Heat dissipation in subterranean rodents: the role of body region and social organisation

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The relatively warm and very humid environment of burrows presents a challenge for thermoregulation of its mammalian inhabitants. It was found that African mole-rats dissipate body heat mainly through their venter, and social mole-rats dissipate more body heat compared to solitary species at lower temperatures. In addition, the pattern of the ventral surface temperature was suggested to be homogeneous in social mole-rats compared to a heterogeneous pattern in solitary mole-rats. To investigate this for subterranean rodents generally, we measured the surface temperatures of seven species with different degrees of sociality, phylogeny, and climate using infrared thermography. In all species, heat dissipation occurred mainly through the venter and the feet. Whereas the feet dissipated body heat at higher ambient temperatures and conserved it at lower ambient temperatures, the ventral surface temperature was relatively high in all temperatures indicating that heat dissipation to the environment through this body region is regulated mainly by behavioural means. Solitary species dissipated less heat through their dorsum than social species, and a tendency for this pattern was observed for the venter. The pattern of heterogeneity of surface temperature through the venter was not related to sociality of the various species. Our results demonstrate a general pattern of body heat exchange through the three studied body regions in subterranean rodents. Besides, isolated individuals of social species are less able to defend themselves against low ambient temperatures, which may handicap them if staying alone for a longer period, such as during and after dispersal events.

The heat exchange between an endotherm and its environment is mediated via radiation, conduction, convection, and evaporation (e.g.¹). In mammals, the transfer of excess heat to the environment is facilitated by so-called thermal windows. These sparsely furred body regions are usually found at the body extremities, e.g. ear pinnae²,³, the feet³–⁶, and the tail⁷, but may also occur on the trunk⁸, and on the ventral body side⁹–¹³. Together with behavioural regulation, such as posture changes, or seeking convenient microhabitats, heat transfer in these body parts is regulated mainly by vasodilatation and vasoconstriction¹.

Mammalian thermal biology is influenced by multiple factors, but body size plays a crucial role. Compared to their larger counterparts, small mammals have to compensate for the relatively higher heat losses in cold environments due to their larger surface-to-volume ratio¹⁴. There are various strategies as to how small mammals can minimise heat loss at low ambient temperature (Tₘᵐᵦ). For example, an individual curled up into a ball reduces its surface-to-volume ratio¹⁵–¹⁷. Similarly, huddling as a mechanism of social thermoregulation decreases heat loss rate (e.g.¹⁸–²⁰). At higher Tₘᵦ, rapid heat dissipation is crucial, especially in situations where animals produce a surplus of metabolic heat, for example due to heavy physical activity. Animals move to a place with a more suitable microclimate or increase their evaporative water loss by sweating and/or panting. Thermal windows may also be actively exposed to the environment at high Tₘᵦ¹²,²¹.

Mammals living in subterranean burrows face a very challenging environment including difficulties in heat dissipation. The burrow environment is relatively warm and very humid (> 80% relative humidity even in very arid areas) with limited ventilation, and such a combination presents a problem for their thermoregulation²²–²⁵. In addition, excavation of burrows, which is the main way to reach food, increases metabolic rate up to five times that of resting²²–²⁵. Thus, the surplus body heat related to such increase needs to be effectively dissipated to

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avoid overheating\textsuperscript{22,29}. Although subterranean mammals live in a thermally relatively stable environment whose overall \( T_b \) does not decrease much below the thermoneutral zone (TNZ), most of them have dense fur that well conserve body heat\textsuperscript{30–33}. This may complicate heat offloading at higher \( T_a \)s or after digging. Finally, these mammals have reduced or even lack most body extremities such as tails and ear pinnae used for heat dissipation in non-fossorial mammals.

From this point of view it has for a long time been an enigma as to how subterranean mammals avoid overheating, especially during highly heat-producing activities. It was speculated that the excess metabolic heat is dissipated mainly through the venter in the Talas tuco-tuco \( \textit{Ctenomys talare} \)\textsuperscript{34}. This heat dissipation pathway was later supported by the analysis of surface temperatures (\( T_s \)), i.e. temperature of the fur surface facing to the environment, in five African mole-rats (Bathyergidae, Rodentia)\textsuperscript{11,35}. Both studies demonstrated that the feet which are generally less haired compared to other body regions in all bathyergids also play a relevant role in heat dissipation. It was also shown that two mole-rat species, the giant mole-rat \( \textit{Fukomys mechowi} \) and the silvery mole-rat \( \textit{Heliophobius argenteocinereus} \), cool themselves very effectively, while burrowing via contact of their body with the colder surrounding soil, especially when the soil is wet\textsuperscript{36}. Although interspecific differences in heat dissipation in mole-rats could be attributed mainly to the climate of the habitats\textsuperscript{37}, remarkable differences were found, surprisingly, also between species from the same climatic conditions and habitats. Thus, social \( \textit{F. mechowi} \) has a shorter and sparser fur allowing more effective body heat dissipation and thus higher \( T_c \) compared to the solitary \( \textit{H. argenteocinereus} \) which has longer and denser fur across most of its body\textsuperscript{38}. Higher heat dissipation for social species is disadvantageous at lower \( T_s \)s, but is reduced by huddling\textsuperscript{37,38}. Both species also differed in the pattern of \( T_c \) on the venter. Whereas \( \textit{F. mechowi} \) had a uniformly high \( T_c \) distributed across its venter, \( \textit{H. argenteocinereus} \) had a smaller area of high \( T_c \) on the chest, and the rest of the ventral surface was remarkably colder making the venter heterogeneous in terms of \( T_c \)\textsuperscript{39}. However, interpretations regarding the heterogeneity of thermal windows related to differences in social organisation are preliminary because only one solitary and one social species have been compared so far (cf.\textsuperscript{31}).

