., 2014; Kim et al., 2011; Pérez et al., 2009; Seluanov et al., 2009; Tian et al., 2013).

For several decades, the furred African mole-rats remained in the shadow of the naked mole-rat. Due to their common ancestry and long history of life in subterranean environments, we may assume that hairy mole-rats share many physiological, behavioural and life history traits with *H. glaber*. In other words, many traits (of course, apart from the nakedness) which are usually interpreted as species-specific peculiarities of the naked mole-rat might characterize also other bathyergid species, but as of yet they have not been searched for. Confirmation of common traits in mole-rats originated from studies on furred mole-rat species, predominantly during the last decade. For example, some other mole-rat species were found to be also long-lived (Dammann and Burda, 2006; Dammann et al., 2011; Schmidt et al., 2013; R. Šumbera unpubl. data for *Heliophobius*), insensitive to capsaicin, probably lacking pain related neuropeptides (Vole et al. unpubl. data) and eusocial (Patzenhauerová et al., 2013). Interestingly, recent research showed that some of these characteristics convergently evolved also in other unrelated subterranean rodents. For example, longevity and cancer resistance have been found in the blind mole-rat *Spalax* (Gorbunova et al., 2012; Manov et al., 2013). Thus, it is possible that most of these highlighted phenomena are consequences of living in this particular ecotope and characterise not only the naked mole-rat, but also other bathyergids and - to a larger or lesser extent - subterranean mammals in general.

It is surprising that, although African mole-rat ecophysiology has been studied for several decades, there has not yet been a review of their thermal biology. Apart from reviewing bathyergid thermal adaptations and the factors influencing it, such a review would be valuable also because mole-rats combine several unusual phenomena in mammals, which may attract interest not only of "subterraneanologists", but also the wider scientific community of mammalogists, ethologists,

**Box 2**
Bathyergid social organisation

There are three solitary and three social genera among the bathyergids (Fig. 1). In solitary species, adults of the opposite sex probably meet only for a short period during the mating season. Longer social contact probably occurs only between mother and offspring for a period of several weeks or months. Although solitary mole-rats were originally assumed to be monogamous or polygynous, recent genetic analyses indicate that females can mate with several partners during one mating season (Bray et al., 2012; Patzenhauerová et al., 2010).

Among social genera, two species have long been thought to be exceptional with respect to their social organisation. Some authors suggested *F. damarensis* and *H. glaber* as the only eusocial mammals, whereas the remaining social mole-rats were considered as "only" social. Eusociality is a social system with a high reproductive skew where only one female breeds and her "sterile" offspring assist her in raising younger siblings. According to parentage analyses and ecological data, it seems that *F. anselli* and probably other species of the genus *Fukomys* share the same social organisation with these two traditionally eusocial species, which is based on extended cooperative monogamy (Patzenhauerová et al., 2013). On the contrary, the mating system of *Cryptomys,* another social genus, seems to be less monogamous or potentially even polyandrous, because of the high occurrence of extrapair and extrafamilial paternity (Bishop et al., 2004). Despite the fact that *H. glaber* is the most studied bathyergid, there is a lack of parentage analysis of families originating in nature.

**Box 3**
African mole-rat world

African mole-rats occupy various savannah habitats from sea level up to high mountains. They can survive in different soil types varying from soft sandy substrates to seasonally very hard soils. Bathyergids feed mainly on subterranean storage organs of geophytes, i.e. plants with resting buds growing below the soil surface such as roots, bulbs, corms, rhizomes, etc. A sufficient density of such plant organs together with a layer of workable soil are the most important preconditions for mole-rat presence.

Bathyergid burrow systems can be relatively simple structures, with a few branches of a main tunnel and a total length of several tens of metres in some solitary species. However, highly social species can have extremely complicated networks comprising several kilometres of tunnels (Fig. 2). The shallow foraging burrows usually lay at a depth of 10–20 cm where most food sources are located and usually form about 80–90% of the total length of a burrow system. In burrow systems of some species, straight axial tunnels can be identified. These tunnels are usually situated deeper than the foraging ones. There are also other burrow components such as nests, food chambers, and sanitary areas. The deepest parts of a burrow system are dead-end burrows (Fig. 3) reaching a depth of around one or two metres with presumed antipredator and thermoregulatory functions. Excavated soil is deposited aboveground in mounds or is pushed into older burrows. The whole burrow system is a dynamic structure with new burrows continuously excavated and older burrows abandoned or backfilled.

physiologists and evolutionary biologists. Due to their strict subterranean way of life in complexes of burrows (Box 3), mole-rats must deal with life in an environment with high air humidity complicating heat dissipation. They feed almost exlusively on underground storage organs of plants, which are often widely spaced or patchily distributed in African savannahs, so intensive burrowing is unavoidable for securing enough food resources. Such physical activity inevitably produces an enormous surplus of heat, which has to be dissipated to avoid overheating. From this point, the ways that these mammals handle surplus heat is extremely interesting. Furthermore, mole-rats are exceptional among mammals due to the diversity of their social organisations. Because all mole-rats share the same strictly subterranean lifestyle with minimal confounding effects of different ecologies, the family is very suitable for studying the relationship between sociality and thermoregulatory abilities. Such an overview would be useful also because of the diversity of thermoregulatory modes ranging from so-called poikilothermy in the naked mole-rats through a tendency to poikilothermy in some furred species, to endothermy in the remaining species. In fact, this family was denoted as a model for the evolution of endothermy (Bennett, 2009).

In this review, I focus on different aspects of mole-rat life which are relevant with respect to their thermal biology. I reviewed all relevant information on the environment in the burrows, which is definitely the main selection pressure shaping the physiology of these strictly subterranean mammals. I provide an overview of the various adaptations that help mole-rats to face thermal stress, how they deal with a surplus of metabolic heat originating from energetically costly activities and how the burrow thermal environment influences their daily activity patterns. Solitary and social species are then compared to reveal how mole-rat thermal biology is related to different levels of social organisation, and to describe postnatal development of the thermal abilities and thermal biology of breeding individuals. Finally, I include an ordination analysis testing the relationship of the main physiological parameters, such as body temperature, resting metabolic rate, width of the thermoneutral zone and thermal conductance, to several explanatory, mainly climatic, variables.

## 2. Characteristics of mole-rat burrow environment

Spatially, a burrow system can be a very complex structure (Box 3, Figs. 2, 3) with its environment deviating from aboveground conditions in many aspects. Soil mounds together with a layer of soil and vegetation above the burrows provide isolation and buffering of the burrow environment, as well as diurnal and seasonal stability (Bennett et al., 1988; Burda et al., 2007; Holtze et al., 2018; Šumbera et al., 2004).

### 2.1. Ambient temperature

It should be mentioned, it is difficult to measure $T_a$ and other microclimatic characteristics in occupied burrows or nests, because mole-rats readily damage the measuring devices. However, we may expect the same $T_a$ in the burrow and surrounding soil when under the same conditions and depth (Holtze et al., 2018). Therefore, if not written explicitly, belowground $T_a$ in this review is temperature measured either in burrows or in soil, usually at the depth of the foraging tunnels.

For mammals, living in an environment with a stable and relatively high $T_a$ such as in burrows (Table 1), it is energetically profitable, because of the lower costs of body cooling or warming. Belowground $T_a$ is primarily determined by aboveground $T_a$, which is related mainly to latitude and altitude. The extent of its diurnal buffering depends on soil characteristics, such as porosity, hardness, colour and water content, depth of the burrows, and vegetation cover (cf. Burda et al., 2007). The amplitude of the daily change of $T_a$ decreases with the depth (Table 1). Such changes have been shown to be negligible (< 1 °C) at the depth of 50–60 cm at sites of the silvery mole-rat *H. argenteocinereus* in Malawi (Šumbera et al., 2008), the giant mole-rat *F. mechowii* (Lövy et al., 2013), Ansell's mole-rat *F. anselli* (Šklíba et al., 2014) in Zambia, the Damaraland mole-rat *F. damarensis* (Streicher et al., 2011) in South Africa and *H. glaber* in Ethiopia and Kenya (Holtze et al., 2018).

The belowground $T_a$ is very relevant for mole-rat thermal biology. Mole-rats usually live in a $T_a$ below their thermoneutral zones (TNZ). After comparison of data in Tables 1, 2, it is possible to see that the mean belowground $T_a$ is usually about 5–10 °C below the TNZ. Nevertheless, $T_a$ could fall well below this level. For example, soil temperature at the depth of the foraging burrows may decrease to 10 °C even in tropical mountains in Malawi (Lövy et al., 2012). Although relevant data about belowground $T_a$ are missing, we may expect much colder conditions in burrows of the Lesotho mole-rat *Cryptomys hottentottus mahali* in the Drakensberg Mountains in Southern Africa, which are more than 3 000 m a.s.l., because of the generally cold climate in this area (see Table A.1). Some species may face the opposite extremes. For example, in *F. damarensis*, the maximum of $T_a$ may exceed TNZ of the species in burrows 25–30 cm deep (Lovegrove and Knight-Eloff, 1988), while still being within the TNZ one metre deep during summer (Streicher et al., 2011) (Table 1). These temperatures increase the risk of mole-rats overheating, especially when burrowing.

The daily amplitude of belowground $T_a$ is also of importance, especially for large mole-rats, because temperature changes during day cannot be dealt with effectively by acclimatisation. In some species, the amplitude is indeed found to be relatively high. In *F. damarensis,* the amplitude was 10–14 °C at a depth of 15–46 cm (Bennett et al., 1988; Roper et al., 2001). Such an amplitude is not expected in the tropics. For example, it was found to be only 1–2 °C at a depth of 26–40 cm in

**Fig. 1.** Representatives of six mole-rat genera. The three social genera are represented by *Cryptomys h. hottentotus*, *Fukomys mechowii* and *Heterocephalus glaber* (from top left), whereas the three solitary taxa are represented by *Bathyergus suillus*, *Georychus capensis* and *Heliophobius argenteocinereus* (from bottom left) (photos by Radim Šumbera).

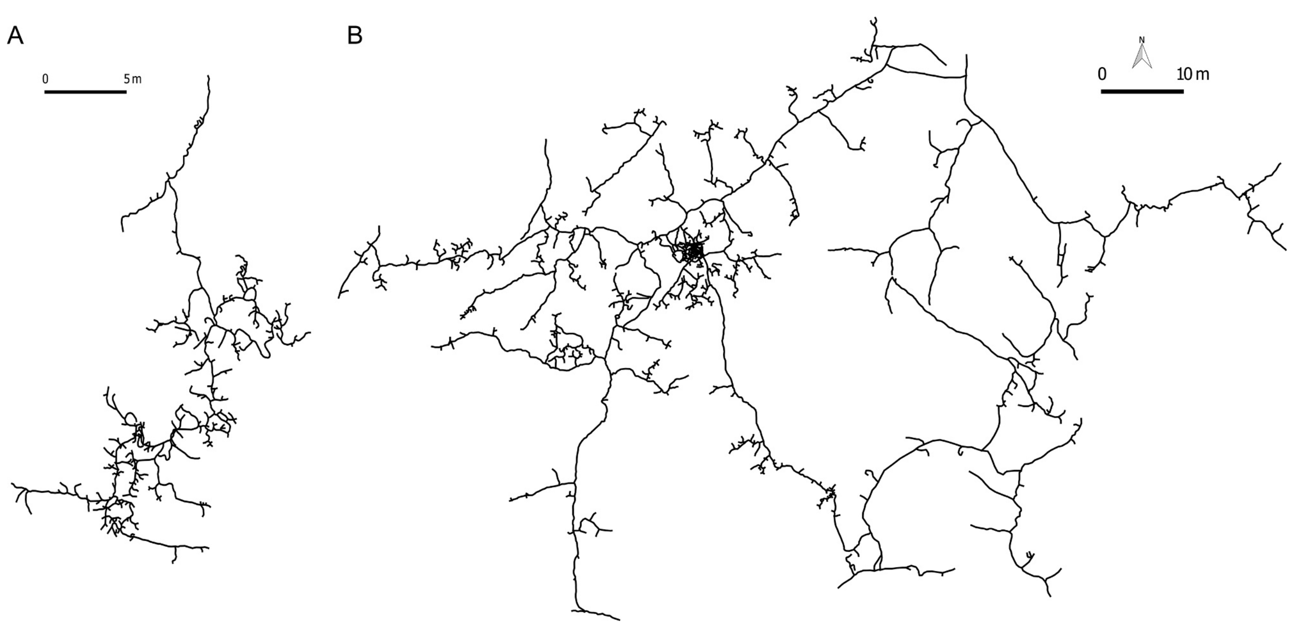


**Fig. 2.** An example of burrow systems of the solitary *Heliophobius argenteocinereus* (a) and social *Fukomys anselli* (b) from Miombo woodland in Malawi and Zambia respectively. Total length of the burrows is 214 m in the former and 1200 m in the latter.

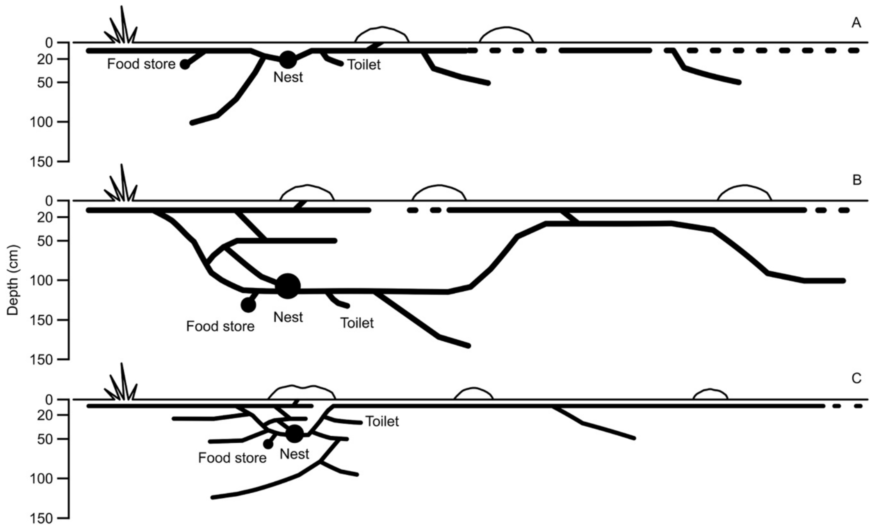


**Fig. 3.** A schematic lateral view on burrow systems of *Heliophobius argenteocinereus* (a), *Fukomys mechowii* (b) and *Fukomys anselli* (c). Note the differences in nest depths among the species and the higher proportion of deep tunnels in the giant mole-rat burrow systems. Size differences in the horizontal plane are not maintained in the pictures. Modified from Šklíba et al. (2016).

the naked mole-rat (Bennett et al., 1988; Jarvis, 1979; McNab, 1966) (Table 1). Nevertheless, systematically collected data in a recent study (Holtze et al., 2018) revealed larger diurnal fluctuations ranging from 25 to 49 °C in naked mole-rat burrows with a mean depth of 30 cm.

The belowground $T_a$ and its daily amplitude may differ markedly across one burrow system at the same depths if the vegetation cover is heterogeneous. In *F. anselli*, the amplitude was 8.0 °C at the depth of the foraging tunnels in a site where soil was exposed to sun, while only 1.8 °C in a site with abundant vegetation (Šklíba et al., 2014). The remarkable buffering effect of vegetation on temperature amplitude is reported in other studies (Holtze et al., 2018; Šumbera et al., 2004). In this situation, mole-rats may select colder parts of a burrow system for burrowing to avoid the risk of overheating as indicated by the naked mole-rat preference to dig in colder soil (Holtze et al., 2018). Alternatively, warmer sites could be used for obtaining heat, by the phenomenon known as basking (Brett, 1991; Buffenstein et al., 1996).

A high thermal capacity of soil is responsible for the delay in the daily cycle of belowground $T_a$ compared to the temperature cycle on the surface. Soil retains heat longer after sunset and remains cold for longer in the morning. Ambient temperature cycles in burrows decrease in amplitude and lag more behind the surface cycles with increasing depth. A lag time ranging from less than one hour through to up to about half a day was recorded in territories of African mole-rats (Table 1). This delay may influence the timing of activity of the mole-rats if related to $T_a$.

Seasonal variations of belowground $T_a$ are also predictable as they are based on the climate of the area. Similar to the daily amplitudes, seasonal changes are lower in the tropics (Bennett et al., 1988). The difference in the amount and pattern of precipitation between different areas of the same region is also relevant, because the belowground $T_a$ during winter differs from that in summer by more than 15 °C in xeric subtropics, but only by 5–7 °C in mesic subtropics (Bennett et al., 1988). Such a difference could be attributed to the higher vegetation cover in the mesic areas. A rapid change of belowground $T_a$ may follow a sudden change of some ecological factor, such as fires burning the insulative layer of vegetation or the onset of the rainy season. A rapid drop of about 11 °C in belowground $T_a$ at the depth of the foraging burrows of *H. argenteocinereus* was found because of the cooling effect of rains after the beginning of the rainy season (Šumbera et al., 2004) (Fig. 4).

