Surprisingly low risk of overheating during digging in two subterranean rodents

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HIGHLIGHTS

- Two mole-rat species increased body core temperature after digging.
- Surprisingly, both species decreased surface temperature (T_s) remarkably.
- The decrease of T_s was especially distinct on head and trunk regions.

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ABSTRACT

Capacities for and constraints of heat dissipation are considered to be important factors governing maximum intensity and duration of physical activity. Subterranean mammals are endurance diggers, but because of lack of air currents in their burrows, high relative humidity and other physical constraints, the capacity of common mammalian cooling mechanisms underground is very limited. We analyzed surface and body core temperature changes after digging in soft and hard substrates in two species of African mole-rats (Bathyergidae, Rodentia); the social giant mole-rat *Fukomys mechowii* and the solitary silvery mole-rat *Heliophobius argenteocinereus*. As expected, we observed an increase of body core temperature in both species after digging in both substrates. Surprisingly, and contrary to our expectations, we observed remarkable decrease of mole-rats' surface temperature immediately after the end of the digging trials. This decrease was greater in soft and moister soil than that in hard and drier soil. Our results suggest that mole-rats may effectively avoid overheating in burrows by effective cooling while digging, especially in wet soil. This indicates that burrowing in soils moistened by rains could be easier than previously thought contributing thus to mole-rats success in challenging environment of subterranean burrows.

1. Introduction

Physical activity of animals leads to production of metabolic heat and increase of body temperature. Due to high thermal capacity of water and its high content in tissues, heat can be partly buffered without significant increase of body temperature. Because the increase of body temperature beyond certain critical limit eventually results in irreversible tissue damage and successive death, it is crucial that the heat production and the heat dissipation are in balance. Apart from cardiovascular scope, pulmonary gas-exchange capacity or muscle performance, it is also the heat dissipation capacity that imposes upper boundary for maximal metabolic rate [1]. Diverse high energy consuming activities such as thermoregulation at low ambient temperatures and locomotion increase metabolic rate substantially. For example, flight might increase metabolic rates up to ten or twelve times in birds or bats respectively (e.g., [2,3]), burrowing through solid substrate about five times in the degu (*Octodon degu*) [4], and cold stress up to almost 13 times in the kowari (*Dasyuroides byrnei*) [5]. One of the largest energetic increases in mammals was found in high speed running horses with almost 32 fold metabolic increase [6]. However, smaller mammals are not able to increase their metabolic rate to more multiples of their resting metabolic rate because the extent of metabolic rate increase is positively correlated with the animal weight (reviewed in [7]).

Among mammals, subterranean mammals live and forage in self-constructed underground burrows facing very challenging living conditions. Similar selection pressures on subterranean mammals of different phylogenetically unrelated taxa have induced convergent evolution of

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morphological, behavioral, and physiological adaptations [8–11]. Important eco-physiological adaptations for life underground include low resting metabolic rate, high conductance, and low body temperature [8,10]. The underground ecotope is characterized by low food availability, high relative humidity, and necessity to dig through mechanically resistant substrate (cf. [11]). In subterranean rodents, digging of new burrows in order to find food and sexual partner and to disperse is probably the most energy consuming activity because the ratio of the digging metabolic rate to resting metabolic rate ranges up to 5.0 [see [12] for a review]. Remarkably increased heat production probably requires effective heat dissipation to avoid body overheating and risk of death.

However, sealed burrows of subterranean mammals are remarkable for high relative humidity, absence of ventilation, and stable temperature [13]. These factors together with usually good insulating pelage bring subterranean dwellers severe problems regarding heat dissipation and body cooling [8,9,14]. Common cooling mechanisms typical for aboveground mammals thus do not work effectively here. Heat loss by water evaporation is limited by high relative humidity in burrows and heat loss by radiation is limited by reduced or missing body appendages in subterranean mammals. The only efficient heat loss pathway is supposed to be conduction by soil. Conductive heat loss is enabled by high conductance of most subterranean mammals (e.g., [15,16]). It is expected that vasodilatation in some bared body parts such as feet or rhinarium could enable heat dissipation [8]. Interestingly, it was shown that thin and short pelage on the ventral side of the body probably play a key role in exchanging heat in two species of African mole-rats [17]. This body part was found to be important for heat dissipation also in other mammals [18–21]. However, the question arises how effective dissipation of metabolic heat might be just after energetically demanding activity such as excavation of new burrows in thermally challenging environment such as in closed humid burrows.