Apart from fur, heat dissipation through a particular body region could be influenced by the characteristics of skin and fat tissue as exhibited in aquatic mammals\textsuperscript{39}, or small terrestrial mammals\textsuperscript{40}. Nevertheless, to be able to move easily through burrows, mole-rats and probably also other subterranean mammals do not store fat as a subcutaneous layer\textsuperscript{41,42}. A recent analysis did not show any remarkable differences in parameters of skin and fat tissue between the dorsum and venter in \( \textit{F. mechowi} \) which supports an exclusive role of fur in heat dissipation through the integument\textsuperscript{43}. Different fur characteristics can thus have relevant behavioural and ecological consequences in subterranean rodents. For example, it has been suggested that well insulating fur allows \( \textit{H. argenteocinereus} \) to colonise the highest altitudes of the Nyika Plateau in Malawi, whereas the sympatric social Whyte's mole-rat \( \textit{Fukomys whytei} \) occurs at lower altitudes\textsuperscript{44}. We may predict that individuals of social species, when dispersing singly, have higher thermoregulatory costs due to a less insulating fur because they cannot decrease heat losses by huddling, one of the most efficient energy saving mechanisms in small social mammals\textsuperscript{40}. Although it is very difficult to obtain data on the duration of staying alone in social subterranean species in nature, several records indicate solitary individuals of social mole-rats stay for weeks, months or even years on their own\textsuperscript{45–48}.

In the current study, we recorded \( T_s \) using infrared thermography (IRT), and core body temperature (\( T_b \)) to analyse heat dissipation ability, the presence of thermal windows, and the role of social organisation in seven species of subterranean rodents over a \( T_a \) gradient from 10 to 35 °C. The studied species originated from different phylogenetic lineages (families Bathyergidae, Octodontidae, Spalacidae), climatic zones, and continents with representatives from both social and solitary species (for details see Table 1). As \( T_c \) may differ among the tested species, we introduce \( T_{diff} \) parameter defined as the difference between \( T_c \) and \( T_s \) of a particular body region (the dorsum, venter, and feet) at each \( T_a \) to quantify heat dissipation. Higher values of this parameter indicate lower heat dissipation from the respective body region to its surrounding. Since \( T_{diff} \) is determined mainly by the value of \( T_c \), while \( T_s \) changes much less, we did not test \( T_c \) in most analyses to avoid redundant results similar to those of \( T_{diff} \). We focused mainly on both extreme \( T_a \)s (10 and 35 °C), and a \( T_a \) within TNZ of all species (30 °C). We hypothesized that:

(a) Smaller \( T_{diff} \) will be found on the venter compared with the dorsum and feet at lower \( T_a \)s confirming the existence of the ventral heat dissipation surface in all species. At these low \( T_a \)s, larger \( T_{diff} \) on the feet and dorsum is a consequence of vasoconstriction in the feet, and better fur insulation of the dorsum. Furthermore, \( T_{diff} \) will be smaller in all three body regions at the highest \( T_s \) when body heat needs to be dissipated at the highest possible rate from all body surfaces to avoid overheating.

(b) \( T_{diff} \) will be generally smaller on the venter and dorsum in social compared to solitary species indicating easier heat dissipation through these regions in social species. No differences in \( T_{diff} \) are expected for the feet because they are less haired in both solitary and social species.

(c) The pattern of \( T_{diff} \) along the ventral body region will be homogeneous in social species, and heterogeneous in solitary species. The heterogeneity in \( T_{diff} \) in solitary species will be caused by smaller \( T_{diff} \) on the less furred chest compared to higher \( T_{diff} \) of other areas of the venter. Next, the venter will be homogeneous in \( T_{diff} \) in all species at highest \( T_s \)s, when body heat needs to be dissipated by the whole ventral surface to avoid overheating.

Material and methods

Tested animals. Altogether 73 individuals from seven species of subterranean rodents differing in body mass, phylogenetic relatedness, and sociality were studied (Table 1). All animals were adult non-breeders, or their breeding history was unknown in solitary species, but none of them showed signs of recent breeding, which may theoretically influence measured parameters. For the purpose of this study, we used the following taxa.
Table 1. Characteristics of seven studied species of subterranean rodents and their habitats. Means ± SD of body masses are given. Numbers in parentheses after the species names represent sample sizes. TNZ, thermoneutral zone; AP, annual precipitation; AMT, annual mean temperature; MT, minimal temperature; TAR, temperature annual range (climatic parameters were downloaded from the Worldclim database49; due to the unknown locality of S. cyanus, climatic data from the whole species range were used). 1J. Okrouhlík, unpublished data, soil temperature 10 cm deep, yearly range in 2017/2018, measured every hour. 2M. Lövy, unpublished data, soil temperature 20 cm deep, yearly range in 2014/2015, measured every 15 min. 3Upper limit is not known, but our unpublished data indicate that it is above 33 °C in N. galili. 4Winter season.

| Species (n) | Social organisation | Body mass (g) | TNZ (°C) | Burrow temperature (°C) | Altitude (m a.s.L) | Locality (GPS) | Climatic zone | AP (mm) | AMT (°C) | MT (°C) | TAR (°C) |
|-------------|---------------------|---------------|----------|-------------------------|-------------------|----------------|---------------|---------|---------|---------|---------|
| B. suillus (10) | Solitary | 694 ± 146 | 25–31 | 12.4–31.6 15 | 252 | Darling, R. of South Africa (33° 22’ S, 18° 25’ E) | Subtropics | 435 | 17.6 | 6.7 | 20.8 |
| G. capensis (9) | Solitary | 148 ± 48 | 26.3–34 2 | 12.0–30.7 3 | 252 | Darling, R. of South Africa (33° 22’ S, 18° 25’ E) | Subtropics | 435 | 17.6 | 6.7 | 20.8 |
| C. hottentotus (10) | Social | 71 ± 13 | 27–30 | 15.9–27.8 | 252 | Darling, R. of South Africa (33° 22’ S, 18° 25’ E) | Subtropics | 435 | 17.6 | 6.7 | 20.8 |
| F. anselli (10) | Social | 80 ± 11 | 26–30 1 | 18–26 4 | 1320 | Lusaka, Zambia (15° 28’ S, 28° 25’ E) | Tropics | 824 | 19.9 | 7.7 | 22.2 |
| F. “Nsanje” (10) | Social | 139 ± 27 | 27–34 5 | 53 | Nsanje, Malawi (16° 55’ S, 35° 16’ E) | Tropics | 842 | 25.7 | 14 | 21.8 |
| S. cyanus (5) | Social | 101 ± 19 | 26–33 6 | 8–32 7 | Not known | Not known, Chile | Subtropics/ temperate | 377 | 13.1 | 1.9 | 22.0 |
| N. galili (20) | Solitary | 171 ± 32 | 26.4–(>33) 8 | 5.4–34.6 | 770 | Gush Halav, Israel (33° 02’ N, 35° 27’ E) | Subtropics | 791 | 16.7 | 1.3 | 28.2 |