## 2.2. Air humidity

Humidity is probably the most stable parameter of the burrow environment as the air of the burrows is almost saturated with water (Burda et al., 2007). Although its high value contributes to a water balance minimising pulmocutaneous evaporative water loss, it concurrently limits evaporative cooling. This represents a problem for heat dissipation, especially after energy consuming activities such as burrowing. In *F. anselli*, *F. mechowii* and *H. argenteocinereus*, humidity in foraging burrows ranged from 80% to 93% (Table 1). Even in *H. glaber*, a species living in arid habitats, humidity in its relatively shallow burrows approaches 60%. Compared to deeper burrows, where humidity exceeds 90% and is stable, lower and more variable values in superficial burrows is probably related to the unique way *Heterocephalus* deposits soil aboveground, known as volcanoing, during which burrows may be open for several hours (Holtze et al., 2018).

## 2.3. Gas composition

Subterranean mammals have been implicated in experiencing hypoxic and hypercapnic conditions due to poor ventilation of sealed burrow systems (Buffenstein, 2000; McNab, 1966). Many studies on African mole-rats assume very hypoxic and hypercapnic conditions in their burrows. Low $O_2$ and high $CO_2$ values would increase the breathing frequency, which requires energy, influencing heat production and the need to dissipate it.

Surprisingly, available information on gas composition from the burrows of African mole-rats in nature does not support pronounced hypoxy and hypercapny. The amount of $O_2$ and $CO_2$ in the burrows of four mole-rat species from different regions, such as *F. damarensis*, the Cape mole-rat *Georychus capensis*, *H. argenteocinereus* and *H. glaber*, did not deviate much from the aboveground atmosphere (Holtze et al., 2018; Roper et al., 2001; Šumbera et al., 2004) (Table 1). Even the first systematically collected data from the burrows of the naked mole-rat, i.e. the species supposed to live in atmosphere so different from aboveground, did not support it; the $O_2$ and $CO_2$ concentrations were 20.5% and 0.17% respectively. The variation in gas concentrations found in the mainly shallow burrows of these species are too small to cause any respiratory stress. We can assume that normoxic conditions is the rule rather than the exception in burrows of African mole-rats, however, in some cases hypoxia and hypercapnia may temporarily arise, which would explain their adaptations against hypoxia (Larson and Park, 2009).

Rain is an important factor that may dramatically change gas composition in burrows. This may be relevant especially in heavy soils, because compact substrates hinder burrow ventilation (Roper et al., 2001; Šumbera et al., 2004). There are no data available for bathyergids, but it is known that heavy rains decreased $O_2$ concentration up to 12.7% and increased $CO_2$ concentration to 5.6% in burrows of the Mediterranean blind mole rat *S. ehrenbergi* in some types of soil (Shams

**Table 1**
Microclimatic characteristics in burrows of African mole-rat species, subspecies and populations: ambient temperature ($T_a$) and its delay compared to aboveground temperature, humidity, $O_2$ and $CO_2$ concentrations. Aridity index (AI) and Annual Precipitation are characteristics of the climate in the sites from where these data were obtained. Aridity index showing dryness of the climate in the given location is calculated according to Tabuco and Zomer 2009 (http://www.csi.cgiar.org). Annual Precipitation data were obtained from Wordclim database (http://www.wordclim.org). "Season" includes the information when the data were collected (months I-XII) and for how long: D - days, W - weeks, M - months, Y - years. Country codes: ET – Ethiopia, MW – Malawi, NA – Namibia, KE – Kenya, ZA – South Africa, ZM – Zambia.

| Species | AI | Annual precipitation (mm) | Site (Country) | Season (months) | Altitude (m.a.s.l.) | Ta (°C) | Range of Ta (°C) | Delay of Ta (hours) | Humidity (range) | % $O_2$ (range) | % $CO_2$ (range) | Depth of measurement (cm) | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *G. capensis* | Dry sub-humid | 565 | Rondenbosch (ZA) | summer (I) | 17 | 26.1 ± 2.2 | 22.9–29.7 | | | | | 11.5 | Bennett et al. (1988) |
| *G. capensis* | ” | ” | Rondenbosch (ZA) | winter (VII) | ” | 12.2 ± 1.1 | 10.2–13.8 | | | | | 14.0 | ” |
| *G. capensis* | ” | ” | Cape Town (ZA) | summer (III)$^{2D}$ | ” | 21.7 ± 1.2 | 18.5–24.2 | 1.5–2 | | 20.4 (19.8 -) | 0.4 (- 1.2) | 14.9 | Ropper et al. (2001) |
| *C. h. hottentotus* | ” | 650 | Welington (ZA) | late summer (IV) | 122 | 25.1 ± 2.0 | 21.0–27.8 | | | | | 14.0 | Bennett et al. (1988) |
| *C. h. hottentotus* | Semi-arid | 449 | Darling (ZA) | winter (V) | 117 | 17.5 ± 1.0 | 15.9–18.8 | | | | | 20.0 | ” |
| *F. damarensis* | Arid | 336 | Dordabis (NA) | winter (VIII) | 1635 | 18.6 ± 2.7 | 15.0–22.8 | | | | | 13.0 | ” |
| *F. damarensis* | Semi-arid | 434 | Otjiworongo (NA) | summer (I) | 1501 | 34.8 ± 4.9 | 26.2–40.0 | | | | | 14.5 | ” |
| *F. damarensis* | Arid | 209 | Twee Rivieren (ZA) | summer (II) | 921 | 31.9 ± 1.0 | 29.9–33.0 | | | | | 38.0 | ” |
| *F. damarensis* | Semi-arid | 434 | Otjiwarongo (NA) | summer (I) | 1501 | 26.1 ± 1.1 | 23.6–29.6 | | | | | 23.5 | ” |
| *F. damarensis* | Arid | 228 | Kalahari (ZA) | summer (I)$^{3D}$ | 985 | 33.5 ± 1.3 | | 6–10 | | | | 25.0 | Lovegrove and Knight-Eloff (1988) |
| *F. damarensis* | ” | ” | ” | winter (VII)$^{3D}$ | ” | 18.8 ± 0.1 | | | | | | 30.0 | ” |
| *F. damarensis* | Semi-arid | 367 | Hotazel (ZA) | summer (III)$^{2D}$ | 1075 | 24.8 ± 3.1 | 19.6–29.3 | 4.5–5 | | 20.4 (19.9 -) | 0.4 (- 6.4) | 46.5 | Ropper et al. (2001) |
| *F. damarensis* | ” | ” | ” | summer (XII - III) | ” | 31.1 ± 0.5/29.7 ± 0.3/27.5 ± 0.4 | | | | | | 50/100/200 | Streicher et al. (2011) |
| *F. damarensis* | ” | ” | ” | winter (IV - IX) | ” | 17.5 ± 2.5/19.4 ± 2.4/21.3 ± 2.2 | | | | | | ” | ” |
| *H. argenteocinereus* | Humid | 1170 | Blantyre (MW) | dry (VI - X)$^{4M}$ | 1120 | 21.3 ± 3.1 | 16.5–28.3 | | 85 ± 1.2 (83.3–87) | | | 15.0 | Šumbera et al. (2004), unpubl. data |
| *H. argenteocinereus* | " | " | ” | rainy (XI - IV)$^{6M}$ | ” | 22.8 ± 1.2 | 20.2–26.9 | | | 19.2 ± 0.8 (17.8–20) | | ” | |
| *H. argenteocinereus* | | 1678 | Chipoka (MW) | dry (V - VI)$^{B}$ | 620 | 22.4 ± 1.0 | 20.6–23.6 | | 84.5 ± 6.0 (69 – 91) | 19.8 ± 0.4 (19.2–20.4) | | 24.0 | ” |
| *H. argenteocinereus* | ” | 1231 | Nyika NP (MW) | dry (VII)$^{4D}$ | 2090/2340 | 13.3 ± 0.1/11.7 ± 0.3 | 12.9–13.5/11.0–12.2 | 10/7 | | | | " | Lövy et al. (2012), unpubl. data |
| *H. argenteocinereus* | ” | 1713 | Mulanje mts (MW) | dry (VIII)$^{2D}$ | 1300/1840 | 19.0 ± 0.4/14.7 ± 0.4 | 18.4–19.5/14.0–15.3 | 8/7.5 | | | | 20.0 | ” |
| *H. argenteocinereus* | ” | 1143 | Zomba (MW) | dry(VII)$^{26D}$/dry(VIII)$^{19D}$/dry(XI)$^{7D}$ | 1070 | 17.7 ± 0.6/19.8 ± 1.1/23.4 ± 0.4 | 16.3–19.1/17.9–22.2/22.7–24.2 | 2/2/6 | 81 ± 1.3 (78–86) | | | 15/15/20 | Šklíba et al. (2007), Šumbera et al. (2008), unpubl. data |
| *H. argenteocinereus* | Semi-arid | 616 | Kapiti plains (KE) | end of dry (III)$^{1D}$ | 1524 | 26.0 | 23.2–26.8 | | | | | 15–60 | McNab (1966) |
| *H. glaber* | ” | 429 | Lerata (KE) | dry (VIII) | 833 | 29.6 ± 0.4 | 29.0–30.0 | | | | | 31.0 | Bennett et al. (1988) |

(*continued on next page*)

**Table 1** (*continued*)

| Species | AI | Annual precipitation (mm) | Site (Country) | Season (months) | Altitude (m.a.s.l.) | Ta (°C) | Range of Ta (°C) | Delay of Ta (hours) | Humidity (range) | % $O_2$ (range) | % $CO_2$ (range) | Depth of measurement (cm) | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *H. glaber* | ” | ” | Archers (KE) | dry (VII) | ” | 31.1 ± 0.6 | 30.5–32.0 | | | | | 26.0 | ” |
| *H. glaber* | ” | 645 | Kamboyo/ Tsavo (KE)[2Y] | (1982–1983) | 851 | 25.6 ± 2.0, 31.5 ± 2.5[C] /28.0 ± 2.2/ 27.5 ± 2.0 | | | | | | 10/30/60 | Brett (1991) |
| *H. glaber* | " | 647 | Mtito Andei (KE) | n.a. | 758 | 32(30–34)[A] | 30.4–36.6/ 31.1–32/ 31.3 | | 92 ± 1.2 (85–100) | | | 5/50/100 | Withers and Jarvis (1980) |
| *H. glaber* | ” | ” | ” | End of dry (III) [1D] | ” | 30.1 | 29.1–30.6 | | 95.6 ± 1 | | | 40 | McNab (1966) |
| *H. glaber* | ” | 621 # | Babile, Dire Dawa (ET) | dry (XII)[1D] | 1363 # | 39 ± 5.5 | 24.6–48.8 | | 56 ± 13.5 (31.2–89.7) | 20.5 ± 0.3 (19.9–20.9) | 0.17 ± 0.09 (0.05–0.4) | 30 ± 10 | Holtze et al. (2018) |
| *H. glaber* | ” | " | ” | ” | ” | | | | 91.3 ± 0.7 (90.1–92.8) | | | 50 | ” |
| *H. glaber* | ” | 527 | Meru (KE) | beginning of dry (VI) [8D,E] | 590 | | 23–26 | 2 | | | | ” | ” |
| *F. mechowii* | Humid | 1224 | Ndola (ZM) | dry (V - VI)[6W] | 1290 | 18.6 ± 0.9/19.1 ± 0.5 | 16.1–20.5/ 18.1–19.9 | 5.5/12 | | | | 10/30 | Lövy et al. (2013), Šumbera et al. (2012), unpubl. data |
| *F. anselli* | Dry sub-humid | 824 | Lusaka (ZM) | dry (V - VI)[8W] | 1320 | 20.9 ± 2.5 | 17.6–25.4 | 2 | | | | 10 | Šklíba et al. (2014), unpubl. data |
| *F. anselli* | ” | ” | Lusaka (ZM) | Dry (VIII)[1D] | 1229 | | 18–22 | | 92–93 | | | 13–16 | Marhold and Nagel (1995) |
| *F. whytei* | Humid | 1266 | Nyika (MW) | dry (VIII)[4D] | 1600/ 2100 | 18.8 ± 0.9/15.5 ± 1.1 | 17.0–20.6/ 14.0–18.1 | 3.5/1.5 | | | | 10 | Lövy et al. (2012), unpubl. data |

A – values in a burrow, B – data were collected irregularly during daylight, C – the higher value is mean maximum temp at 3 p.m., the lower value means minimum at 9 a.m. in 10 cm, # – a mean value of four sites, E- measurements were carried out only from 6 a.m. to 8 p.m.

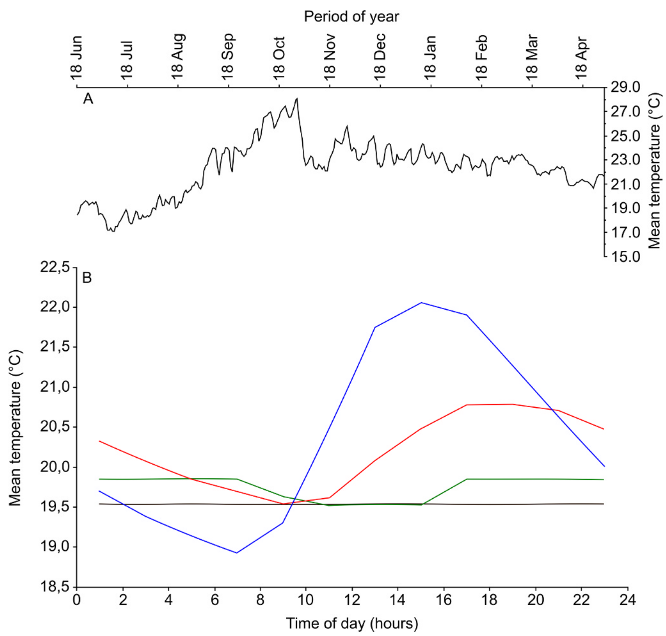


**Fig. 4.** Annual temperature soil profile at the depth of the foraging burrows (a) and diurnal profiles of soil temperatures at four depths where most *Heliophobius argenteocinereus* burrows occur (b). (blue = 5 cm, red = 15 cm, green = 30 cm and black 50 cm). Modified from Šumbera et al. (2004, 2008).

et al., 2005). Moreover, mole-rats may face temporary hypoxic and hypercapnic conditions when more individuals rest in one nest at the same time. Family size can exceed 10 individuals in furred social species, and even more than 100 in the naked mole-rat. Thus, changes in gas composition in the nest chamber could be fast and dramatic (note that furred bathyergids are larger, so the rate of $O_2$ depletion of a family comprising of ten giant mole-rats could be comparable to a family of 100 naked mole-rats). In such situations, the ability of the naked mole-rat to decrease its metabolic rate and breathing frequency in a low $O_2$ atmosphere (Pamenter et al., 2015) may be a useful adaptation to hypoxia, while resting in a crowded nest. Finally, mole-rats probably face hypoxic and hypercapnic conditions during digging in dead-end burrows. It would be interesting to investigate how the burrow atmosphere changes during burrowing, because physical activity leads to increased metabolic rates and breathing. We may speculate that increased hypoxia and hypercapnia in close vicinity of the head of a burrowing mole-rat, because of an increased need for $O_2$ and because the area between the nose and soil is probably not well ventilated. No such data exist for bathyergids, but in this respect it could be relevant that Seymour et al. (1998) found that the partial pressure of $O_2$ in interstitial surroundings in dune sand was only 0.9 Kpa lower near the nose than ambient in the subterranean Namib mole *Eremitalpa granti*. (It should be mentioned that 1 Kpa is about 1% of the normal atmosphere, i.e. the decrease was approximately to value of 19%). We could expect lower values of $O_2$ during digging by African mole-rats in compact soils due to lower gas exchange.

### 2.4. Burrow ventilation

The high and stable humidity and gas concentrations in burrows are related mainly to the limited ventilation of the burrow system. No air movement was recorded in burrows of *G. capensis* (Roper et al., 2001), but we cannot exclude a mechanism of ventilation such as that described for the European mole (Olszewski and Skoczen, 1965), when wind above soil mounds creates lower pressure and "sucks" air out of the sealed burrows. In addition, the piston-like pushing of the air by moving mole-rats, the presence of vertical "chimneys" ending a few centimetres below the surface or in vegetation as found for *H. argenteocinereus* burrows, open burrows leading to the surface in *F. mechowii* and *F. anselli* (R. Šumbera unpubl. data) or tunnels opened during burrow excavation (Holtze et al., 2018) could further contribute to burrow ventilation. A different thermal gradient between soil layers may also be relevant in the mixing of air between burrows at different depths (Kennerly, 1964). Holtze et al. (2018) even speculated that the differences in $T_a$ in deep and shallow tunnels during 24-h could drive air convection in burrows (during the day shallow burrows are warmer than deeper ones, but this relationship is inversed during the night).