The aim of this study was to analyze temperature changes in two similarly sized subterranean rodent species with different social systems, the solitary silvery mole-rat (*Heliophobius argenteocinereus*) and the social giant mole-rat (*Fukomys mechowii*). In particular, we focus on differences in body temperature and surface temperature after burrowing in two different substrates, hard and soft. We predicted that (a) body temperature will increase substantially in both species during digging; (b) surface temperature will increase during digging on less haired body regions, especially on the ventral side of the body and on feet, in order to facilitate heat loss; (c) increase of surface temperature will be greater during digging in hard substrate than that in soft one because of higher mechanical resistance of the former; and (d) increase of surface temperature will be smaller in the solitary *H. argenteocinereus* than that in the social *F. mechowii* because its denser and longer pelage prevents effective cooling (cf. [17]).

2. Materials and methods

2.1. Tested animals

Seven adult giant mole-rats *F. mechowii* (five males and two females; mean weight 399 ± 93 g) and seven adult silvery mole-rats *H. argenteocinereus* (four males and three females; 239 ± 56 g) were analyzed. Both species originate from the Zambezian region in central and eastern Africa, and they live in similar habitats (grassland, woodland, and agricultural fields). Mole-rats were born or kept for at least 4 years in captivity and were accustomed to handling. Parental giant mole-rats were captured in Ndola (Zambia) and the wild-born silvery mole-rats in Blantyre-Limbe and Mulanje (Malawi). Giant mole-rat families were housed in large terrariums with a home box and plastic tubes. Silvery mole-rats lived in systems of interconnected Perspex tunnels with two home boxes. Horticultural peat was used as bedding and tissue paper as nest material. Mole-rats were fed on carrots, potatoes,

apples, lettuce, and rodent pellets. All experiments on animals were approved by the Ethical Committee of the University of South Bohemia.

2.2. Measurements of temperature

The body temperature was measured by a digital thermometer (Thermalert TH-8, Physitemp Instruments, Inc.) inserted at least 2 cm into the rectum. The surface temperature (T_s) of four defined body parts (head, trunk = dorsum + flanks, ventrum and feet) was determined from infrared images (see below) of the body surface from dorsal, lateral, and ventral side, captured perpendicularly to avoid possible errors due to angle distortion [see [17]]. For the evaluation, the mean temperature of the respective body parts was taken. Eyes, ears, and nose were excluded from the head temperature measurements.

Infrared images (thermograms) of the body surface were obtained by a thermographic camera AGA 570 (Agema infrared systems AB, Danderyd, Sweden, long wave, 7.5–12 μm, 24 FOV lens). To obtain correct values of surface temperatures by compensating for the effects of different radiation sources, the following parameters were supplied for the camera: emissivity of the subject, reflected temperature, distance between the subject and the camera, and relative humidity. Air temperature, relative humidity, reflected temperature, and air flow rate were recorded by thermometers TESTO 415, 615, and pyrometer TPT 64+. All thermograms were evaluated using analytical software (Irwin 5.3.1, Agema infrared systems AB, Danderyd, Sweden).

2.3. Experimental design

The Perspex tunnel system consisted of a starting chamber (75 × 75 × 300 mm), separated from the digging tunnel (75 × 75 mm square cross-section) by a partition. The tunnel was filled with one of the two tested types of substrate: compressed peat (water content 29 ± 3.5%) simulating soft soil or dried clay (water content 9.5 ±1.8%) simulating hard soil. The tunnel length was 60 cm (for hard substrate) or 90 cm (for soft substrate).

Tested animals were removed from their housing setting and let to acclimatize individually in boxes (40 × 23 cm) with food and bedding for 1 day before the experiment. Then the body temperature and the surface temperature of mole-rats in the rest were measured, and the animal was put into the starting chamber of the digging system and let to calm down for another 30 min. After this period, the partition between the starting chamber and the digging tunnel was removed and the animal was allowed to dig for 15 min or alternatively until it reached the end of the tunnel. The animals usually started to dig immediately. At the end of the trial, the animal was removed from the tunnel and post-digging body, and surface temperatures were measured immediately. All temperatures were measured three times, during resting and after digging in soft and hard soil.

The ambient temperature and humidity during the whole experiment was 23.7 ± 0.5 °C and 43.6 ± 2.0%. The temperature of hard and soft soils was 22.3 ± 0.3 °C and 22.2 ± 0.8 °C, respectively.

2.4. Statistical analysis

Because there was no effect of mole-rat weight or sex on resting body temperature in both species (ANCOVA; Wald statistics = 0.286; df = 1, p = 0.59; and Wald statistics = 0.344; df = 1; p = 0.56, respectively), the effect of these predictors was not considered in the following test. Body temperatures while resting, after digging in soft and hard substrate were analyzed in both species by repeated measures two-way ANOVA. Within-factor differences were identified by the Tukey HSD test (Statistica 10).

We analyzed differences in surface temperatures prior to and after digging (dependent variable) by mixed-effect mode using the R 2.14.1 (R development core team, package lme4.), assuming the Gaussian distribution (link identity). First, we extended the null model to include