African mole-rats (Bathyergidae): the social Ansell’s mole-rat *Fukomys anselli* (Burda, Zima, Scharff, Macholán & Kawalika 1999) occupies the miombo in a small area near Zambia’s capital Lusaka; another social species of the genus *Fukomys* is named here as *Fukomys “Nsanje”* because founders of the breeding colony were captured near town Nsanje in south Malawi. Although we used name *Fukomys darlingi* (Thomas 1895) for mole-rats from this population in previous studies (e.g.38,49), its taxonomic status is still not resolved; the social common mole-rat *Cryptomys hottentotus hottentotus* (Lesson, 1826) occurs in mesic and semi-arid regions of southern Africa; the solitary Cape dune mole-rat *Bathyergus suillus* (Schreber, 1782) inhabits sandy soils along the south-western coast of South Africa; and the solitary Cape mole-rat *Georychus capensis* (Pallas, 1778) occupies mesic areas of the South Africa25. In addition, we studied the social coruro *Spalacopus cyanus* (Molina, 1782) (Octodontidae) occupying various habitats in Chile21; and the solitary Upper Galillee Mountains blind mole rat *Nannospalax galili* (Nevo, Ivanitskaya & Belles 2001) (Spalacidae) from Israel25. Further information about the species including number of individuals used in the study, their physiology and ecology is shown in Table 1.

All experiments were done on captive animals. *Georychus capensis*, *C. hottentotus*, and *B. suillus*, were captured about four months before the experiment, and kept in the animal facility at the University of Pretoria, South Africa (temperature: 23 °C; humidity: 40–60%, photoperiod: 12L:12D). The animals were housed in plastic boxes with wood shavings used as a bedding. *Cryptomys hottentotus* and *G. capensis* were fed with sweet potatoes; *B. suillus* with sweet potatoes, carrots, and fresh grass. *Fukomys anselli*, F. “Nsanje”, N. galili, and S. cyanus were kept for at least three years in captivity (or born in captivity) before the experiment in the animal facility at the University of South Bohemia in České Budějovice, Czech Republic (temperature: African mole-rats 23 °C, N. galili and S. cyanus 23 °C; humidity: 40–50%, photoperiod: 12L:12D). The animals were kept in terraria with peat and sweet potatoes, beetroot, apple, and rodent dry food mix ad libitum.

**Experimental design.** We measured *Tb* and *Tf* in all species at six *Ts* (10, 15, 20, 25, 30 and 35 °C). Each individual of all species was measured only once in each *Tc*. Measurements were conducted in temperature controlled experimental rooms in České Budějovice and Pretoria. Each animal was tested on two experimental days. The animals were placed in the experimental room individually in plastic buckets with wood shavings as bedding. On the first day, the experimental procedure started at *Tf* 25 °C. They spent 60 min of initial habituation in the first *Tf* after which *Tc* and *Tf* were measured as described in the following paragraphs. The *Tb* was then increased to 30 °C and 35 °C, respectively. After the experimental room reached the focal *Tc*, the animals were left minimally 30 min in each *Tf* to acclimate, and the measurements were repeated. Considering their relatively small body size, tested animals were very likely in thermal equilibrium after this period because mammals of a
comparable body mass are thermally equilibrated after similar period of acclimation. On the second day, the procedure was repeated with the initial $T_a$ 20 °C and decreasing to 15 °C and 10 °C, respectively. The time span between the measurements of the same individual in different $T_a$ was at least 150 min. Between experimental days, the animals were kept at 25 °C in the experimental room (individuals of social species were housed together with their family members).

**Body temperature measurements.** We used two sets of equipment to measure animal $T_b$ and $T_a$. In *B. suillus*, *G. capensis*, and *C. hottentotus*, $T_b$ was measured by intraperitoneally injected PIT tags (<1 g, LifeChip with Bio-Thermo Technology; Destron Fearing Corp., Dallas, Texas, USA, accuracy 0.5 °C, resolution 0.1 °C). A vet injected the tags under anaesthesia (Isoflurane) three months before the experiment. The tags were calibrated by the manufacturer and were read using a Global Pocker Reader EX (Destron Fearing Corp., Dallas, Texas, USA). $T_a$ was measured by FLIR SC325 thermal camera (FLIR Systems, Inc., Wilsonville, Oregon, USA; sensitivity < 50 mK, accuracy ± 2%, frame rate 31 fps, calibrated by the manufacturer).

Core body temperatures of *F. "Nsanje"*, *F. anselli*, *N. galili*, and *S. cyanus* were measured using a RET-2 temperature probe (Physitemp Instruments LLC., Clifton, New Jersey, USA; tip diameter 3.2 mm, inserted at least 2 cm in the rectum, accuracy 0.1 °C) connected to Thermalert TH-8 (Physitemp Instruments LLC., Clifton, New Jersey, USA; resolution 0.1 °C). This procedure took less than 30 s. The apparatus was verified against a thermometer (EL-US-2-LCD+; Lascar Electronics Ltd., Salisbury, UK; overall accuracy 0.45 °C) calibrated by an accredited laboratory. Both means of measuring $T_b$ have been shown to provide almost identical results in small mammals including one species belonging to African mole-rats.

Surface temperature was measured using a Workswell WIRIS thermal imaging system (ver. 1.50, Workswell s.r.o., Praha, Czech Republic, sensitivity 30 mK, accuracy ± 2%, frame rate 9 fps, calibrated by the manufacturer). Both thermal cameras were calibrated prior to measurement of each animal, and we used the same software to process the raw thermograms (see below).

To measure $T_b$, a focused radiometric video of the animal was taken with its different body parts exposed perpendicularly to the camera. More specifically, the animals were held hanging by the loose skin around the tail, and their dorsal and ventral body regions were sequentially exposed to the camera. This procedure took less than 30 s. To ensure unbiased $T_b$ measurements, all fans in the experimental room were switched off during measurements, and a non-uniformity correction (type of calibration of the camera) was performed just before measuring each animal. Since the seven tested species were of different sizes, and the lenses of the two thermal cameras had different focal lengths, and thus field of views, the animals were filmed at different distances from the camera to fully utilise the resolution of the two cameras. Distances of animals to the camera lens were 38–42 cm for *N. galili*, *F. anselli*, *F. "Nsanje"*, and *S. cyanus*, 53–57 cm for *C. hottentotus*, 64–68 cm for *G. capensis*, and 86–92 cm for *B. suillus*. Room air temperature and humidity were monitored throughout the trials (EL-US-2-LCD+; Lascar Electronics Ltd., Salisbury, UK; calibrated by a certified laboratory). Humidity in both labs ranged from 47 to 72% during all experiments.