### 2.5. Microclimatic conditions in the nest

In nature, mole-rats spend the majority of their time in the nest (Šklíba et al., 2007), where the microclimate is probably more stable because of its depth (Fig. 3). The conditions in the nest could rapidly change when one or more individuals remain there for extended times (see above). Unfortunately, information about microclimate in occupied nests is completely devoid, because it is very difficult to get such data in nature. It is speculated that the depth of the nests is selected to ensure that subterranean mammals has enough $O_2$. At depths down to 30 cm, the exchange of $O_2$ and $CO_2$ with the surface atmosphere might equilibrate (Kennerly, 1964). Some mole-rat species have relatively shallow nests (Fig. 3), for example, the top of the nest of the silvery mole-rat is at a depth of about 15 cm (Šumbera et al., 2004). Many other, mainly social, mole-rat species have deeper nests, which probably severely restrict ventilation. In such cases, branched burrows around nests, as found in some social species (Šklíba et al., 2012; Šumbera et al., 2012), and nests having several openings (Holtze et al., 2018) could contribute to gas exchange in compact soils.

Sparse anecdotal data regarding microclimatic conditions in bathyergid nests are limited mainly to $T_a$ in empty chambers. In *F. mechowii, H. argenteocinereus* and the Whyte's mole-rat *Fukomys whytei*, nest $T_a$ was found to be below 20 °C (Burda et al., 2007), however, without further information about $T_a$ in the burrows, soil, or on the surface, such information is difficult to interpret. Other anecdotal findings provide indications of convenient microclimatic conditions in deep nests. Marhold and Nagel (1995) found $T_a$ to be 26–28 °C in a nest 70 cm below the ground compared to 20 °C in 14 cm deep burrows of the Kafue mole-rat, *Fukomys kafuensis,* during the cold season. If nests are shallow, there could be a fluctuation not only in $T_a$, but also in gas concentrations (see above). In the only systematic study analysing gas composition in nests of the any African fossorial rodent, we detected significant, but not large, increases of $CO_2$ and $CH_3$ concentrations in the morning, after the resident animal spent the entire night in nest in *T. macrocephalus* (J. Šklíba unpubl. results). There was no substantial variation of $O_2$ in the nests during the day.

## 3. Mammalian energetics

Mammals use energy from food mainly to fuel various processes such as growth, reproduction, heat production and to build energetic reserves. Most energy is eventually dissipated as heat. The minimal rate of energy expenditure in an endotherm at rest is the basal metabolic rate (BMR). This parameter is measured mainly as the amount of energy spent or $O_2$ consumed per unit of time by an unstressed, adult individual in a metabolically neutral $T_a$. The measured animal should be resting, but not sleeping, and in postabsorptive state, when no energy is spent for digestion, but not starving. The range of $T_a$ under which the metabolism is minimal is the TNZ. Within this zone, demarcated by lower critical temperature (LCT) and upper critical temperature (UCT), the metabolic rate is regulated primarily through skin blood flow and the control of dry or sensible heat loss (Gordon, 1990). Below and above the TNZ, individuals must expend energy to maintain a stable $T_b$, either by increasing heat production below the TNZ or by increasing heat dissipation above the TNZ. Nevertheless, measuring BMR is complicated, since we usually do not know exactly whether a tested animal is stressed and when it is in a postabsorptive state. Therefore, another parameter called the resting metabolic rate (RMR), which is defined as the metabolic rate in the TNZ of a resting individual, which is not necessarily in a postabsorptive state, is used. Compared to BMR, values of RMR are usually 10–25% higher (Sherwood et al., 2005).

Below the TNZ of a species, a decrease in $T_a$ causes an increase in heat loss due to the greater temperature gradient between the skin and $T_a$. Mammals may use various mechanisms to regulate heat transfer and keep a stable $T_b$. The heat losses may be minimised by increased vasoconstriction and a counter-current heat exchange system, especially in body extremities. They could react also by changing body posture and body insulation, locomotion, finding refuge with a more convenient microclimate, building nests and huddling. Furthermore, they can react by shivering and nonshivering thermogenesis or decreasing $T_b$ and going into torpor.

When $T_a$ increases above a species' TNZ, the animals can react by changing posture, insulation or by finding a colder refuge. They may increase grooming to increase water loss, or intensify breathing. In such a situation, evaporative water loss can become a significant avenue for heat dissipation by passive water loss. This can be realised by diffusion through skin via sweating, panting, and application of saliva and urine on the body surface. Animals may also increase tissue processes, peripheral circulation and elevate $T_b$.

## 4. Resting metabolic rate and daily energetic expenditure in mole-rats

A number of studies attempted to measure BMR or RMR in bathyergids. For mole-rats, it may be better to use RMR instead of BMR, due to the fact that food restriction of the tested animals varied substantially from three to 16 h (see Table 2 for details). In some studies, the animals were not even fasted before the experiments (Jarvis, 1978; Lovegrove, 1986a, 1987). Mole-rats are probably not in a postabsorptive state with less than three hours of starvation. Similar to other subterranean rodents, African mole-rats have a low RMR compared to other rodents of a similar body size (Table 2).

Apart from the period of food deprivation, there is another factor, which may complicate attaining a minimal value of metabolic rates. To get such information, the individuals are usually tested singly. In highly social mammals, stress from isolation may contribute to higher values in the resting individual. Contrary to the energetic savings obtained from huddling, which is testable at a $T_a$ below the TNZ, this so-called socio-physiological factor should be visible mainly during measurements within the TNZ when the effect of energetic savings of huddling should not exist. Wiedenová et al. (2018) found that $O_2$ consumption of the Mashona mole-rat *F. darlingi* decreased by 5% per individual when two adult individuals of the same group were measured together. This indicates that, if a socio-physiological factor exists in this species, it is probably negligible. This is in contrast with the study of Kotze et al. (2008), who found extremely high savings in two mole-rat species. Energetic costs per animal of *F. damarensis* and the Natal mole-rat, *C. h. natalensis,* decreased from 0.44 and 0.42 ml $O_2$ $g^{-1}$ $h^{-1}$ when the mole-rats were measured alone to 0.05 and 0.08 ml $g^{-1}$ $h^{-1}$ while mole-rats were measured in groups (energetic savings were thus 89 and 81%), respectively. This phenomenon in African mole-rats definitely deserves further investigation.

The relatively low metabolic costs of mole-rats are also reflected in their lower daily energy expenditures. Indeed, in *F. darlingi*, daily energy expenditure (DEE), i.e. energy which an organism spends during various activities per day, was only 67% (P. Wiedenová and R. Šumbera unpubl. data) of the value predicted for rodents of similar body mass (McNab, 1966; Nagy et al., 1999).

In mole-rats, it was predicted that energetically costly activities such as territory defence and search or fighting for sexual partners, could be mirrored in an increased DEE. Scantlebury et al. (2006a) measured DEE in the sexually monomorphic *G. capensis* and dimorphic Namaqua dune mole-rat *Bathyergus janetta* to test if these behaviours potentially associated with such dimorphism are reflected in higher DEE. The higher absolute values of DEE, but not for mass independent DEE, in males of the dimorphic species (Table 3) suggests that the energetic cost of dimorphism is primarily the cost of maintaining large male body sizes than associated behaviours related to different breeding systems.

We may predict that DEE is influenced by fundamental environmental factors such as the change between the dry and wet seasons, which is typical for habitats of all mole-rats. Indeed, it was found that the onset of the rainy season increased DEE, while RMR remained the same in the silvery mole-rat (Zelová et al., 2011). An increase in DEE after the first rains is indicative of increased activity, probably digging, in soil moistened by water. In the study of Scantlebury et al. (2006b), breeding females and larger individuals of *F. damarensis* increased DEE after rains, whereas smaller ones did not. It appears that the smaller mole-rats are probably active all year round. These authors suggested that the larger individuals, which they call infrequent workers, constitute a physiologically distinct caste, which builds up a body reserve for dispersal instead of helping in the family. If true, we may assume that frequent workers face higher thermoregulatory challenges due to their higher activity.

### 4.1. Hypothesis explaining low RMR in subterranean rodents

Three hypotheses have been put forward to explain low RMR in subterranean rodents (see Zelová et al., 2007 for a review). According to the *respiratory stress hypothesis,* low RMR contributes to normalizing the partial pressures of $O_2$ and $CO_2$ in the blood and tissues under hypoxic conditions in sealed burrows (e.g. Arieli, 1979). The *cost of burrowing hypothesis* proposes that low RMR compensates for the energetic demands of subterranean foraging and represents an energy saving mechanism lowering food and water requirements (e.g. Vleck, 1979). Finally, the *thermal stress hypothesis* suggests that lower RMR minimises the risk of overheating in burrows by decreasing heat production (e.g. McNab, 1966).

There is still no consensus about what selection pressures are responsible for low RMR and which of the hypothesis is most relevant in the African mole-rats and other subterranean mammals. The finding that concentrations of respiratory gases in burrows of African mole-rats do not differ much from aboveground (see Table 1) undermines the *respiratory stress hypothesis*, because burrow air might not be as stressful as originally considered (Contreras and McNab, 1990). Nevertheless, we may still expect hypercapnic and hypoxic conditions in the deeper parts of burrow systems, nests or in the burrows after heavy rains. The *cost of burrowing hypothesis* is generally accepted for bathyergids, especially because of low and widely spaced food resources in mole-rat habitats (Jarvis, 1978; Jarvis et al., 1998; Lovegrove, 1986a; Lövy et al., 2012) and their energetically costly search. Finally, there is also support for the *thermal stress hypothesis.* Bathyergids have a higher thermal conductance than expected for rodents of comparable body sizes (Table 2). This indicates easier heat losses from the body, which may be viewed as an adaptation to cope with thermal stress, similar to low RMR.

The three hypotheses are not mutually exclusive, so they could contribute together to explain low RMR. This has been supported by the meta-analysis of White (2003), who compared RMR/BMR across various burrowing mammals from all over the world. He analysed mammals foraging below and above the soil surface (White's terms "fossorial" and "semi-fossorial" represent the same lifestyles as "subterranean" and "fossorial" respectively in this text) to test the *cost of burrowing hypothesis* and *thermal stress hypothesis*. He found that rodents from arid environments have lower RMR/BMR than those from mesic areas indicating that cost of foraging is important, because food supply is expected to be lower and/or more difficult to obtain in arid environments. He then analysed subterranean and fossorial species separately within arid and mesic environments. He predicted that if the cost of burrowing is relevant, the species feeding underground would

**Table 2**
The body mass, sociality and thermal characteristics of African mole-rat species, subspecies and populations: body temperature ($T_b$), resting metabolic rate (RMR), thermoneutral zone (TNZ), thermal conductance (C) and experimental conditions of their obtaining. Aridity index (AI) and Annual Precipitation are characteristics of the climate at the localities from where studied mole-rats or their progenitors were collected. Aridity index showing dryness of the climate in the given location is calculated according to Trabucco and Zomer (2009) (http://www.csi.cgiar.org.). If the information on locality is missing or mole-rats from different sites were studied, the value for whole geographic distribution was calculated (marked by #). The information about sample size and acclimatisation in captivity before measurement (length and $T_a$) is also included: W- weeks, M - months, Y - years.

| Species | Body mass (g) | Tb (°C) | Length and $T_a$ of aclimatisation | Starvation (h) | RMR (ml $O_2$ $g^{1}$ $h^{-1}$) | TNZ (°C) | C (ml $O_2$ $g^{-1}$ $h^{-1}$ $C^{-1}$) | AI | Annual Precipitation (mm) | Sociality | N | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Cyptomys h. hottentotus* | 75 | 34.4 | < 3 W (26°C) | 3 | 1.38 | 27–30 | 0.14 | Arid | 118 | Social | 6 | Bennett et al. (1992) |
| *Cyptomys h. hottentotus* | | | 3 M (25 °C) | ” | 0.92 | | | ” | ” | ” | ” | ” |
| *Cyptomys h. pretoriae*[a] | 95 | 35.8 | > 3W (22–25 °C) | | 0.68 | 30–32 | 0.144 | Semi-arid | 700 | ” | 7 | Haim and Fairall (1986) |
| *C. h. mahali* $^{low}$ | 57 | 35.2 | 3W (25 °C) | ” | 1.23 | 30–36 | 0.26 | Humid | 1008 | ” | 12 | Broekman et al. (2006) |
| *C. h. mahali* $^{high}$ | 84 | 35.6 | ” | ” | 1.19 | 28–36 | 0.25 | ” | 928 | ” | 6 | ” |
| *C. h. nimrodi* $^{highveld}$ | 81 | 34.4 | N.a. (26 °C) | ” | 0.83 | 31–32 | 0.17 | Semi-arid | 612 # | ” | 6 | Bennett et al. (1996) |
| *C. h. nimrodi* $^{lowveld}$ | 99 | 34.0 | ” | ” | 0.95 | 28–30 | 0.14 | Arid | 341 | ” | 6 | ” |
| *C. h. natalensis* | 102 | 33.8 | fresh (n.a.) | ” | 1.03 | 30–31.5 | 0.13 | Humid | 986 # | ” | 7 | Bennett et al. (1993b) |
| *C. h. natalensis* | | | 2 M (26 °C) | ” | 0.80 | | | ” | 986 | ” | ” | ” |
| *F. darlingi* | 60 | 33.3 | ” | ” | 0.98 | 28–31.5 | 0.19 | Dry sub-humid | 890 | ” | 7 | Bennett et al. (1993a) |
| *F. darlingi* | 143 | 33.0 | Y (25 °C) | 12 | 0.76 | 27–34 | 0.12 | Semi-arid | 842 | ” | 10 | Zemanová et al. (2012) |
| *F. bocagei* | 94 | 33.7 | 2 M (26 °C) | 3 | 0.74 | 31.5–32.5 | 0.12 | Dry sub-humid | 861 | ” | 4 | Bennett et al. (1994a) |
| *F. damarensis* | 130–192 | 35.1 | 2W (26 °C) | ” | 0.66 | 28–31 | 0.065 | Arid | 296 | ” | 6 | Bennett et al. (1992) |
| *F. damarensis* | | | 2.5 M (26 °C) | ” | 0.69 | | | ” | ” | ” | ” | ” |
| *F. damarensis* | 124.5 | 35.2 | 1–5Y (23 °C) | No | 0.57 | 27–31 | 0.085 | ” | 213 | ” | 7 | Lovegrove (1986a) |
| *F. mechowii* | 267 | 34 | 2 M (26 °C) | 3 | 0.60 | 29–30 | 0.09 | Humid | 1207 | ” | 6 | Bennett et al. (1994a) |
| *F. anselli* | 82 | 36.1 | Y (n.a) | 16 | 0.76 | 32.5 | 0.144 | Dry sub-humid | 842 | ” | 10 | Marhold and Nagel (1995) |
| *F. anselli*[b] | 77 | 33.8 | 2 M (26 °C) | 3 | 0.63 | 28–32 | 0.12 | ” | 816 | ” | 7 | Bennett et al. (1994a) |
| *H. glaber* | 39.5 | 32.1 | ? (24 °C) | | 0.64 | 31–37 | 0.39 | Semi-arid | 619 # | ” | 14 | McNab (1966) |
| *H. glaber* | 42.8 | 33 | Y (30 °C) | ” | 1.00 | 31–34 | 0.5 | ” | 372 | ” | 17 | Buffenstein and Yahav (1991) |
| *G. capensis* | 193 | 36.4 | M (23 °C) | No | 0.59 | 26.3–34 | 0.046 | Humid | 646 | Solitary | 8 | Lovegrove (1987) |
| *H. argenteocinereus* | 89 | 35.1 | n.a. (24°C) | ” | 0.87 | 28–33 | 0.128 | Semi-arid | 616 | ” | 2 | McNab (1966) |
| *H. argenteocinereus* | 223 | 33.6 | Y (25 °C) | 3 | 0.68 | 25–33 | 0.077 | Humid | 1424 # | ” | 8 | Zelová et al. (2007) |
| *B. janetta* | 406 | 34.7 | > 2 M (23 °C) | ” | 0.54 | 27.5–33.2 | 0.069 | Arid | 48 | ” | 3 | Lovegrove (1986b) |
| *B. suillus* | 712 | 35.3 | > 2 M (23 °C) | ” | 0.45 | 25–31 | 0.038 | Semi-arid | 469 # | ” | 5 | Lovegrove (1986b) |
| *Rattus norvegicus* | 160 | 37.5 | | | 1.31 | 25–31 | 0.09 | Humid | | Social | | Hart (1971) |
| *Meriones unguiculatus* | 70 | 38.2 | | | 1.40 | 30–40 | 0.14 | Arid | | ” | | Hart (1971) |
| *Cavia porcellus* | 570 | 38.0 | | | 0.70 | 21–29 | 0.042 | Humid | | ” | | Hart (1971) |

[a] Probably *C. h. pretoriae*, because caught in Zwavelpoortu near Pretoria.
[b] Denoted as C. amatus in the original study.

have lower RMR/BMR due to the higher costs of obtaining food. The absence of a difference between the surface and subterranean foragers would support the validity of the *thermal stress hypothesis*, because both groups stay in humid burrows. He found support for the thermal stress hypothesis in species from mesic areas and in larger ($> 77$ g) species in arid areas. In smaller species ($< 77$ g) from arid environments, the subterranean species had lower metabolism than the fossorial ones. This indicates that the *cost of burrowing hypothesis* could be relevant for them, because lower RMR/BMR may compensate for the high energetic costs of subterranean foraging in arid areas (cf. White, 2003).