To assess the heat dissipation (which is related mainly to insulative properties of the integument) of each species regardless of their actual value of $T_b$, we introduced $T_{diff}$ parameter defined as the difference between $T_b$ and $T_a$ of a particular body region of each individual (the dorsum, the venter, and the feet) at each $T_a$.

Handling stress may influence $T_b$ and may also evoke vasoconstriction on the periphery and thus potentially affect $T_{diff}$. To test the potential influence of handling procedures employed in our study on $T_b$ and $T_{diff}$, we carried out several simple experiments. Firstly, we measured $T_b$ of three individuals of *F. mechowii* (species not included in the present study, but in3) by intraperitoneal probes (G2-HR E-Mitter, Starr Life Sciences Corp., Oakmont, Pennsylvania, USA; the only species with these probes in our breeds), and found no significant differences in $T_b$ prior to or after the 30 s handling period ($T_b$ was 34.0 ± 0.6 °C and 34.1 ± 0.7 °C before and after handling, respectively; paired t-test: $t = 0.42$, $df = 3$, $p = 0.69$). Secondly, to exclude the possibility of a long-term effect of repeated handling on $T_b$, we simulated the measurement procedure with another three individuals of the same species with intraperitoneally injected PIT tags obtaining $T_b$ without direct contact. We placed mole-rats singly in a bucket and after 150 min we measured their $T_b$s. Lifting of the mole-rats and temperature measurement was repeated once again (Note that 150 min is the minimal period between two manipulations of each individual in our experiment). The $T_{diff}$ did not change during these three subsequent measurements (Generalized Least Squares model [GLS]: $F = 0.7$, $p = 0.544$; $T_b$ values were 33.14 ± 0.6, 33.13 ± 0.77 and 33.23 ± 0.92 °C). Thirdly, to rule out a possible effect of handling on $T_{diff}$, we measured dorsal $T_b$ in ten individuals of *F. "Nsanje"* (species included in the present study) before and after the handling period which took usually less than 30 s. Similarly, we did not find significant differences ($T_b$ was 30.5 ± 1.1 °C and 30.3 ± 1.1 °C before and after the 30 s handling, respectively; paired t-test: $t = 1.78$, $df = 9$, $p = 0.11$). It should be noted that all animals are accustomed to this handling, as they undertake it on a weekly basis during routine activities, such as weighing, cleaning of terraria, and miscellaneous behavioural and physiological experiments. We therefore suggest that the different approaches in obtaining $T_b$, and different time in captivity for experimental animals did not affect our results substantially.

**Thermogram processing and analysis.** The thermographic camera produces (sequences of) images in the infrared range, so-called thermograms. Sharp and high contrast radiometric thermograms of the dorsum, the venter and hind foot as a representative of the feet, were captured from the raw radiometric video in the software CorePlayer (ver. 1.7.70.320; Workswell s.r.o., Praha, Czech Republic; https://workswell-thermal-camera.com/workswellthermoformat). These parameters were entered as follows: fur emittance was...
Set to 0.97 (e.g.60); air humidity, air temperature, and reflected temperature were entered as means of experimental room humidity and air temperature during the course of $T_s$ measurement of each species at given $T_a$; distance was set as the distance of camera lens from the animal. Although Šumbera et al.31 identified a few other body surface areas through which body heat is mainly passively dissipated in mole-rats (peripalpebral, nose, and ear area), we did not include them in our study due to their relatively small area, and thus very low contribution to overall heat dissipation.

Processed thermograms were used to infer mean $T_s$ of the whole ventral and dorsal body region, and the feet necessary for the calculation of $T_{\text{diff}}$. The analysed body regions were manually marked out with a polygonal region of interest in the CorePlayer (see Fig. 1 as an example for polygon of the whole venter). The region of interest was adjusted to fit onto the part of the body region of the particular individual perpendicularly oriented to the camera lens. Additionally, the venter was divided in the anterior–posterior axis into five areas (Fig. 1: 1—between the front legs, 2—to the widest part of the chest, 3—to the end of the rib cage, 4—to the hips, and 5—between hind legs without the anogenital area).

**Data analyses.** In all analyses performed in this study, $T_{\text{diff}}$ was used as a dependent variable assuming Gaussian error distribution. In all models described below, body region (the dorsum, the venter, and feet), social organisation (social and solitary), and ventral area (1–5) were treated as explanatory categorical variables, whereas $T_s$ was treated as a covariate. Means ± SD are given throughout the text. The sex of the tested animals was not included as an explanatory variable, mainly because of a relatively low number of males and females tested. Nevertheless, we did not expect any differences because there are no remarkable sex differences in thermal biology of subterranean rodents apart from body mass if females are not pregnant or lactating pups25. To test our hypotheses, we fitted the models on subsets of data divided according to body region and selected $T_a$ values. All analyses were carried out in R61 and all figures were edited using the program Inkscape 0.92 (https://inkscape.org/).

**Figure 1.** A schematic illustration of the layout of the five ventral areas for which surface temperatures were measured. The background is an infrared thermogram of the Ansell’s mole-rat, *F. anselli* taken after acclimation at 10 °C. The figure was prepared using the program Inkscape 0.92 (https://inkscape.org/).
Tдв, T₂, and Tдв over the Tₙ gradient. Prior to testing of our hypotheses, we performed the following basic statistical exploratory analyses of Tдв and T₂. For each species, we firstly calculated a piecewise linear regression implemented in the R package Segmented to assess whether there is a breakpoint Tₛ, at which the regression curve characterising the change in Tдв (expressed as mean values for each Tₙ for each species) for a given species changes its slope. Secondly, we calculated a linear regression to characterise a change in Tдв (expressed as mean values for each Tₛ for each species) in response to increasing Tₙ. We used Bonferroni procedure to correct the α of the tests since we calculated one piecewise linear regression for Tдв for each of the seven species (adjusted α = 0.0071) and 21 linear regressions for Tₛ (adjusted α = 0.0024).

For each species separately, we tested whether Tдв differs amongst the three body regions, i.e. the dorsum, the venter, and the feet, using GLS marginal models implemented in the nlme package. One GLS model was calculated for each of three Tₙ = 10 and 35 °C as extremes in order to obtain information about Tдв in cold and hot conditions, respectively, and 30 °C which represents TNZ of all the studied species (Table 1). In all GLS models, the body region was the explanatory variable, and the identity of tested individuals was included to avoid pseudo-replication. We used the Bonferroni procedure to correct the significance level of the tests because we tested each Tₛ separately for seven species and three Tₛ (adjusted α = 0.0024), and then performed a similar post-hoc comparison 13-times (adjusted α = 0.0038).

For each species separately, we first calculated three linear regressions to test whether the slope characterising the change of Tдв in response to increasing Tₙ for each of the three body regions is different from zero. For each body region, Tдв value for a given Tₙ was calculated as the mean obtained from all individuals within a given species, for which we obtained a complete set of Tₛ values from all three body regions at all six Tₛ. Afterwards, a homogeneity-of-slopes model was calculated to test whether these three regression lines are parallel to each other, i.e. there is no interaction between body region and Tₙ. The function "emmeans" implemented in the R package emmeans was used to calculate post-hoc comparisons to find differences between the slopes for the dorsum, the venter, and the feet in these models. We used the Bonferroni procedure to correct the significance level of the tests we performed for each of the seven species: (a) three similar regression models (adjusted α = 0.0024) and (b) altogether seven homogeneity-of-slopes models with a post-hoc test (adjusted α = 0.0071).

Tдв of the three body regions in solitary and social species. To assess the effect of the social organization on Tдв (expressed as a mean value for each Tₙ for each species) in each of the three body regions, we fitted Generalized Linear Mixed Models in a Bayesian framework using Markov Chain Monte Carlo sampling algorithm (MCMC) implemented in the R package MCMCglmm. This approach was used to account for non-independence in Tдв measurements arising due to shared phylogenetic ancestry, and therefore a random effect of phylogeny was included in all models. We controlled for phylogenetic relatedness using the subset tree of the mammal phylogeny by Upham et al. The set of subtrees was retrieved via an online tool: vertlife.org/phylo-subsets/. The maximum credibility tree was then inferred using the R package phangorn, and taxa labels were changed using the R package phytokit in order to merge the taxa with the comparative dataset.

Parameter estimates for fixed and random effects of each model were obtained from sampling posterior distributions by running 2,500,000 MCMC iterations with a burn-in period of 20% and a thinning interval sampling each 1000th iteration. Estimates of each parameter are thus based on 2000 samples from a posterior distribution. In all models, we used weakly informative priors for variance components (V = 1, v = 0.02), and a default prior specification for fixed effects, i.e. mean centred on zero with a very large variance (µ = 0, V = 10⁰⁰), to let the posterior be determined mostly by the information in the data. Mixing and convergence of MCMC chains were assessed by visual inspection of both time-series and density plots, as well as by calculating autocorrelation among successive MCMC samples. There was no apparent trend among MCMC samples in time-series plots, and autocorrelation was low in each fitted model. Effective sample size was ~ 2000 for all estimated parameters in all models, suggesting generally good mixing and convergence properties of MCMC chains.

For each of the three body regions separately, we fitted a model of the formula: Tдв ~ Tₙ + social organisation + Tₛ; social organisation (the same Tдв datasets as for linear regressions were used for these models). Beside the random effect of the phylogeny accounting for evolutionary history of the studied taxa, we included also a random effect of species to account for species-specific effects on the variability in Tдв in response to Tₙ. This model allowed us to test whether the slopes for the change in Tдв as a response to increasing Tₙ differ between solitary and social species. Interaction term was considered only when its effect in a model was significant (see highest posterior density (HPD) intervals and/or PPMC in Table 3), and the deviance information criterion (DIC) indicated a better fit (lower DIC) of the model with than without interaction. If the effect of interaction was not significant, we ran the model without the interaction term, and interpreted only the effects of Tₙ and social organisation, respectively.

Tдв along the venter in solitary and social species. For each species individually, we tested whether Tдв differs among the five ventral areas using GLS models. One GLS model was calculated for each Tₙ of 10, 30 and 35 °C. In all GLS models, the ventral area was the explanatory variable (a factor with five levels: ventral area 1—ventral area 5, see Fig. 1). We used the Bonferroni procedure to correct the significance level of the tests since we tested each of three Tₛ separately for seven species (adjusted α = 0.0024). In all GLS models, an identity of tested individuals was included to avoid pseudo-replication.

In addition, for each of the three Tₛ, we fitted one MCMCglmm of the form: Tдв ~ ventral area + social organisation + ventral area: social organisation, with random effects of the phylogenetic relatedness and species. This model allowed us to test whether the pattern of mean change in Tдв (calculated as the mean from all individuals of each species entering GLS analysis mentioned above) across five ventral areas differed between solitary and social species. The effect of interaction term was considered significant if the HPD intervals did not
| Species          | Tb breaking point for Tā (°C) | Slope before the breaking point of Tb (p value) | Tā breaking point for Tb | Tā Dorsum (F and p value) | Tā Venter (F and p value) | Tā Feet (F and p value) |
|------------------|-------------------------------|-----------------------------------------------|-------------------------|---------------------------|---------------------------|-------------------------|
| B. suillus       | 27.5 ± 0.9                    | 0.052 ± 0.010 (0.035)                         | 0.244 ± 0.033           | 609.6, 1.6 × 10⁻⁴        | 850.9, 8.2 × 10⁻⁴        | 125.5, 3.6 × 10⁻⁴       |
| G. capensis      | 28.6 ± 1.4                    | 0.048 ± 0.020 (0.137)                         | 0.264 ± 0.066           | 386.6, 3.9 × 10⁻⁴        | 157.5, 2.3 × 10⁻⁴        | 216.1, 1.2 × 10⁻⁴       |
| C. hottentotus   | 29.3 ± 0.2                    | 0.069 ± 0.005 (0.004)*                        | 0.397 ± 0.015           | 615.7, 1.6 × 10⁻⁴        | 263.6, 8.4 × 10⁻⁵        | 56.1, 0.0017*           |
| F. anselli       | 28.8 ± 0.9                    | 0.072 ± 0.019 (0.064)                         | 0.361 ± 0.067           | 137.3, 3.0 × 10⁻⁴        | 74.1, 0.001*             | 160.0, 2.3 × 10⁻⁴       |
| F. "Nsanje"     | 26.8 ± 0.5                    | −0.030 ± 0.012 (0.131)                        | 0.054 ± 0.040           | 309.1, 6.1 × 10⁻⁴        | 52.1, 0.002*             | 1229.7, 3.9 × 10⁻⁵*     |
| S. cyanus        | 23.1 ± 1.1                    | 0.002 ± 0.025 (0.942)                         | 0.274 ± 0.035           | 1060.3, 5.3 × 10⁻⁴       | 670.9, 1.3 × 10⁻⁵        | 350.4, 4.8 × 10⁻⁵       |
| N. galili        | 26.6 ± 1.6                    | 0.059 ± 0.013 (0.047)                         | 0.192 ± 0.044           | 1036.3, 5.5 × 10⁻⁴       | 921.5, 7.0 × 10⁻⁴        | 382.4, 4.0 × 10⁻⁵       |