### 4.2. Factors influencing RMR in African mole-rats

In mammals, body mass explains the most variability in RMR at the intraspecific and interspecific levels. Mole-rats are no exception, because it can explain up 87% of the variability in RMR within species (e.g. Scantlebury et al., 2006a; Zelová et al., 2010, 2011).

At the interspecific level, the situation was not so equivocal during the history of bathyergid research. African mole-rats were for a long time considered exceptional with respect to the relationship between metabolism and body mass, because their RMR was found to be independent of body mass (Lovegrove and Wissel, 1988). The body mass independent metabolism was thus considered to be advantageous in social species, in which a higher number of small individuals having the same total biomass as one individual of a larger solitary species would have no extra metabolic costs. A family of smaller individuals would thus represent an increased workforce with no additional energetic costs related to their smaller body mass. This was supposed to be useful in areas with widely spaced food resources. Body mass independent metabolism was thus established as an important precondition for evolution of sociality, termed as "Risk-Sensitive Metabolism" (Lovegrove, 1991; Lovegrove and Wissel, 1988), later modified this as the "Aridity Food Distribution Hypothesis" (Jarvis et al., 1994). Zelová et al. (2007) tested the body mass independent metabolism on a large number of bathyergid taxa, including data from studies published after the original Lovegrove and Wissel's study (Bennett et al., 1992, 1993a, 1994a; Marhold and Nagel, 1995; Scantlebury et al., 2006a). This meta-analysis using independent contrasts showed that metabolism across the African mole-rats has a typical mammalian pattern with body mass explaining 48% of the variability in RMR.

Apart from body mass, differences in energetics and thermoregulatory capabilities in African mole-rats were supposed to be related mainly to the environmental conditions of particular populations, related particularly to aridity and altitude. Lovegrove (1986a) found that the RMR of subterranean rodents from arid areas was lower in comparison to species from mesic regions and that *F. damarensis* from an arid site has a lower RMR than those from a less arid site. This would support the *cost of burrowing hypothesis*. However, this finding is no longer supported in his following study, where solitary *G. capensis* from mesic areas had very low RMR (Lovegrove, 1987, Table 2). In addition, no relationship between RMR and aridity was found across seven *Fukomys* and *Cryptomys* taxa (Bennett et al., 1994a).

Considering altitude, Bennett et al. (1996) found RMR of high altitude Matabeleland mole-rats *Cryptomys hottentotus nimrodi* to be 87% compared to individuals from lower altitudes, either as a consequence of lower $O_2$ partial pressure in the burrows (this is thus a variant of the *respiratory stress hypothesis*) or alternatively by the need to maintain higher $T_b$ in colder conditions. Both conditions should prevail at higher altitudes. No data about partial $O_2$ pressure were provided, but we may assume that the differences between the two altitudes (1330 and 457 m a.s.l) - if they exist - are too small to cause any respiratory stress, especially in mammals resistant to hypoxia. In this context, it should be noted that no differences in RMR were found in *C. h. mahali* from areas with larger differences in altitudes, 1600 vs. 3200 m a.s.l. (Broekman et al., 2006). The explanation regarding colder microenvironments at higher altitudes seems to be more plausible, especially if we consider that mole-rats from higher altitudes might face higher $T_a$ fluctuations, also due to the fact that nests are probably shallower because of the relatively thin layer of soil which is typical for mountain ecosystems (cf. Bennett et al., 1996). Unfortunately, the absence of any data about food supply, gas partial pressure and nest depths precludes any convincing evaluation of these factors.

Mole-rats could adjust RMR relative to food supply. In a study on *H. glaber*, it was found that 1–2 weeks of food restriction (60–70% of ad libitum consumption) caused a 25% reduction of metabolic rates (Goldman et al., 1999). Food consumption remained lower even after a return to the original amount of food. This indicates that African mole-rats, or at least the naked mole-rat, is capable of long-lasting metabolic adaptations to cope with a restricted food supply.

## 5. Thermoneutral zone and metabolic rates in $T_a$ below and above TNZ

The width of the TNZ and value of LCT depends ultimately on the effectiveness of thermoregulatory mechanisms that do not require significant energy. In mammals, insulation by means of fur and fat are major factors influencing these characteristics. Lower LCT allows animals to save energy and maintain $T_b$ at a lower $T_a$. The LCT could be seasonally adjusted by insulatory thickness, behaviour, and integration with the hypothalamus.

In solitary African mole-rats, the width of the TNZ is relatively large (5–8 °C) with LCT shifted to a lower $T_a$ (around 25–27 °C; Table 2; Fig. 5). This is probably a consequence of the colder climate and impossibility to save energy by huddling. Afrotropical silvery mole-rat, which generally live in higher altitudes (Lövy et al., 2012; Šumbera et al., 2007a) may face similar seasonal $T_a$ fluctuations as the species from the subtropics, such as the Cape dune mole-rat, *B. suillus, B. janetta* and *G. capensis* (Table 1).

Among the social mole-rats, the width of the TNZ is rather variable with the differences being mainly among mole-rats from different climatic regions (Table 2, Fig. 5). In *H. glaber,* the width of the TNZ was found to be 3–6 °C with LCT of 31 °C (Buffenstein and Yahav, 1991; McNab, 1966). In *Fukomys* species from the tropics, the width of the TNZ is relatively small ranging from 1 to 5 °C and LCT is between 27 and 32 °C. The lowest LCT was found in *F. damarensis,* the southernmost species of all congenerics. In *F. mechowii* (Bennett et al., 1994a) and *F. anselli* (Marhold and Nagel, 1995), the width of the TNZ is very narrow, being only one degree Celsius. (But see study of Bennett et al. (1994a) for wider TNZ in the latter species, which was denoted as *C. amatus*)). In *Cryptomys* species from Southern Africa, the width of the TNZ varies from 1 to 8 °C and LCT between 27 and 30 °C. The widest TNZ (8 °C) was found in *C. h. mahali* living at 3200 m a.s.l. Their TNZ was wider and with lower LCT than a population from a lower altitude (Broekman et al., 2006). This together with lower thermal conductance and greater thermogenic capacity (see below), while keeping the same RMR, is probably an adaptation for life in colder $T_a$. These mole-rats also face the lowest mean annual temperature among all mole-rats (Table A.1).

Metabolic rates increase above and below the TNZ, first to avoid hyperthermia and second hypothermia. This increase of metabolic rates at low $T_a$ can be very high as in *F. anselli* and *F. darlingi* (see Fig. 5c). On the contrary, the increase of metabolic rate is very low in the largest bathyergids *B. suillus* even at lowest $T_a$ (Fig. 5a). A small increase in the metabolic rate was found also in the large social mole-rats *F. mechowii* and *F. damarensis* (Fig. 5c,d). Mole-rat responses to $T_a$ below the TNZ can also be very different between populations of the same species. In addition to the different TNZ, LCT and C, Broekman et al. (2006) found that metabolic rates in *C. h. mahali* far below the LCT ($T_a = 5$ °C) increased five times in individuals from low altitudes, but only twice in those from higher altitudes indicating better adaptation to cold in later ones.

Different methodological approaches, equipment used, and sample size could lead to different values of $O_2$ consumption and related

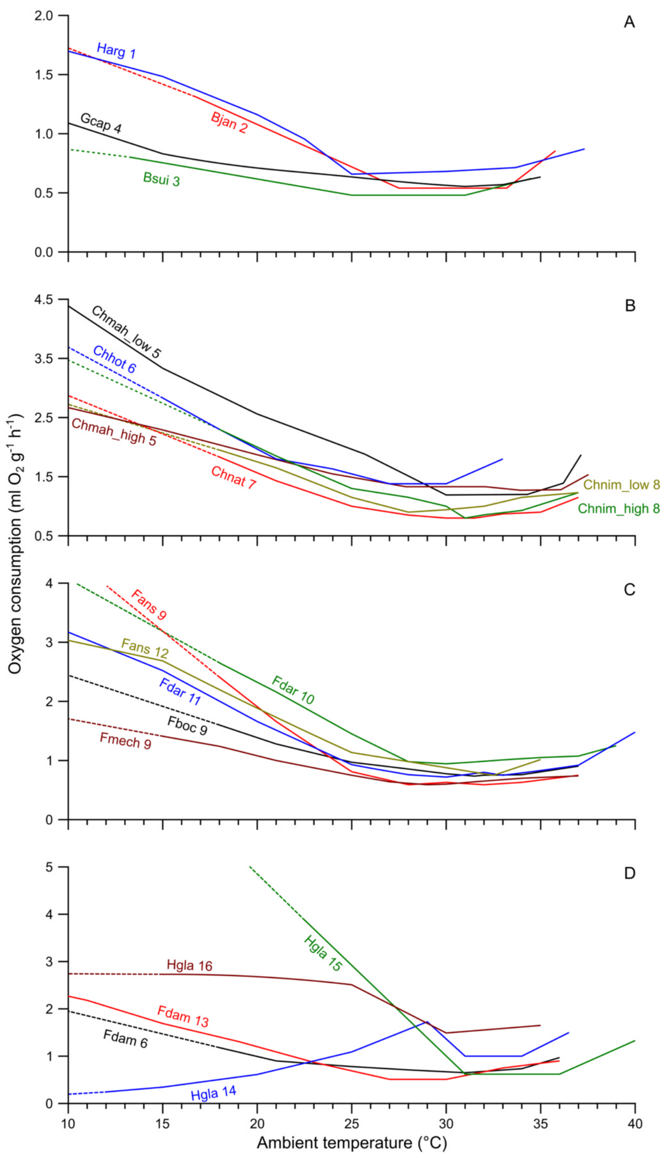


**Fig. 5.** Oxygen consumption of African mole-rat species as a function of $T_a$: a) solitary species of the genera *Bathyergus*, *Georychus* and *Heliophobius*; b) social species of *Cryptomys*; c) social species of genus *Fukomys* (except of *F. damarensis*); d) social *F. damarensis* and *H. glaber*. The thermoneutral zone is roughly indicated by a horizontal line. The dashed part of the lines is an extension of the trend of $O_2$ consumption at temperatures up to 10 °C below TNZ to make species energetic costs comparable. Species codes: Harg – *Heliophobius argenteocinereus*, Bjan – *Bathyergus janetta*, Bsui – *Bathyergus suillus*, Gcap – *Georychus capensis*, Chhot – *Cryptomys h. hottentotus*, Chmah – *Cryptomys h. mahali (low* – lowland and *high* – highland populations), Chnat - *Cryptomys h. natalensis*, Chnim - *Cryptomys h. nimrodi*, Fans – *Fukomys anselli*, Fdar – *Fukomys darlingi (zim* – Zimbabwe, *mal* - Malawi, Fboca – *Fukomys bocagei*, Fmech – *Fukomys mechowii*, Fdam – *Fukomys damarensis*, Hgla – *Heterocephalus glaber*.
*Sources* (numbers behind species codes): 1 - Zelová et al. (2007), 2, 3 - Lovegrove (1986b), 4 - Lovegrove (1987), 5 - Broekman et al. (2006), 6 - Bennett et al. (1992), 7 - Bennett et al. (1993b), 8 - Bennett et al. (1996), 9 - Bennett et al. (1994a), 10 - Bennett et al. (1993b), 11 - Zemanová et al. (2012), 12 - Marhold and Nagel (1995), 13 - Lovegrove (1986a), 14 - Buffenstein and Yahav (1991), 15 - McNab (1966), 16 - Withers and Jarvis (1980).

physiological parameters. The length of acclimation before testing is also a very important factor. Table 2 shows that, in some studies, physiological parameters were assessed in mole-rats kept in captive conditions for only a few weeks after capture, whereas others were done on mole-rats staying in captivity for months, years or on animals born in captivity. Such differences surely influence the results, at least in some species, resulting in decreased RMR in individuals acclimated for a longer period. Higher values of wild caught individuals could be influenced by the stress originating from capture. Similarly, a lack of measurements across a sufficient range of $T_a$s could bring large differences between results of different studies on the same species (Fig. 5). For example, McNab (1966) (Hgla 15 in Fig. 5d) showed a rapid and constant increase of $O_2$ consumption in $T_a$ below the TNZ suggesting that metabolism in the naked mole-rat is positively related to a decrease in $T_a$. On the contrary, two other studies demonstrated either a halt in the increase (Hgla 16 in Fig. 5d) (Withers and Jarvis, 1980) or a decrease of $O_2$ consumption (Hgla 14 in Fig. 5d) (Buffenstein and Yahav, 1991), in lower $T_a$ indicating the inability of the naked mole-rat to control its thermoregulation at colder environments. Instead of there being a different pattern of thermoregulation, it is probable that measurements in lower $T_a$s in McNab's study ended too early to provide a complete picture of naked mole-rat energetics.

## 6. Thermal conductance (C)

Thermal conductance is a parameter describing how easily an animal can dissipate heat through the body surface to the outside environment via conduction, convection, radiation and evaporation. Its efficiency depends on the insulative quality of fur, vascularisation of skin, tissue chemical composition and body mass. We should be aware that this parameter is a simplification of complex heat exchange processes. To obtain information about the potential for heat dissipation in a species, the surface area should be measured, however, due to difficulties to get such information body mass is usually used as a proxy. If the calculation of thermal conductance is based on body mass, the term "whole body thermal conductance" should be used (Gordon, 1990). For the purpose of this review, I use the term conductance (C).

In African mole-rats, C is usually higher compared to same sized surface dwelling mammals, indicating that handling of a surplus of heat is important for them (Table 2). A higher C is an effective tool to avoid overheating (Buffenstein, 2000; Contreras and McNab, 1990; McNab, 1966). It could also be considered as an energy and water saving adaptation, because the animals are not forced to fully employ energetically costly cooling mechanisms.

It is not surprising, that the highest C is found in the naked mole-rat. Withers and Jarvis (1980) estimated C in this species to be about twice that to a surface dwelling mammal of the same body mass. Such high C reduces the risk of hyperthermia in warm burrows, but it, together with a small body mass probably prevents its dispersal through the cooler highlands, which set the northern and western borders of its distribution and thus limits its occurrence to lowland areas of East Africa (cf. McNab, 1979).

However, not all mole rats have a high C. The social *F. damarensis* has a C comparable to the value predicted for aboveground rodents (Lovegrove, 1986a) while the solitary *G. capensis* has the lowest C among mole-rats i.e. only 62% of the predicted value (Lovegrove, 1987) (Table 2). The low values in both species may be explained by the colder climate. *Fukomys damarensis* faces low night temperatures during winter at least in some part of its distribution (Table 1). The good insulation quality of its fur could be important during dispersal, because it is known that dispersing mole-rats may stay alone (with no access to the advantages of social thermoregulation) for months or even years (K. Finn, pers. comm). On the other hand, good insulation limits the time in hot burrows. Indeed, from radiotracking, Lovegrove (1988) found that *F. damarensis* avoids the risk of overheating by short bouts of activity. The influence of $T_a$ on C can be visualised also by comparing populations from different altitudes. Broekman et al. (2006) found a higher C in *C. h. mahali* from lower and warmer altitudes compared to animals from higher and colder altitudes.

## 7. Core body temperature ($T_b$)

Core body temperature represents a balance between metabolic heat production and heat loss to the environment. Keeping a high $T_b$ is energetically costly, because it needs precise behavioural and physiological thermoregulatory mechanisms.

Compared to most placental mammals, which maintain $T_b$ of between 36 and 38 °C, African mole-rats have lower $T_b$, of around 34 °C in the TNZ (Table 2). Apart from anecdotal information, such as mean $T_b$ of the naked mole-rats just after capture (33.9 °C in $T_a$ = 32 °C; Withers and Jarvis, 1980), there is a lack of data on $T_b$ collected systematically in free-living mole-rats and with no stress of handling. Only Streicher et al. (2011) measured $T_b$ using intraperitoneal dataloggers in free ranging *F. damarensis*. They found that mole-rat $T_b$ was individually variable within one family and there was a seasonal variation in $T_b$ in the respective individuals. Some mole-rats exhibited a unimodal 24-h pattern, some bimodal, some had multiple rhythms of $T_b$ and others were arrhythmic. The daily variation in $T_b$ was greater during winter than summer and greater in males than in females. Body mass or $T_a$ did not easily explain these differences.

The value of $T_b$ can be influenced by changes in $T_a$ in some species (see below) and also by physical activities (Lovegrove and Muir, 1996; Riccio and Goldman, 2000), especially if they are energetically demanding (Lovegrove, 1989; Zelová et al., 2010). Marhold and Nagel (unpubl. data in Marhold and Nagel, 1995) measured $T_b$ of *F. anselli* digging in a tube filled with soil. Body temperature increased quickly to a point when the animals stopped digging probably to dissipate heat to avoid overheating. After $T_b$ dropped, mole-rats started to dig again.