Table 2. Results of piecewise linear regressions characterising a change in core body temperature (Tb) and linear regressions characterising a change in the surface temperature (Tā) for three body regions in response to increasing ambient temperature (Tā) in seven subterranean rodent species. Breaking points and slopes are provided as mean ± SEM; p values for the slopes before the breaking point are in parentheses; statistically significant tests after the Bonferroni procedure α = 0.0071 for Tb and α = 0.0024 for Tā are marked with asterisks.

include zero (see HPD intervals and/or pMCMC in Table 4), and DIC of the model with interaction was lower than that of the model without it.

Ethical approval. The experimental procedures in the Czech Republic were approved by the University of South Bohemia Animal Welfare committee and Ministry of Education, Youth and Sports of the Czech Republic (Permission no. MSMT-26065/2014-12). The experimental procedures in South Africa were approved by University of Pretoria Ethics Committee (Permission no. EC069-16). All procedures were performed in accordance with relevant guidelines and regulations.

Results

Tb, Tā, and Tādiff over the Tā gradient. In all species apart from C. hottentotus and S. cyanus, Tb was stable from 10 up to 25 °C (the slopes of segmented regressions were close to 0), showing breaking points between 26.6 and 28.8 °C, after which Tb started to increase (see Table 2 for details). For C. hottentotus, Tb increased across the whole Tā range (the slope was significantly different from 0 for Tā values before the breaking point), but there was a relatively steeper increase between 30 and 35 °C (breaking point at 29.3 ± 0.2 °C, Table 2). For S. cyanus, Tb was stable only from 10 to 20 °C, with a breaking point at Tā of 23.1 ± 1.1 °C.

Surface temperature for the dorsum, the venter, and the feet increased in all species over the range of Tā (Table 2). For each of the seven species, Tādiff differed among the three body regions at 10 °C (p < 0.0001, Supplementary Table S2). In N. galili, F. anselli, F. "Nsanje", and S. cyanus, Tādiff was the lowest for the venter, and the highest for the feet, with the dorsum having intermediate Tādiff significantly different from both (p < 0.001, for all pairwise comparisons see Supplementary Table S2). In B. suillus, G. capensis, and C. hottentotus, Tādiff was lower only for the venter than the dorsum (p < 0.001), and the feet did not differ from either of the two.

At 30 °C, Tādiff differed among the three body regions in N. galili, B. suillus, and F. anselli only (p < 0.0001, Supplementary Table S2). While both the venter and the feet had significantly lower Tādiff than the dorsum in N. galili (p < 0.001), Tādiff was lower for the feet than for both the venter and the dorsum in B. suillus (p < 0.001). In F. anselli, the ventral Tādiff was lower than the dorsal one, with Tādiff of the feet being the highest (p < 0.001).

At 35 °C, Tādiff differed among the three body regions only in N. galili, B. suillus, and G. capensis (p < 0.0001, Supplementary Table S2). The feet of N. galili had lower Tādiff than the venter and the dorsum, with the latter having the highest Tādiff (p < 0.001). In both B. suillus and G. capensis, the feet had lower Tādiff than both the dorsum and the venter (p < 0.001) which had similar Tādiff.

For each of the seven species, Tādiff decreased with increasing Tā in all three body regions (see Table 3 for statistical details and Fig. 3). Among the three body regions, the ventral Tādiff showed the smallest change in response to increasing Tā (i.e. a less steep slope), and it differed significantly from those of both the dorsum and the feet in five species. In S. cyanus, it differed from the feet only, and in C. hottentotus, no differences among all three respective slopes were found. Besides, the slopes for the dorsum were significantly steeper than slopes for the feet in F. anselli, F. "Nsanje", S. cyanus, and N. galili.

Tādiff of the three body regions in solitary and social species. The comparison among the slopes of regression lines characterising the response of Tādiff to increasing Tā for the dorsum, the venter, and the feet differed between solitary and social species (Fig. 4). For the dorsum, Tādiff was significantly higher in solitary than in social species across the whole Tā range (pMCMC < 0.0001), and it decreased relatively more in solitary (slope = −0.52) than in social species (slope = −0.39) for a given increase in Tā (Fig. 4A and Table 4, DIC = 134.4 and 119.8 for models without and with the interaction between Tā and social organisation, respectively). For the venter, the slopes characterising the change in Tādiff in response to increasing Tā did not differ between solitary and social species (slope = −0.23, DIC = 93.4 and 95.6 for models without and with the interaction between Tā and...
social organisation, respectively; pMCMC = 0.884), but there was a tendency (pMCMC = 0.079) for higher T_{diff} in solitary compared with social species (Fig. 4B and Table 4). For the feet, T_{diff} did not differ between solitary and social species across the T_a range (slope = −0.59, Fig. 4C, and Table 4, DIC = 145.8 and 148.1 for models without and with the interaction between T_a and social organisation, respectively; pMCMC = 0.902).

T_{diff} along the venter in solitary and social species. The T_{diff} for the five ventral areas varied for each of the seven species at T_a of 10, 30, but not at 35 °C (Table 5; Supplementary Fig. S1; see also Fig. 5 for the comparison of T_s pattern of the venter at 30 °C for one solitary and one social mole-rat). In the N. galili, F. anselli, F. "Nsanje", T_{diff} varied among the five ventral areas at both 10 and 30 °C, whereas for C. hottentotus and S. cyanus, it differed at 30 °C only. At 35 °C, there were no differences in T_{diff} among the five ventral areas in all species. In solitary B. suillus and G. capensis, the venter was thermally homogeneous at all T_a. There were no significant differences in the pattern of the T_{diff} change among the five ventral areas between solitary and social species in either of the three T_a (see Table 6 for statistical details; at 10 °C: DIC = 65.2 and 72.7, at 30 °C: DIC = −3.6 and 3.1 and at 35 °C: DIC = −44.1 and −42.5; the first and second DIC value are for models without and with the interaction between the ventral area and social organisation, respectively).

Figure 2. Core body temperatures and surface temperatures of the dorsum, the venter, and the feet measured across the range of ambient temperatures in seven subterranean rodent species. Means ± SD are depicted. The figure was prepared using the program Inkscape 0.92 (https://inkscape.org/).
ratio bringing additional energetic savings70 (note that the same posture is adopted also by torpid small non-
animals not only minimise heat losses through their venter, but also reduce their effective surface-to-volume
dissipation can be advantageous as its heat flow may be controlled behaviourally12,21,31,69. Although we did not
up into a ball was observed in most individuals at lower Tas (see Supplementary Fig. S2). Adopting this posture,

| Species          | Dorsum (R2 adj)  | Venter (R2 adj) | Feet (R2 adj) | Body region × Tb | p value of post-hoc comparison |
|------------------|------------------|----------------|---------------|------------------|-------------------------------|
|                  | t = −11.1, p < 0.001* (0.96) | t = −6.1, p < 0.001* (0.88) | t = −7.1, p = 0.002* (0.91) | F = 12.1, p = 0.001* | 0.003* 0.003* 0.999 |
| G. capensis      | t = −38.0, p < 0.001* (1.00) | t = −10.0, p < 0.001* (0.95) | t = −21.4, p < 0.001* (0.99) | F = 54.2, p < 0.001* | < 0.001* < 0.001* 0.552 |
| C. hottenrotus   | t = −13.3, p < 0.001* (0.97) | t = −10.4, p < 0.001* (0.96) | t = −11.8, p < 0.001* (0.97) | F = 8.5, p = 0.005* | 0.013* 0.008* 0.956 |
| F. anselli       | t = −25.0, p < 0.001* (0.99) | t = −10.0, p < 0.001* (0.95) | t = −13.4, p < 0.001* (0.97) | F = 66.2, p < 0.001* | 0.004* < 0.001* < 0.001* |
| F. ’Nsanje’      | t = −16.0, p < 0.001* (0.96) | t = −14.9, p < 0.001* (0.98) | t = −14.2, p < 0.001* (0.98) | F = 31.7, p < 0.001* | 0.007* < 0.001* 0.003* |
| S. cyanus        | t = −10.5, p < 0.001* (0.96) | t = −8.4, p < 0.001* (0.93) | t = −10.1, p < 0.001* (0.95) | F = 21.1, p < 0.001* | 0.231 < 0.001* 0.002* |
| N. gailli        | t = −12.4, p < 0.001* (0.97) | t = −14.4, p < 0.001* (0.98) | t = −11.6, p < 0.001* (0.96) | F = 31.4, p < 0.001* | 0.004* < 0.001* 0.006* |

Table 3. Results of the linear regressions testing whether the slopes characterising a decrease in the change of the difference between core body and surface temperatures (Tdiff) in response to increasing ambient temperatures (Ta) differ from zero for the dorsum (D), venter (V) and feet (F) and of the homogeneity-of-slope models (Body region × Tb) testing whether these slopes differ among the three body regions in seven subterranean rodent species. The degrees of freedom were 1 and 4 for the linear regressions and 2 and 12 for the homogeneity-of-slope models; the goodness of fit of the regression is presented by the adjusted R2; the p value of post-hoc pairwise comparisons for the homogeneity-of-slope models are shown in the columns V vs. D, V vs. F, and D vs. F; statistically significant results after Bonferroni correction α = 0.0024a or α = 0.0071b applied are marked with an asterisk.

Discussion
To the best of our knowledge, this study represents the highest number of endotherm species, where heat dissipation has been analysed within a single study using the IRT approach. In several aspects, this allows us to generalise our findings for subterranean rodents. We found that the main heat dissipation areas in all species are present at the venter and the feet. With respect to the effect of sociability, solitary species dissipate less heat through the dorsum than social species and the same tendency was found for the venter. For the feet, there were no differences between both groups. Finally, the pattern of heat dissipation along the venter was not consistent between species and could not be attributed to sociability.

For the purpose of our study, we defined Tdiff as the difference between Tb and Ts in each individual and each Tb measured. The value of this parameter is predominantly driven by Tb which increases remarkably over the gradient of Tb for all three body regions with Tb being much more stable (Fig. 2). Applying this approach can be important especially in comparative studies using multiple species differing in Tb and species-specific change of Tb over the gradient of Tb. This can be illustrated by the results of the segmented analysis when the increase of Tb over the gradient of Ta. This can be illustrated by the results of the segmented analysis when the increase of Tb over the gradient of Ta. This can be illustrated by the results of the segmented analysis when the increase of Tb over the gradient of Ta. This can be illustrated by the results of the segmented analysis when the increase of Tb over the gradient of Ta.

Our results demonstrate that the tested body regions play different roles in heat dissipation in subterranean rodents. As predicted (based on31,34), at the coldest Tb measured (10 °C) we found lower Tdiff on the venter compared to the dorsum in all studied species (and in F. anselli, F. ‘Nsanje’, S. cyanus, N. gailli also compared to the feet) showing relatively higher heat dissipation from this body region (Fig. 3 and Supplementary Table S2). The warmer venter in lower Tbs compared to other body surfaces was recently also found in three social mole-rat species35. This finding corresponds with the pattern found in some other mammals. A venter suitable for heat dissipation can be advantageous as its heat flow may be controlled behaviourally12,21,31,69. Although we did not quantify the behaviour of all individuals during the experiments, closing of a ventral thermal window by curling up into a ball was observed in most individuals at lower Tbs (see Supplementary Fig. S2). Adopting this posture, animals not only minimise heat losses through their venter, but also reduce their effective surface-to-volume ratio bringing additional energetic savings70 (note that the same posture is adopted also by torpid small non-volant mammals71). On the contrary, at high Tbs (≥ 30 °C), tested animals usually exposed their venter to the environment mainly by lying on their back with the legs outstretched trying to maximize heat transfer to the surroundings (Supplementary Fig. S2). A large ventral thermal window should thus be advantageous, especially in subterranean mammals because they are predicted to lose the excessive metabolic heat during digging by means of conduction when the venter is in direct contact with the excavated soil and burrow floor69.