## 8. Relationship of mole-rat physiological parameters to climatic characteristics of their habitats

I explored the relationships of bathyergid $T_b$ in the TNZ, RMR, width of the TNZ and C and several climatic characteristics downloaded from the Wordclim database (http://worldclim.org) and used as explanatory variables in a Principal component analysis (PCA) performed in CANOCO version 5 (ter Braak and Šmilauer, 2012). Of the 18 available climatic characteristics, I selected the five most relevant for mole-rat survival: Annual Precipitation BIO12, Annual Mean Temperature BIO1, Temperature Annual Range BIO7 (expressed as the difference between Max Temperature of Warmest Month and Min Temperature of Coldest Month), Precipitation Seasonality (Coefficient of Variation) BIO15 and Min Temperature of Coldest Month BIO6. Due to the fact that the last two variables were highly correlated with other Worldclim characteristics selected (own pilot test), I excluded them from further analyses. I included also body mass as an explanatory variable, because of its importance in influencing physiological parameters in mole-rats and other mammals.

The first two axes of the PCA (Fig. 6a) explained 70.3% of the variance in the entire physiological data set. The first axis was positively related to both C and RMR and negatively to body mass, which accounted for 44.6% of the variance. Solitary species clustered together. These species generally have a larger body size, low C and RMR. High values of C and RMR were found in smaller mole-rats, especially *H. glaber* from the study of Buffenstein and Yahav (1991) (Hgla2). The second axis explained 25.8% of the variance, which could be attributed mainly to the gradient of TNZ width. Whereas a wider range of TNZ is typical for solitary mole-rats, *F. darlingi* from Malawi, and the naked mole-rat from the study of McNab (1966) (Hgla1), the remaining mole-rats usually have a narrow TNZ (showed by a negative relationship to the TNZ). From the environmental variables, TNZ width is negatively correlated with Temperature Annual Range.

I performed a Redundancy analysis (RDA) to test whether the influence of the four explanatory variables on the main physiological parameters of mole-rats is significant. All four variables together explained 41.3% of the variation in the entire physiological data set and

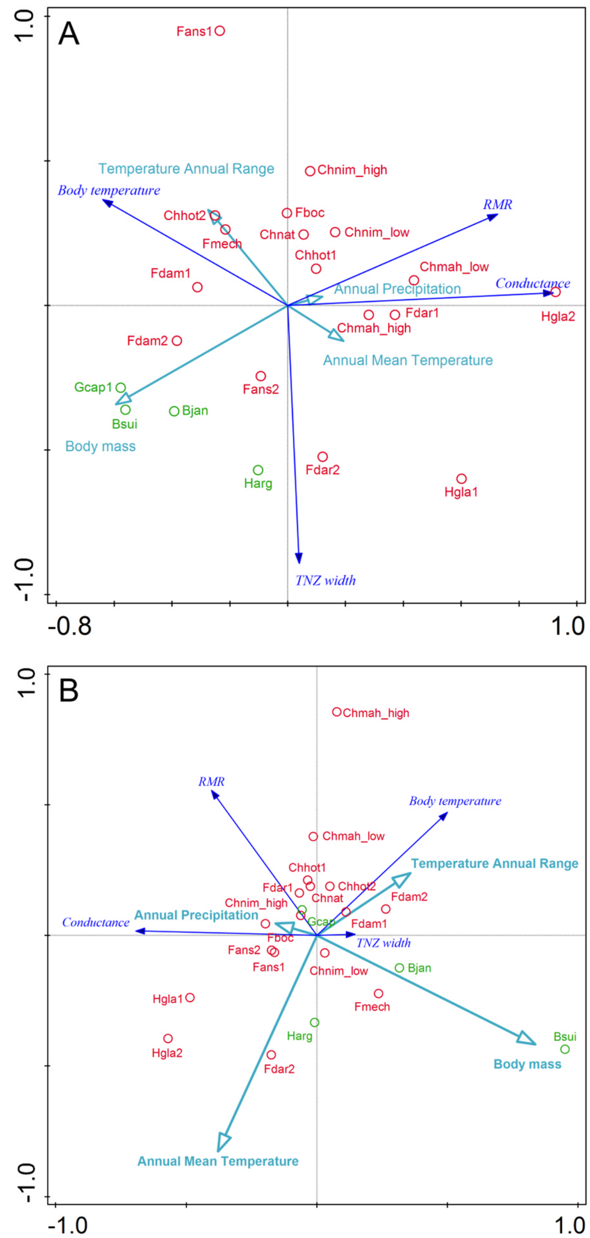


**Fig. 6.** Ordination plots showing interrelationships among mole-rat physiological parameters (depicted as dark blue arrows) and environmental variables for particular localities and body mass (light blue arrows). Environmental variables are either passively projected to the diagram using PCA (a) or their effect tested using RDA (b). In both diagrams, the two first axes are plotted. For *B. suillus,* parameters from the whole distribution range were used, because locality from where the tested specimens originated is missing in the reference. Red circles represent social mole-rats, green circles solitary mole-rats. Data from the same species from different localities are treated as independent. The numbers behind species names indicate the data source: Harg – *Heliophobius argenteocinereus* (Zelová et al., 2007), Bjan – *Bathyergus janetta* (Lovegrove, 1986b), Bsui – *Bathyergus suillus* (Lovegrove, 1986b), Gcap – *Georychus capensis* (Lovegrove, 1987), Chhot – *Cryptomys h. hottentotus* (1 - Bennett et al., 1992, 2 - Haim and Fairall, 1986), Chmah – *Cryptomys h. mahali* (Broekman et al., 2006), Chnat - *Cryptomys h. natalensis* (Bennett et al., 1993b), Chnim - *Cryptomys h. nimrodi* (Bennett et al., 1996), Fans - *Fukomys anselli* (1 - Marhold and Nagel, 1995, 2 - Bennett et al., 1994a), Fdar - *Fukomys darlingi* (1 - Bennett et al., 1993a, 2 - Zemanová et al., 2012), Fboc - *Fukomys bocagei* (Bennett et al., 1994a), Fmech - *Fukomys mechowii* (Bennett et al., 1994a), Fdam - *Fukomys damarensis* (1 - Bennett et al., 1992, 2 - Lovegrove, 1986a), Hgla - *Heterocephalus glaber* (1 - McNab, 1966, 2 - Buffenstein and Yahav, 1991) – Environmental characteristics of Buffenstein and Yahav study are represented by the average value for climate in the species distribution in Northern Kenya, because of no other information about locality where the progenitors were caught was provided.

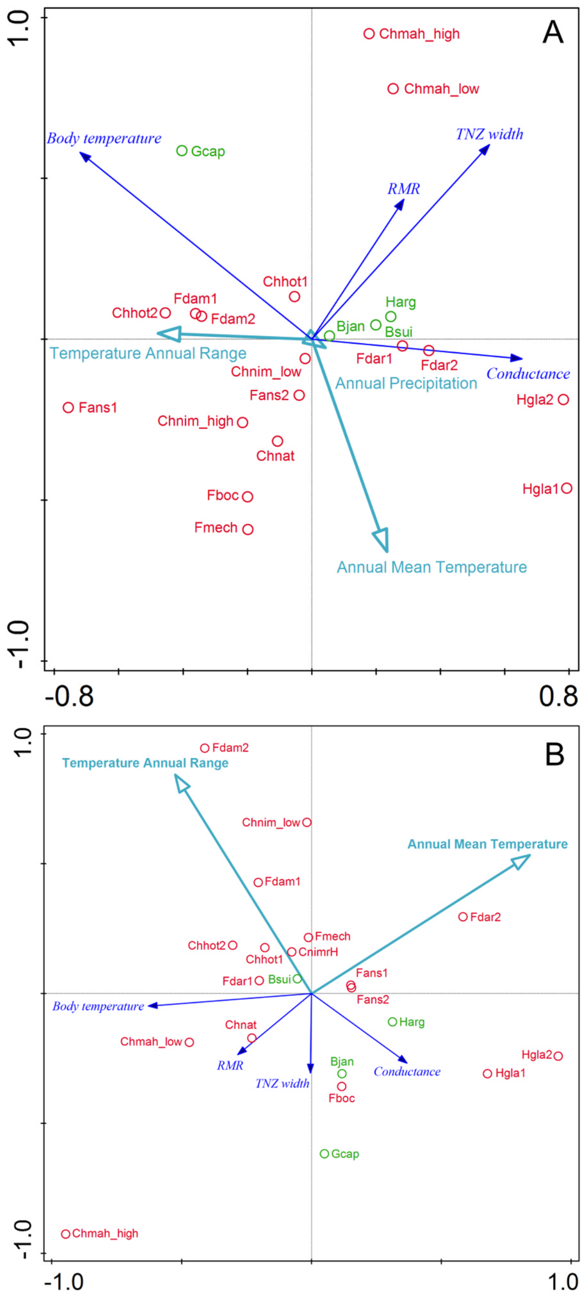


**Fig. 7.** Ordination plots showing interrelationships among mole-rat physiological parameters (depicted as dark blue arrows) and environmental variables for the particular localities and body mass (light blue arrows) with the effect of body mass removed using a covariable. Environmental variables are either passively projected to the diagram using PCA (a) or tested using RDA (b). In both diagrams, the first two access are plotted. For *B. suillus,* parameters for the whole distribution range were used, because the locality from where the tested individuals originated was missing in the reference. Red circles represent social mole-rats, green circles solitary mole-rats. Data from the same species from different localities are treated as independent. Codes for species are the same as in Fig. 6.

the model was significant (F = 2.8, p = 0.002, Fig. 6b). When the simple effect of each variable was tested independently, the highest explanatory power was found for body mass which explained 18.9% of the data variance (F = 4.4, p = 0.012), followed by 12.8% for Annual Mean Temperature (F = 2.8, p = 0.04). Temperature Annual Range and Annual Precipitation explained only 6.9% and 1.3%, respectively, and neither of them significantly influenced the data (F = 1.4, p = 0.28 and F = 0.2, p = 0.914, respectively).

Since body mass is the main factor overriding the effect of climatic explanatory variables, I did the same visualisation and tested the relationships with body mass as a covariate (Fig. 7a). The main difference is that all solitary species, except for *G. capensis* which has a high $T_b$, are in the centre of the ordination plot indicating the absence of particular relationships of their physiological parameters and environmental characteristics. Using body mass as a covariate, the PCA analysis confirms many of the main relationships visualised in Fig. 6a. The first two axis of the PCA explained 68.7% of the variance in the physiological data, from which the first axis accounted for 41.1% and was positively related to C and negatively to $T_b$. There was a negative relationship between C and both $T_b$ and Temperature Annual Range demonstrating that small mole-rat species with a high tendency to heterothermy live in areas with smaller annual temperature extremes. Species occurring in warmer areas (higher Annual Mean Temperature) are characterised by a narrower TNZ and lower RMR. Contrary to the previous ordination, there was no close relationship between high C and high RMR.

To test the effect of environmental variables on the physiological parameters after removing the effect of body mass, I performed a RDA with forward selection to choose the optimal set of variables explaining the largest amount of variability in the data (Fig. 7b). The largest amount of variability of the physiological parameters was explained by Annual Mean Temperature (15.4%, F = 3.3, p = 0.026), followed by Temperature Annual Range, which showed a marginally significant conditional effect (i.e. its size and significance depended on the variables already selected, i.e. Annual Mean Temperature; 10.3%, F = 2.4, P = 0.066). Adding Annual Precipitation did not improve the model fit (F = 0.4, p = 0.78), as it has almost no explanatory power, explaining only 6.9% of the variance in the data. Accordingly, $T_b$ and RMR in bathyergids seemed to increase with decreasing Annual Mean Temperature, whereas both C and the TNZ width likely decreased with increasing Temperature Annual Range.

Based on these ordinations, several generalisations about the relationships between bathyergid physiological parameters and the environmental characteristics that characterise climate in a particular area could be made. It seems that aboveground $T_a$ and its seasonal range are highly relevant for a combination of physiological parameters. In addition, the ordinations clearly showed that there are no remarkable differences in energetics between solitary and social mole-rats, apart from those related to the larger body size of solitary species, as they do not form any distinct clusters in the multidimensional space defined by the mole-rat physiological parameters. Finally, the influence of precipitation, which is frequently mentioned as a crucial environmental factor for many aspects of mole-rats biology, seems to be negligible as can be inferred from the almost absent explanatory power of this variable on the variance of the physiological data.

## 9. Mole-rats' preference for ambient temperature

Seeking for a place with optimal $T_a$ is a common thermoregulatory strategy. It needs relatively little energy, so it precedes activation of autonomic thermoregulatory defences. Each mole-rat species or population may have a preference for a particular range of $T_a$s, which does not necessarily correspond with their TNZ. When such preferences were tested in *F. anselli, F. micklemi, H. argenteocinereus,* and *H. glaber*, the mole-rats chose a $T_a$ within or slightly below their respective TNZ (Begall et al., 2015). Only *F. mechowii* preferred a $T_a$ about 4 °C below the TNZ, probably due to a more favourable surface to volume ratio and its ability to keep heat (larger species lose relatively less heat due to a relatively smaller surface area).

The social context could also be relevant for selection of $T_a$ for resting. The naked mole-rat selects 34.2 °C if tested individually, whereas 30.3 °C is selected when in groups (Jarvis, 1978). Nevertheless, individuals spent only a brief period to "warm up" in a higher $T_a$ and afterward selected a lower one for sleeping. No differences in thermal preference in relation to group size, from two to eight, was found in Ansell's mole-rats (Begall et al., 2015).

African mole-rats are limited in their preference for a thermal environment, because they can find suitable microsites only within their burrow systems. Daily changes of $T_a$ are mainly in burrows close to the surface, so mole-rats may move to deeper parts avoiding adverse microclimatic conditions both diurnally and seasonally as speculated by several researchers (Jarvis, 1978; Lovegrove and Knight-Eloff, 1988). Burda et al. (2007) suggested that subterranean mammals, if the $T_a$ is predictably fluctuating, do not need special thermoregulatory adaptations, because they can simply time digging in relation to burrow $T_a$. Nevertheless, this has never been proven either in nature or in an artificial burrow system simulating natural burrow stratification and temperature cycling. On the contrary, more evidence exists that mole-rats tend to select a thermally-optimal period of the day for physical activity and spend the remaining part of the day mostly inside the nest (see Šklíba et al., 2007, 2014). The existence of many morphological, behavioural and physiological adaptations for dealing with temperature extremes indicates that African mole-rats challenge relevant temperature stress.

## 10. How mole-rats defend low ambient temperatures

Cold is potentially a very stressful factor, especially if it lasts for a long period and is coupled with food shortage. For African mole-rats, a low $T_a$ and probably also seasonal food shortages are not so pronounced, because of the buffering effect of soil and the availability of subterranean parts of plants during the whole year. However, they still may face relevant changes in both factors thus causing problems in filling energy needs.

### 10.1. Behavioural adaptations

To improve thermal balance, mole-rats could passively warm themselves by basking (Brett, 1991; Buffenstein et al., 1996). This way of warming can be widespread, because burrow systems may lay in a heterogeneous habitat in terms of exposure of soil to sunlight and thus belowground temperatures (Holtze et al., 2018; Šklíba et al., 2014; Šumbera et al., 2004). Apart from finding a warmer microsite, there are other behaviours in which mole-rats may immediately deal with decreased $T_a$. They can curl into a ball to minimize heat losses or increase activity, especially locomotion (Boyles et al., 2012; Buffenstein and Yahav, 1991; S. Marhold and A. Nagel unpubl. data in Marhold and Nagel, 1995).

Subterranean rodents can actively improve their thermal environment. In nature, African mole-rats use for that purpose dry plant parts or even unnatural material such as plastic bags, nylon, cloths (Burda et al., 2007). In the lab, adding cotton to a nest results in energetic savings of individuals, or small groups of *H. glaber* in $T_a$ under the TNZ (Withers and Jarvis, 1980). An animal's presence in the nest, especially if more individuals are present, may increase nest $T_a$, but unfortunately, there are no data about the magnitude of such an "igloo effect" in mole-rats. A peculiar way of improving nest thermal conditions was found in the fossorial rodent East African root rat *Tachyoryctes splendens*, which uses the heat from decaying nesting material and faeces (Jarvis and Sale, 1971). Compared to burrows, nest $T_a$ was about 5–7 °C higher (Rahm, 1980). Such "faeces fuelled heating" does not seem to be the case for African mole-rats, because bathyergids use dead-end burrows as a sanitary area.

Another way to reduce heat loss in cold is social thermoregulation. Huddling in groups reduces the exposed surfaces of each individual for heat dissipation. In the first study on this topic in bathyergids, Jarvis (1978) found that four huddling naked mole-rats had less than half of the metabolic rate per individual compared to a single individual at 25 °C. In a following study, Withers and Jarvis (1980) also demonstrated high energetic savings in groups of two and four *H. glaber* at $T_a$ below the TNZ. Finally, Yahav and Buffenstein (1991) analysed the effect of groups of two, four and eight individuals of *H. glaber* on their thermoregulatory parameters. Contrary to the previous study, the authors found that $O_2$ consumption decreased with decreasing $T_a$ below the TNZ in a poikilothermic manner irrespective of group size. At higher $T_a$, the poikilothermic patterns changed to endothermic based on group size (25 °C for groups of eight, 27 °C for groups of two). Huddling contributed also to decreased $O_2$ consumption in the TNZ (32 °C), because groups of eight mole-rats attained only 78% of resting metabolism per individual (this could be attributed to a socio-physiological effect, see above).

Kotze et al. (2008) measured the extent of social thermoregulation at different $T_a$ in two haired mole-rat species. Both species saved energy with increased group size, but *F. damarensis* had higher savings than *Cryptomys h. natalensis*. The authors suggested that the interspecific difference is related to climatic differences, because the species from an arid environment (*F. damarensis*) could be more prone to lose heat at low $T_a$, especially in small groups. A higher temperature stress in habitats of *F. damarensis* may be indicated by deeper nests, but it should be noted that not all of its populations have deep nests (Thomas et al., 2016). Surprisingly, both species showed extremely high energetic savings while huddling in the whole range of $T_a$. Thus, $O_2$ consumption per individual at 22 °C in *C. hottentotus* decreased four-fold (from 0.53 to 0.13 ml $O_2$ $g^{-1}$ $h^{-1}$), and as much as nine-fold in *F. damarensis* (from 0.74 to 0.09 ml $O_2$ $g^{-1}$ $h^{-1}$), which means 75 and 87% energetic savings, compared to a single individual. In *F. darlingi*, the energetic savings was largest (32%) in groups of up to four individuals, a value which corresponds with other mammal species (Wiedenová et al., 2018).

### 10.2. Morphological protection

In mammals, fur and fat layers are effective barriers to heat exchange. The insulative value of fur is mainly a function of hair length and density. There is not much information about fur characteristics in African mole-rats. No differences were found in the length of pelage between populations of *C. h. mahali* from two altitudes (Broekman et al., 2006). The existence of a denser pelage in *C. h. natalensis* compared to *F. damarensis* was mentioned by Kotze et al. (2008). The thinner pelage in the latter species was supposed to be useful in warm burrows, although it has low C (Lovegrove, 1986a) (Table 2). Contrary to previous studies, Šumbera et al. (2007b) provided detailed information about mole-rat fur characteristics. The authors showed that remarkable differences in pelage characteristics exist in furred mole-rats. Although conspicious at first sight, the extent of the interspecific differences in fur between *H. argenteocinereus* and *F. mechowii* is surprising. In *H. argenteocinereus*, fur on the trunk is 17 mm long, with a density of 16,500 hairs per $cm^2$, whereas *F. mechowii* fur has a length of 7 mm and density of only 11,200/$cm^2$. The silvery mole-rat has a longer but thinner pelage on the ventral part of the body: 11 mm and 1800 hairs/$cm^2$ vs. 7.5 mm and 2800 hairs/$cm^2$ in *F. mechowii*.

One may expect no remarkable seasonal differences in fur characteristics in subterranean rodents due to the buffering effect of soil. However, seasonal moulting was mentioned in some species (Hislop and Buffenstein, 1994). This could be useful in the regions where $T_a$ seasonally fluctuate substantially (Bennett et al., 1988). In *G. capensis* and *C. hottentotus*, its was speculated that changes in burrow $T_a$ provide a cue for the onset of moulting in bathyergids from the subtropics (Bennett et al., 1988), but no data were provided.

Heat exchange between a mole-rat's surface and the environment and thus the insulation effectiveness of fur can be surveyed using infrared thermography (IRT). In addition to the pelage characteristics in two mole-rats, Šumbera et al. (2007b) analysed surface temperatures ($T_s$) using IRT along a $T_a$ gradient (10–35 °C). The authors found remarkable interspecific differences at lower $T_a$ (below 25 °C), when $T_s$ of large haired areas, such as the head and trunk, were 2–4 °C higher in the social *F. mechowii* than in the solitary *H. argenteocinereus* (Fig. 8). Since

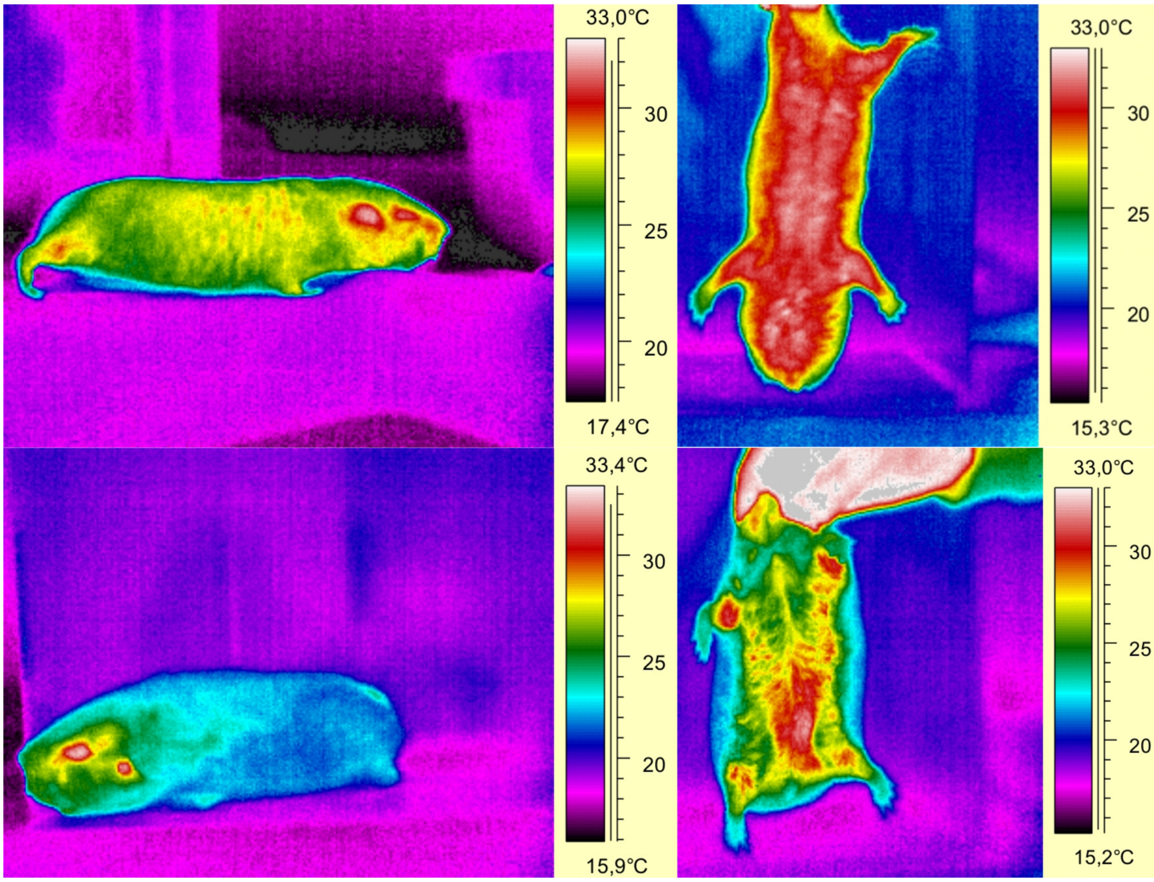


**Fig. 8.** Surface temperatures (lateral and ventral view) recorded by infrared camera of *Fukomys mechowii* (top) and *Heliophobius argenteocinereus* (bottom) in $T_a$ = 20 °C. Note the generally higher $T_s$ in the giant mole-rat and its different pattern on the ventral side between both species (Photos made by Petr Kunc).

both species are comparable in size and live in the same climate and habitats, we may assume the differences are related mainly to the option for social thermoregulation and no need for long and/or dense fur in social species. Whereas *F. mechowii* rests freely outstretched in a group of family members, *H. argenteocinereus* rests singly, curled into a ball. This position reduces the surface-to-volume ratio and covers the less insulated ventral body part. Compared to social species, solitary ones probably need to conserve energy by having dense and long fur, which on the other hand increases the risk of overheating (Okrouhlík et al., 2015). In *Heliophobius*, a large patch with less hair was found on the ventral body side (Fig. 8), which probably serves for quick heat loss. At colder $T_a$, this area could be effectively "closed" by rolling the body into a ball. The short sparse hairs in *F. mechowii* are advantageous in warm conditions and during digging, because of faster heat dissipation. It would be very interesting to know if such differences between solitary and social species exist in other mole-rats as well.

In contrast to densely furred mole-rats, the naked mole-rat lacks fur on most of its body. The absence of fur is supposed to be partially compensated for by a thicker epidermal layer and reduction in sweat glands (Daly and Buffenstein, 1998). It is clear that the absence of fur and characteristics of skin contribute to its poikilothermic responses.

Exact data about the presence of subcutaneous fat and vascularisation in African mole-rats are almost non-existent. The naked mole-rat lacks a subcutaneous fat layer; there are only a pair of fat bodies surrounding the follicles of sensory hairs, scattered fat deposits in the corium (Thigpen, 1940) and dispersers have more fat especially in the belly and neck regions (O'Riain et al., 1996). It has been repeatedly pointed out that *Fukomys* mole-rats (particularly females) do not store subcutaneous fat (Burda, 1990, 1999). This author even suggested that prolonged bathyergid prenatal and postnatal development (and the need of helpers in social species) could be related to the inability of breeding females to store body fat. Later, Bennett et al. (1994b) mentioned that freshly captured mole-rats of *F. darlingi*, *F. damarensis, F. anselli* (in that study denoted as *C. amatus*), *C. hottentotus* and *G. capensis* are able to store fat with no difference between breeders and non-breeders in the social species. Unfortunately, neither of the authors provided any data and it is not clear if they meant subcutaneous fat or another type of fat. If some mole-rats are not able to store body fat, or alternatively if they store it mainly in the abdominal cavity, it should have relevancy also for their thermal biology. This topic deserves further studies.

### *10.3. Mole-rat potential for heterothermy*

Small mammals can save energy in the cold by temporarily abandoning normothermia, which is characterised by inactivity, reduced metabolism and decreased $T_b$. There is a lack of information about estivation or daily torpor in African mole-rats from the field. Anecdotal findings, such as for *G. capensis* found in a torpid state on several occasions (J.U.M. Jarvis unpubl. data in Lovegrove, 1987), indicate that at least some mole-rats are probably able to use heterothermy as an energy saving mechanism. In the absence of such data, information about $T_b$ could be indicative.

Some mole-rat species maintain a stable $T_b$ even at low $T_a$. For example, Lovegrove (1986a) found that *F. damarensis* has a stable $T_b$ at 7 °C. Two solitary bathyergids, *H. argenteocinereus* and *B. suillus*, maintain a stable $T_b$ down to the lowest $T_a$ tested, 10 °C and 13 °C, respectively (Lovegrove, 1986b; Zelová et al., 2007). In *G. capensis*, only a $T_a$ around zero induced signs of hypothermia with decreased metabolic rate to one third of RMR (Lovegrove, 1987). A remarkable decrease of $T_b$ was observed only at 5 °C in the lab in the social highveld mole-rat *Cryptomys h. pretoriae* (Haim and Fairall, 1986).

In contrast, some mole-rats are not able to maintain a stable $T_b$ and they show signs of heterothermy at relatively high $T_a$. The solitary mole-rat species, *B. janetta*, has variable $T_b$ below 24 °C (Lovegrove, 1986b). A tendency for heterothermy is more conspicuous in the Afrotropical social mole-rats. *Fukomys mechowii* and *F. bocagei* are not able to keep a stable $T_b$, as it decreased from 34.0 °C in the TNZ to 31.5 °C between 15 and 18 °C and from 33.7 °C in the TNZ to 32.5 °C between 18 and 21 °C, respectively (Bennett et al., 1994a); but see also Šumbera et al. (2007b) for a less pronounced decrease of $T_b$ in *F. mechowii* at low $T_a$. In *F. anselli,* a drop in $T_b$ of about 3 °C at 10 °C also showed that this species did not keep a constant $T_b$ at lower $T_a$. If combined with starvation, *F. anselli* readily shows torpor at a low $T_a$ (Marhold and Nagel, 1995).

A strong heterothermy was described in the tropical *F. darlingi* from Zimbabwe. The tested individuals were not able to maintain a stable $T_b$ below 25 °C with an observed decrease of 6 °C in their $T_b$ at 14 °C (Bennett et al., 1993a). The authors stressed that this phenomenon was related to a high surface to volume ratio in individuals weighing less than 60 g coupled with species high C. The limited ability to maintain a stable $T_b$ was found also in another study on individuals from the same area (Boyles et al., 2012). Interestingly, *F. darlingi* from Malawi were able to maintain stable $T_b$ even at 10 °C (Zemanová et al., 2012). The remarkable differences in body mass between both populations (the Malawian mole-rats were double the size) might explain the differences. The influence of body size on the ability to keep a stable $T_b$ was found also in one small individual weighting 90 g from the Malawian population. Its $T_b$ depended on $T_a$ in the whole range of the tested temperatures, reaching 24 °C at 10 °C (Zemanová et al., 2012).

Due to the absence of fur, the naked mole-rat is an exception among African mole-rats. Adult $T_b$ was found to be closely related to $T_a$ in the range of 12–37 °C (Buffenstein and Yahav, 1991). At 12 °C, *H. glaber* was not able to move and would probably die if exposed to this temperature for long period of time (Buffenstein and Yahav, 1991; Hislop and Buffenstein, 1994). Its low ability to defend a low $T_a$ was explained by the fact that, in nature, it is not exposed to $T_a$ below 28 °C (Bennett et al., 1988). This species was thus frequently mentioned as a poikilotherm, however, its ability to respond to noradrenalin stimulation by raising the $T_b$ and physiology of pregnant females (see below) showed that it has endothermic characteristics (Hislop and Buffenstein, 1994). New information does not confirm very high and stable $T_a$ in the burrows (Holtze et al., 2018), and the fact that it is capable of unexpected dispersal distances of several kilometres (Braude, 2000) indicate that this species is able to successfully face thermal challenges while in burrows or even on the surface. To do this, it probably combines different ways of maintaining a functional $T_b$, including social thermoregulation, muscle work, ST and NST, the timing of activity with respect to the most convenient $T_a$, etc.

So far, only a single study has evaluated bathyergid potential for heterothermy by mean of hair shaving. Boyles et al. (2012) tested whether two mole-rat species confronted with a $T_a$ below the TNZ would be more heterothermic after artificial increase of heat loss by shaving of the dorsal fur, i.e whether they lower $T_b$, and/or increase activity as a mean of behavioural thermoregulation. Both species increased activity as $T_a$ decreased, but shaving contributed little to this activity increase. Whereas *F. darlingi* decreased its $T_b$, *C. h. pretoriae* maintained the same $T_b$ in colder $T_a$. The difference is explained by the species geographical distribution and size. Compared to the tropical *F. darlingi*, the subtropical *C. h. pretoriae* challenges a more pronounced decrease of $T_a$ in nature. The smaller *F. darlingi* may lack the thermogenic capacity to maintain homeothermy. The absence of influence of fur removal on its $T_b$ indicates that its fur is relatively unimportant for thermoregulation at lower $T_a$. On the contrary, the larger *C. h. pretoriae* is probably better adapted for colder $T_a$ probably due to fur quality (unfortunately, such data are not available), because of decreased $T_b$ after shaving.

### *10.4. Metabolic protection*

If mole-rats are exposed to cold for an extended period, they may react physiologically by generating heat, which requires energy. Apart from an increase in activity, small mammals can produce endogenous thermogenic heat by shivering and nonshivering thermogenesis. The advantage of nonshivering thermogenesis is in the generation of a large amount of heat in a few minutes without interfering muscle function, whereas shivering thermogenesis involves involuntary muscle contractions, which may interfer with the mobility of the animal.

There is not much information about shivering thermogenesis in African mole-rats. Marhold and Nagel (1995) found that most females of *F. anselli* began shivering at 20 °C; the naked mole-rats shiver at 24 °C (Begall et al., 2015). On the contrary, solitary species seem to shiver at a much lower $T_a$. Two small individuals of the Afrotropic *H. argenteocinereus* shivered at 10 and 15 °C, while larger individuals did not shiver at these $T_a$ (Šumbera et al., 2007b). *Georychus capensis* shivered only at temperatures around zero (Lovegrove, 1987).

Non-shivering thermogenesis is a better-known way of heat production in African mole-rats and subterranean mammals. The potential for nonshivering thermogenesis might have important ecological implications, because it seems to be inversely related to annual temperature in the species distributional area. In the blind mole rat *S. ehrenbergi,* a relationship was found between the daily temperature range of different geographic areas in some months and the magnitude of NST (Haim et al., 1984). Among African mole-rats, injection of noradrenalin increased metabolic rates 4.5 times and $T_b$ by about 5.4 °C in *C. h. pretoriae* (Haim and Fairall, 1986). Hislop and Buffenstein (1994) found that *F. damarensis* increased metabolic rates and $T_b$ by 194% and 4.1 °C, whereas for *H. glaber* these numbers were 356% and 2.8 °C, after injection of noradrenalin compared to a control. The smaller increase of $T_b$ in *Heterocephalus* is probably related to its higher heat loss. Similar increases in the metabolic rates and $T_b$ in the naked mole-rat was found also by Goldman et al. (1999). The increased metabolism in anesthetised individuals in this study indicated that the influence of noradrenalin cannot be solely attributed to muscular activity.

Small mammals can increase their capacity for nonshivering thermogenesis if exposed to cold $T_a$ for a longer time. To test this, Woodley and Buffenstein (2002) kept naked mole-rats in colder $T_a$ for more than one year. Surprisingly, they found that the mole-rats did not increase NST capacity. It seems that the high heat loss in this species probably needs to be compensated by continuous maximum stimulation of brown adipose tissue with no potential for a further increase.

## 11. How mole-rats defend a high $T_a$

The upper limit of thermal survival of mammals is determined by many factors including $T_a$ and the length of exposure to it, humidity, water availability, activity, animal insulation, and previous acclimation. At a $T_a$ above the TNZ, mammals rapidly increase their metabolism, $T_b$, heart and breathing rates and they also lose more water. For mammals, hot, arid ecosystems are one of the most challenging environments on Earth. However, several mole-rat species occur in such areas. Living in thermally buffered burrows with water-saturated atmosphere decreasing water loss due to evaporation from lungs, nasal tissues and skin, and the accessibility of year-round geophytes providing water is key to their survival.

### *11.1. Behavioural adaptations*

Similar to the cold, the easiest way to avoid a high $T_a$ for a small mammal is to find a suitable microenvironment. If there is a risk of overheating in the warm burrows, African mole-rats may find more convenient temperatures deeper in the soil, or in burrows under vegetation. If this is not possible, other behaviours may enable them to confront the high $T_a$. For example, *H. glaber* and furred mole-rats maximize the exposed body surfaces by lying on their back with their legs spread to dissipate heat (Goldman et al., 1999; Zelová et al., 2007; own unpubl. observation).

Spreading saliva could assist in avoiding overheating. This is a less effective way of cooling compared to, for example, sweating, because, if not spread on less hairy body areas, the fur has to be soaked with saliva before the heat can move out from the skin. This mechanism is also effective for a relatively short period. Accordingly, *H. argenteocinereus* spreads saliva on the face, head, belly and body sides at $T_a$ above 30 °C (McNab, 1966), however, we did not observe it during different experiments on *Heliophobius* at high $T_a$. This behaviour may occur only in individuals from the hottest part of its distribution. No salivation was observed in *H. glaber* in the same study, probably because of easy heat dissipation through the entire body surface.

### 11.2. Morphological adaptations

Characteristics of the body surface are important not only in preventing heat loss, but also for dealing with a surplus of heat. Mammals may defend themselves against overheating by increased blood circulation in bare and highly vascularised body parts. Areas where pronounced heat exchange occurs are called thermal windows, which are usually relatively large, such as ears or naked tails. Due to the specialization for life belowground, such appendages are reduced in African mole-rats, therefore other body areas must be used to dissipate the heat. Šumbera et al. (2007b) measured $T_s$ using IRT and found that a decrease of $T_a$ causes decreased $T_s$ over all body areas in *H. argenteocinereus* and *F. mechowii* over a large range of $T_a$. In some body parts, such as around the ears, the peripalpebral region, and the ventrum, $T_s$ changed much less than on the head, trunk, and feet. All these areas play a role in heat dissipation due to easy heat exchange through the less haired surfaces. Because of the size of the ventrum, this part probably plays the main role in heat dissipation, especially if pressed to a colder burrow floor.

On the contrary, sparsely furred feet are probably relevant for active heat dissipation. It was observed that some shivering silvery mole-rats had substantially higher $T_s$ in one or two feet compared to others at 10 and 15 °C. The difference between the colder and the warmer foot was about 10 °C in one individual of *H. argenteocinereus* (Šumbera et al., 2007b). This indicates that these extremities effectively and probably actively dissipate surplus heat (produced by ST or NST or both) at low $T_a$. These body areas work in the same way at a higher $T_a$, because of their very high $T_s$ observed in the silvery mole-rat at 35 °C (Šumbera et al., 2007b). A similar response to cold in the feet and tail was demonstrated in an anesthetised rat, in which tail blood flow decreased sharply as $T_a$ decreased from 40 to 10 °C. A further decrease of $T_a$ resulted in elevated tail blood flow (Berry et al., 1984). This increase is supposed to be an adaptive response to protect exposed tissues against hypothermia.

The effectiveness of heat dissipation by increased blood circulation in other relatively small less haired body areas, such as the nose and tail in haired African mole-rats is questionable, even though the short tail in subterranean rodents can be an important venue for heat dissipation. When subjected to 35 °C, the South-eastern pocket gopher *Geomys pinetis*, with experimentally cut tails, had a $T_b$ 3 °C higher compared to those with tails (McNab, 1966). It was estimated that this species loses up to 30% of heat via the tail. The absence of any $T_b$ increase in the tailless *H. glaber* in the same study indicates easy heat dissipation via the hairless body surface. Nevertheless, heat exchange through the tail in furred mole-rats is not probably of the same importance as in *G. pinetis*, because their tails are shorter and furred.

The naked skin in *H. glaber* is a unique and sensitive organ. Prolonged exposure to low humidity and heat may lead to cracked, dry, peeling skin and even in death by dehydration (Jarvis, 1991a). Whereas *C. hottentotus* and probably other haired mole-rats have a skin typical for homeothermic mammals with sweat glands at the dorsum, the skin of *H. glaber* has no such glands (Daly and Buffenstein, 1998). Naked skin is probably an adaptation to prevent overheating in high $T_a$ in burrows, however, a negative consequence is a very high passive water loss (Tucker, 1981). Thus, loose and folded skin over the whole body and the lack of sebaceous and sweat glands probably assists in prevention of moisture loss (Daly and Buffenstein, 1998). On the other hand, increased skin area expands the surface for heat loss resulting in a higher cooling effect (Tucker, 1981). Moisture loss can also be lower due to high burrow air humidity. It is worth to mention that, even with such skin, the naked mole-rats are able to disperse for hundreds or even thousands of metres aboveground (Braude, 2000). Although exact data are missing, we may assume that mole-rats disperse during night-time to avoid high temperatures and sunlight.

### 11.3. Increase of body temperatures and metabolic rates

An increase in $T_a$ above the TNZ brings substantial energetic costs and higher metabolism in mammals due to the need for cooling. For example, an increase of 5–6 °C above the TNZ caused an increase in RMR of about 60% in *F. damarensis* (Lovegrove, 1986a) and 90% in *F. darlingi* (Zemanová et al., 2012). Although small mammals are limited by body size in the extent to which they can store heat, we may assume that storing of heat in the body is a relevant thermoregulatory mechanism in African mole-rats at high $T_a$. *Heliophobius argenteocinereus, F. darlingi* and *H. glaber* survive a short-term increase in $T_b$ of about 4–6 °C without problems (McNab, 1966; Zelová et al., 2007; Zemanová et al., 2012). The latter two species seem to be very heat tolerant, as they tolerate an increase in $T_b$ of up to 39 °C and 40 °C respectively. Tolerance to high $T_b$ could be considered an adaptation to save energy, similar to the decrease in $T_b$ at lower $T_a$. Such heat storing takes place also within the TNZ, which can be inferred by the fact that the notable increase of $T_b$ was not coupled with a higher $O_2$ consumption, which usually indicates energetically expensive cooling (Bennett et al., 1993a, 1994a; Lovegrove, 1986b, 1987; McNab, 1966; Zelová et al., 2007; Zemanová et al., 2012).

## 12. Acclimation to thermal stress

Organisms acclimate to experimentally-induced changes in a particular climatic factor, such as $T_a$, through adaptive behavioural and physiological changes. This can be characterised as a gradual change of RMR and shift of LCT and UCT towards the $T_a$ to which the animal is exposed. In mammals, the potential to acclimate to thermal stress depends on the environment from which they originated. Individuals from habitats with considerable and extended seasonal changes in $T_a$ usually have a higher potential to acclimate to changing thermal conditions.

Two studies analysed the influence of thermal acclimation on RMR in African mole-rats. Bennett et al. (1992) showed that substantial interspecific differences exist in the ability to acclimate. If maintained at 26 °C, the RMR of *Cryptomys h. hottentotus* decreased by 43% after three months in captivity. On the contrary, no decrease of RMR was detected in *F. damarensis* after a similar period of acclimation (Table 2). The authors explained the difference due to a more constant $T_a$ in deeper nests in the latter species (Bennett et al., 1988, N.C. Bennett unpubl. data in Bennett et al., 1992). A 22% decrease in metabolism after acclimation at 26 °C, which is four degree below the species TNZ, was found in *C. h. natalensis* (Bennett et al., 1993b).

Most measurements of RMR in mole-rats were conducted on animals in captivity for a long time or born in captivity (Table 2). These individuals were acclimatized to laboratory conditions defined by a particular temperature regime and reduced foraging costs and therefore they differed from the freshly captured ones in many physiological characteristics. Similarly, freshly captured animals might be affected by the stress of capture, which can also affect their RMR. These factors were discussed in Bennett et al. (1992) as alternative explanations of the detected decrease of RMR in *C. h. hottentotus* during their three months in captivity, other than acclimation. However, during this period, the tested mole-rats faced the same post-capture conditions as individuals of *F. damarensis*, which did not show any signs of acclimation. This finding supports the existence of interspecific differences in acclimatisation capability.

## 13. Thermal biology of mole-rats during pregnancy and pups

### 13.1. Pregnancy

Pregnancy is energetically costly. African mole-rats have gestation periods of up to four months (Šumbera et al., 2003), so we might expect total pregnancy costs to be higher compared to rodents with a shorter gestation. During pregnancy, the body mass of the female *H. glaber* may increase by as much as 84% (Jarvis, 1991b) and metabolic rates rise 1.4 times (Urison and Buffenstein, 1995). Such changes must influence female thermostability, not only due to their increase of body mass, but also foetal development and progesterone effect. The higher female metabolism is already visible even at less than three weeks of pregnancy (Urison and Buffenstein, 1994). During early pregnancy, peak metabolic rates occurred at $T_a$ = 27 °C and from that temperature metabolism decreased with decreasing $T_a$, reaching lowest values at $T_a$ = 31–34 °C. On the contrary, in late pregnancy (week 9–10), $O_2$ consumption was stable over the whole range of tested $T_a$s (24–36 °C) indicating a fully endothermic pattern of metabolism.

Pregnant naked mole-rat females from the mid stage of pregnancy (weeks 4–7) maintain a higher $T_b$ (of about 1 °C) compared to non-pregnant and early pregnant females (Buffenstein et al., 1996). It is assumed that this increase is caused by the greater body mass together with increased body fat (from 10% to 32%), which reduces the surface to volume ratio (from 2.8 to 2.5). If a heat source is provided, basking of females of this species decreased during later pregnancy probably due to improved insulation by increased body fat (Buffenstein et al., 1996).

Studies on the furred mole-rat are inconsistent in terms of the relation between pregnancy and metabolic rate. Bennett et al. (1993a) found lower metabolic rates in breeding females of *F. darlingi* at $T_a$ below the TNZ. These authors suggested that it might be an adaptation for future energetically costly reproduction. On the contrary, Schielke et al. (2017) demonstrated higher RMR in breeding individuals of *F. anselli*. Another study on the same species indicated that pregnant mole-rat females are more thermolabile in adverse thermal conditions. They might use torpor in lower $T_a$, whereas nonbreeding females do not (Marhold and Nagel, 1995).

### 13.2. Postnatal development of thermoregulatory abilities

Due to the stable microclimate in burrows, the low predation pressure and dispersal timed to a period when ecological conditions are suitable, a "relaxed" postnatal development in African mole-rats reflected in their long pregnancy and slow postnatal development is expected (Bennett et al., 1991). We may thus expect slow development of thermoregulation in bathyergids. M. Zemanová and R. Šumbera (unpubl. results) analysed the development of thermoregulatory abilities in *F. darlingi* pups under two different $T_a$. Newly born pups were altricial with poor fur isolation. At $T_a$ = 20 °C (below the species TNZ), pup $O_2$ consumption was lower than at 30 °C (within the TNZ) up to the age of one month. The highest $O_2$ consumption at 30 °C was at the age of one month (367% RMR per gram of adults), whereas it was at two and half months at 20 °C (721% RMR per gram of adults). Their $T_b$ at two weeks was closely related to the $T_a$ showing that Mashona mole-rat pups are not able to regulate $T_b$ at this age. Thermoregulatory abilities started to develop from the age of three-four weeks when the pups reached a body mass of about 20 g. At 30 °C, they were able to maintain a stable $T_b$ from the age of 45 days, but at 20 °C only at the age of three months. This is in the contrast with the fossorial solitary Tala's tuco-tuco, *Ctenomys talarum*, in which the highest metabolism of the pups is between 10 and 15 days, reflecting fast postnatal development (Cutrera et al., 2003; Zenuto et al., 2002). Since solitary bathyergids have faster postnatal development than the social ones (Bennett et al., 1991; Šumbera et al., 2003), we may predict fast development of thermoregulation in solitary mole-rats as well.

Physical contact with one or both parents decreases the need for producing metabolic heat and contributes to faster growth and development in pups of fossorial species (cf. Cutrera et al., 2003; Zenuto et al., 2002). *Fukomys darlingi* pups had lower $O_2$ consumption when examined in the presence of one or both parents, compared to pups examined alone or with littermates (M. Zemanová and R. Šumbera unpubl. results). This suggests that the presence of one or both parents is important for decreasing the energetic costs of the pups. We can assume that the presence of adults is crucial especially during the early stage of establishing a new family, because of the absence of older litters providing heat to the pups. This topic, which is closely related to the evolution of bathyergid social life, deserves further study.

## 14. Thermoregulation during energy consuming activities

In subterranean mammals, burrowing and the transport of soil are very important activities, because finding food, searching for sexual partners and natal dispersal is usually done by excavation through mechanically resistant soil (Nevo, 1999). In African mole-rats, soil density, cohesiveness, moisture content, and body size have been considered to be the most important factors influencing energetic cost of digging (e.g. Lovegrove, 1989; Zelová et al., 2010, 2011).

### 14.1. Digging metabolic rates

There is a 2.7–5.3 fold increase in metabolism during digging in African mole-rats depending on soil conditions (Table 3). Lovegrove (1989) found that *F. damarensis* and *H. glaber* have higher costs of digging in damp sands, probably due to pushing a heavier mass compared to dry sand. Suprisingly, both species dig faster in wet substrates. In the latter species, there was remarkable drop of $T_b$ (about 2.3 °C) after burrowing in damp sand, but not in dry sand, probably because the heat production cannot compensate for its high loss in a substrate with a higher thermal capacity. *Fukomys damarensis* increased $T_b$ by 1.3 °C after digging in dry sand probably due to its low C (Lovegrove, 1986a). Unfortunately, no data for digging in damp substrate were provided.

Similarly, Zelová et al. (2010) focused on digging costs in two mole-rat species in different substrates. Contrary to the species used in the study of Lovegrove (1986a), *F. mechowii* and *H. argenteocinereus* live in the same habitats. Both mole-rats dug with comparable energetic costs in both substrates, indicating that their digging metabolic rate is independent of substrate quality. They dug faster in softer and wetter soil, while the increase of $T_b$ was higher after digging in harder and drier substrate (Zelová et al., 2010). Similar results were obtained using the same mole-rat species in a separate study (Okrouhlík et al., 2015). The increase in $T_b$ indicates that heat in both species is not sufficiently removed during digging in dry substrates, similar to the finding for *F. damarensis* (Lovegrove, 1989).

### 14.2. Dissipation of heat during work

How do mole-rats dissipate surplus metabolic heat during and after intensive physical activity? Okrouhlík et al. (2015) tested if the thermal windows identified in Šumbera et al. (2007b) are really responsible for the exchange of heat after digging in soft and humid or hard and dry substrates. Surprisingly, $T_s$ was lower after digging in both substrates in all analysed body regions compared to the rest despite an increase of $T_b$ in both species. It appears that mole-rats effectively lose body heat during digging. There was about a 10 °C difference between the initial $T_b$ of the tested animals and soil $T_a$ (24ºC), which is very similar to

**Table 3**
Energetics of African mole-rats during burrowing in a lab and for a longer period in the field. DMR/RMR - the ratio of digging (DMR) to resting metabolic rate (RMR), DEE - daily energetic expenditure, susMS - sustained metabolic scope expressed as the ratio of DEE to RMR.

| Species | Body mass (g) | Type of soil | DMR/RMR | DEE (kJ $g^{-1}$ day $^{-1}$) | % expected DEE[a] | susMS | Source |
|---|---|---|---|---|---|---|---|
| *H. glaber* | 32 | Dry sand | 4.34 | | | | Lovegrove (1989) |
| *H. glaber* | ” | Damp sand | 5.25 | | | | ” |
| *F. damarensis* | 152 | Dry sand | 4.53 | | | | ” |
| *F. damarensis* | ” | Damp sand | 5.02 | | | | ” |
| *F. damarensis* $^{IW}$ | $133^D$, $139^W$ | | | $0.54^D$, $0.82^W$ | $40^D$, $62^W$ | $1.4^D$, $2.2^W$ | Scantlebury et al. (2006b) |
| *F. damarensis* $^{FW}$ | $78^D$, $93^W$ | | | $0.9^D$, $0.88^W$ | $58^D$, $59^W$ | $1.9^D$, $1.9^W$ | ” |
| *F. damarensis* $^{BF}$ | $124^D$, $110^W$ | | | $0.63^D$, $0.97^W$ | $46^D$, $69^W$ | $1.6^D$, $2.5^W$ | ” |
| *G. capensis* | 137 | Sandy | 2.71/ $5.15^B$ | | | | DuToit et al. (1985) |
| *G. capensis* | $137^M$, $127^F$ | Wet | | $1.0^M$, $1.1^F$ | $75^M$, $81^F$ | $1.9^M$, $2.8^F$ | Scantlebury et al. (2006a) |
| *B. janetta* | $423^M$, $291^F$ | Wet | | $0.90^M$, $0.88^F$ | $92^M$, $83^F$ | $3.2^M$, $2.6^F$ | ” |
| *H. argenteocinereus* | $161^D$, $162^W$ | | | $0.76^D$, $1.00^W$ | $60^D$, $82^W$ | $1.5^D$, $2.0^W$ | Zelová et al. (2011) |
| *H. argenteocinereus* | 232 | Hard and dry | 4.10 | | | | Zelová et al. (2010) |
| *H. argenteocinereus* | ” | Soft and wet | 3.79 | | | | ” |
| *F. mechowii* | 320 | Hard and dry | 4.62 | | | | ” |
| *F. mechowii* | ” | Soft and wet | 4.40 | | | | ” |

D - dry season, W - wet season, M – males, F – females, IW – infrequent workers, FW – frequent workers, BF – breeding females, a - % of expected DEE from the equation: DEE = 5.48 body mass$^{0.712}$ for the rodents (Nagy et al., 1999), B - this value is probably underestimated because only the value of resting individuals below TNZ (Ta = 22 °C) were used in the original study. Therefore, the second value based on RMR within TNZ from study of Lovegrove (1987) was calculated.

natural conditions (Tables 1, 2), therefore the body heat could be easily transferred to the substrate via conduction. The decrease of $T_s$ was more pronounced in mole-rats digging in a softer and wetter substrate. Unfortunately, the experimental design did not allow us to distinguish between the effects of soil hardness and humidity, which is in fact difficult, because both of these parameters are highly correlated.

The relationship between soil water content and heat dissipation might have important implications for mole-rat burrowing activity in nature. Based on the appearance of new mounds or an increase in DEE, we may assume that mole-rats increase digging activity at the beginning of the rainy season or even after the first showers (e.g. Brett, 1991 Jarvis et al., 1998; Scantlebury et al., 2006b; Zelová et al., 2011). Although, precipitation moistens the soil, changes its hardness and stimulates plant growth, digging in moist soil might also be very advantageous, because of the efficient increased body heat removal due to higher thermal capacity of such soil (Okrouhlík et al., 2015) allowing the burrowing mammals to dig more intensively and longer as well as the ease of voiding excavated soil.

### 14.3. Digging metabolism and its relation to mole-rat sociality

In social African mole-rats, individuals of the same family cooperate and share the costs of digging. Some bathyergids are known to dig cooperatively in chains, where family members alternate in the construction of burrows (Jarvis and Sale, 1971; Lovegrove, 1986a; Tucker, 1981; own unpubl. observations). Apart from testing substrates, Zelová et al. (2010) analysed the influence of size, species and sex on the digging costs. After removing the effect of body mass as the most important factor, these authors found that *F. mechowii* had a greater digging metabolic rate than *H. argenteocinereus,* suggesting that this social species has a higher energy cost per burrowed distance. It is possible that the presence of more diggers may ease selection pressure on individual digging efficacy in social mole-rats, because the animals share the costs for tunnel construction (cf. Zelová et al., 2010). On the contrary, a solitary *H. argenteocinereus*, living in very similar conditions to *F. mechowii* in terms of soil and food supply (Šumbera et al., 2012), is probably forced to burrow more effectively to reduce the risk of starvation, which is generally higher in solitarily than in cooperatively foraging mole-rats (Spinks and Plaganyi, 1999).

## 15. Timing of activity with relation to thermal environment

The subterranean environment is thermally buffered with a stable food supply and low predation risk, so mammals living there are predicted to be active during both the day and night (Nevo, 1999). Nevertheless, most field studies found a daily periodicity in the activity of subterranean rodents (see Šklíba et al., 2014 for a review).

Although light was found to be a relevant stimulus for maintaining circadian activity in many mole-rats in lab (e.g. Oosthuizen et al., 2003), the influence of the thermal environment cannot be excluded (Bennett and Faulkes, 2000; Šklíba et al., 2014). The simplest example of a relation between the daily pattern of activity and $T_a$ is avoiding thermal discomfort during the time when the burrow temperature is either too warm or cold. For example, radio-tracked Damaraland mole-rats avoid the risk of hyperthermia by constraining the time of burrowing (Lovegrove, 1988) and the naked mole-rat by restricting “volcanoing” to early morning and late afternoon (Jarvis, 1978). On the other hand, mole-rats can also be attracted to warm burrows to obtain heat passively (Brett, 1991). It is reasonable to expect higher mole-rat activity within the part of the day with a lower $T_a$, because they can use metabolic heat for warming their bodies and because it may take longer to overheat. Indeed, Damaraland mole-rats are more active at a $T_a$ below than within the TNZ in captivity (Oosthuizen and Bennett, 2015). Nevertheless, activity data on mole-rats from the field obtained by mean of radiotracking exhibit not so unambiguous relationships.

Šklíba et al. (2007) found that the activity of the silvery mole-rat rose with increased $T_a$ in the soil in the coldest part of the year (Fig. 9a), but was shifted to colder (earlier) hours at the beginning of the hot dry season. Peak activity was further shifted to earlier hours (about two hours) during the late dry season, the warmest period of the year (J. Šklíba unpubl. data). Avoiding activity at a higher $T_a$ (especially if producing large amount of heat) could be highly relevant for this species due to its long and dense fur hindering easy heat dissipation. The activity of *F. mechowii* individuals living in a family had no clear relationship to belowground $T_a$ (Fig. 9b), but a singly living, probably dispersing, female had an activity pattern tightly related to belowground $T_a$ with its peak of activity in the maximum $T_a$. During colder hours, the female stayed in the nest sleeping in a curled-up body position as is typical for solitary silvery mole-rat (Šklíba et al., 2007). Finally, Šklíba et al. (2014) found that the activity of five free-living families of *F. anselli* was tightly related to belowground $T_a$ with a peak of activity around 14:00 (Fig. 9c). Due to their relatively large body surface and high C, this small species has high thermoregulatory requirements to maintain a stable $T_b$ below the LCT. Based on published data on RMR (Table 2), it was estimated that a single individual needs to double the energy expenditure on thermoregulation to deal with the prevailing $T_a$ in burrows (cf. Šklíba et al., 2014). Activities coinciding with a high $T_a$ in burrows could thus be energetically favourable. For

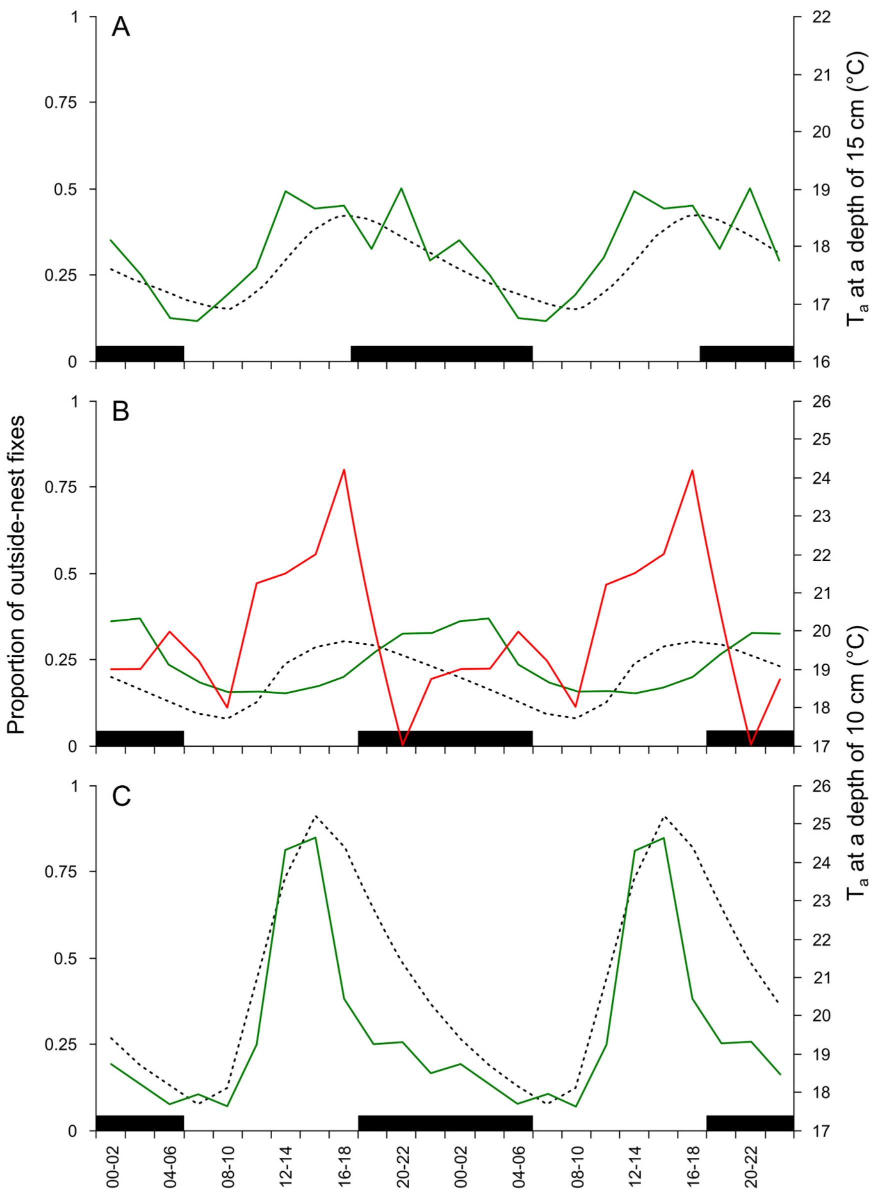


**Fig. 9.** A double-plotted diagram of activity patterns expressed as the proportion of radiotracking fixes when mole-rats were located outside of the nest (and thus active in most cases) to all fixes of the particular 2-h interval of the day (solid lines) in relation to soil $T_a$ at the depths of the foraging tunnels (dashed lines) in *Heliophobius argenteocinereus* (a), *Fukomys mechowii* (b) and *Fukomys anselli* (c). In *Fukomys mechowii*, the green line depicts the mean profile of several members of one family, the red line demonstrates the activity of isolated, probably dispersing, adult females. Modified from Šklíba et al. (2007), Šklíba et al. (2014) and Lövy et al. (2013).

this species, it might be necessary to be better adapted to cope with high $T_a$, as they spend a significant part of the day active in relatively warm burrows. Since the ability to keep heat inside the body when the $T_a$ is below the LCT and the ability to dissipate it when the $T_a$ is above the UCT are interconnected, better adaptation to a low $T_a$ has to result in a worse adaptation to high $T_a$, because better insulation against cold would limit mole-rats in warmer conditions. For Ansell's mole-rat, and probably other mole-rats, it would be better to be protected against higher $T_a$, which are more likely to be fatal in humid burrows. Lower $T_a$ can be coped with by heterothermy, ST and NST thermogenesis, huddling and the proper timing of activity.

It seems that in African mole-rats maintaining daily activity rhythms in relation to $T_a$ fluctuation is influenced by body size and also the social environment. In solitary (Šklíba et al., 2007), small social (Šklíba et al., 2014) and temporarily isolated individuals of large bodied social mole-rat species (Lövy et al., 2013), heating up bodies in warm burrows is probably less energetically costly than spending energy from internal reserves. To confirm function of changing activity as a mean of behavioural thermoregulation related to $T_a$, experimental approaches in temperature-controlled conditions in captivity are necessary.

## 16. Conclusion and perspectives

In this review, I demonstrated the diversity of adaptations in the energetics and thermal biology of African mole-rats, which allow them to thrive in a challenging environment for mammalian inhabitants. Considering the conditions in the burrows, I provided information about the environment in areas from where data on particular species, subspecies, and populations originated, because climatic characteristics, especially temperature, determine the burrow microclimate. Further, I reviewed the available data about belowground $T_a$, humidity and gas concentrations, their diurnal and seasonal changes and factors influencing them. I also gathered published data on mole-rat RMR, $T_b$, TNZ and C for particular species and I reviewed hypotheses explaining their adaptive values and evolution. In addition, I focused on the most typical activity of bathyergids, the excavation of new burrows, and how metabolism increases, and the heat produced is dissipated during this energy-consuming activity. Special attention was paid to the morphological, behavioural, and physiological characteristics that enable mole-rats to face $T_a$ above and below the TNZ to illustrate the diversity of adaptations against thermal stress. All this information provides the exhaustive overview of bathyergid thermal adaptations, which is necessary for understanding their thermal biology.

A glance at the information provided in the Tables allows us to investigate several intriguing relationships between bathyergid thermal characteristics and their environment. Ordination plots and statistical tests on the influence of these environmental variables further support these impressions. At the intra and interspecific levels, body mass explains the most variability in the selected physiological characteristics; however, temperature characteristics of climate related to latitude and altitude also play an important role (Figs. 6 and 7). Surprisingly, the influence of precipitation, i.e. a factor expected to have a fundamental influence on mole-rat life, geographical distribution and sociality, was found to have a negligible effect. Another interesting finding is the absence of any remarkable differences in the selected thermal parameters between mole-rats with different social organisations if we do not consider their different body sizes. The two species mentioned as the only eusocial mole-rat species, *F. damarensis* and *H. glaber*, are not similar in their physiology, since they are found in different parts of the multidimensional ordination space.

The position of the naked mole-rat in the ordination plots is worthy of further comment. Its thermal biology has been considered to be distinct and exceptional among mammals for a long time. Nevertheless, as demonstrated here, its uniqueness is not only related to the absence of fur, but moreover to a very small body mass. A high C and thermolability is found in other small social bathyergids from warmer climates. From the visualisations, it is clear that *H. glaber* is close to other species and is not a notable outlier. In other words, this species is not energetically as unique as previously presumed, but has a largely bathyergid and mammalian pattern of thermal biology.

We are still far from understanding all aspects of bathyergid thermal biology. For many taxa, data are completely lacking; while only anecdotal information is available for some others. The results were frequently obtained by different methods, which limits their comparison, therefore a unification of the methodical approaches used in different research groups would be helpful. A very useful approach is to focus on studying several populations of the same species from different ecological conditions in terms of altitude, aridity, food supply, soil conditions etc. This will enable studying the influence of particular ecological factors and thereby minimising the phylogenetic signal. For this purpose, species with a large geographic distribution covering diverse habitats, such as *F. damarensis* differing in aridity and *H. argenteocinereus* living from the seashore to high mountains, are potentially interesting.

In the field, easily collectable data such as the parameters of a burrow system, its depth, soil, food and vegetation above the burrow should be collected. Food and soil conditions are of special interest as they are the two main determinants of burrowing effort in order to fulfill energy needs. This, together with diurnal and seasonal profiles of belowground $T_a$, gas concentrations and humidity especially in the nests, will allow us to assess the level of environmental challenges that particular species or populations face. It would be also very useful to obtain long-term profiles of $T_b$ especially during ecological extremes such as heavy rains and during the peaks of the hot and cold seasons to see if mole-rats overcome adverse conditions by heterothermy. Application of DLW and radiotracking to follow their activity could be also very useful to know how these natural events are reflected in mole-rat energetics and behaviour.

In the lab, we should study the effects of social thermoregulation and socio-physiological factors. Attention should be paid to the development of thermal biology in pups and how it is influenced by the presence of other family members, because breeding, dispersal and forming of a new family in social species is probably the riskiest period of a bathyergid's life cycle. Due to the advantages of controlled conditions in the lab, testing of phenomena hard to study in the field, such as the influence of $T_a$, soil hardness and water content on the amount of activity, especially burrowing, metabolism and heat dissipation, should be carried out. In addition, studies on fur quality, skin characteristics, vascularisation and subcutaneous fat should be done across many species or subspecies, because such characteristics reflect the thermal environment of particular taxa to some extent.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jtherbio.2018.11.003

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