Our findings also confirm an important role of the feet in thermoregulation of subterranean rodents as has been also shown in two studies on African mole-rats34,35. In laboratory rats, the feet together with the distal parts of legs comprise around 10% of the total body surface and serve as an important heat dissipating region32. The feet of rodents adapted for digging and removing the soil are larger than in non-fossorial rodents73,74, and thus represent a significant proportion of the body surface. The importance of the feet in the thermoregulation of subterranean rodents is likely even higher because of lack of other body appendages, and due to their large surface-to-volume ratio. The feet are usually not well haired which, together with their bare pedal surface, makes them suitable for fast and effective heat transfer. Due to their relatively large size and heat convection via direct
contact with the substrate, the feet are far more effective than small areas around the eyes or ears which were also found to lose heat in mole-rats \textsuperscript{31}.

In this regard, our results indicate very effective vasoconstriction taking place in the feet to decrease heat losses at the lowest \( T_{\text{as}} \). This is supported by the feet being the body region with the lowest \( T_{s} \), and thus highest \( T_{\text{diff}} \) in four of seven tested species at \( T_{a} \) of 10 °C (Fig. 2, 3, and Supplementary Table S2). The absence of significant differences between the feet and the other two body regions at this \( T_{a} \) in \textit{B. suillus}, \textit{G. capensis}, \textit{C. hottentotus} indicates a very effective insulative ability of their haired body surfaces rather than the absence of effective vasoconstriction in their feet. Importantly, at 35 °C, the feet \( T_{\text{diff}} \) was significantly smaller than the \( T_{\text{diff}} \) of other two body regions in three tested solitary species, \textit{N. galili}, \textit{B. suillus}, and \textit{G. capensis} (Fig. 3, Supplementary Table S2). This demonstrates intensive vasodilatation and dissipation of the excessive body heat which cannot be effectively dissipated by other body parts because of the presence of well insulating fur (based on data on fur characteristics for all three species, Vejmělka and Šumbera unpubl. data). Heat dissipation via the feet is likely very relevant, similarly to the venter, especially during digging because of their contact with soil. McGowan et al. \textsuperscript{35} even suggested that the feet with reduced hair coverage are important at high \( T_{s} \) when other conductive heat losses are working at their maximal capacity. Since the feet contribute to increased heat dissipation at high \( T_{s} \), but effectively decrease heat loss at low \( T_{s} \), they serve as a typical body-extremity-located thermal window similarly to other mammals (e.g. \textsuperscript{36}).

**Figure 3.** The difference between core body temperature and surface temperature (\( T_{\text{diff}} \)) for the dorsum, the venter, and the feet across the range of ambient temperature (\( T_{a} \)) in seven subterranean rodent species. Points indicate mean values, straight lines are the regression lines predicted by linear models. The figure was prepared using the program Inkscape 0.92 (https://inkscape.org/).
The importance of the feet in heat exchange was supported also by behavioural observations during the experiment. At low $T_{as}$, we observed that many tested animals were sitting on the hind feet with the front feet not in contact with the cold floor (Supplementary Fig. S2). It was also documented that several individuals of *H. argenteocinereus* had some of their feet surprisingly warm while shivering at 10 °C. This indicates that the feet may play an active role in dissipation of excessive heat produced by shivering as suggested by authors, or alternatively, occasional warming of the feet could be related to protection against cold damage by repeated short-term redirection of blood flow into peripheral colder body parts, as showed across diverse mammalian taxa including foxes, rats, or humans (e.g., 4, 75, 76).

We demonstrated that tested species and probably other subterranean rodents effectively combine heat dissipation through the venter and the feet, yet each of these body regions acts as a different type of thermal exchanger. The first type emits heat more or less continuously (as indicated by constantly relatively low $T_{diff}$, and by its less steep slope over the gradient of $T_a$ compared to the other two body regions; see Fig. 3), and is represented by being less furred, and thus less thermally insulated venter. When necessary in cold conditions, heat dissipation through this surface can be reduced behaviourally by changing the body posture (see above). The second type is represented by the feet with the steeper slope of the $T_{diff}$ change. In the cold temperatures, heat loss may be prevented effectively as for instance indicated in gerbils. In this regard, the way in which these mechanisms, when acting simultaneously, contribute to heat dissipation is intriguing, and needs to be further explored in subterranean rodents and mammals in general.

Considering the effect of sociality on heat dissipation, Šumbera et al. found that social *F. mechowii* had higher $T_v$ on both the venter and the dorsum, but not the feet compared with solitary *H. argenteocinereus*. Our results partially support the effect of sociality on heat dissipation in larger number of species. As expected, the
role of the feet in heat dissipation was independent of social organization, as demonstrated by almost identical regression lines for solitary and social species (Fig. 4C). On the contrary, solitary species had significantly higher T_{diff} on the dorsum across tested T_{as}, especially at lower temperatures (Fig. 4A). Solitary species thus conserve heat more effectively through this body region especially at lower T_{as} (cf.31). Although the mean ventral T_{diff} of solitary species was about 2 °C higher across experimental T_{as} (Fig. 4B), this difference only approached significance. This might be caused mainly by a large intraspecific variability of the ventral T_{diff} among the four studied social species (compare Fig. 4A,B). Indeed, S. cyanus and C. hottentotus had markedly higher T_{diff} than two Fukomys

Table 4. Relationships between the difference between core body and surface temperature (T_{diff}) of the three body regions, ambient temperature (T_{a}), and social organisation (solitary vs. social) in seven species of subterranean rodents. 2.5% HPD and 97.5% HPD represent lower and upper highest posterior density intervals; pMCMC denotes to the p value obtained from MCMCglmm; T_{a} × Social organisation = interaction between T_{a} and social organisation.

| Body region | Fixed term                      | Estimate (β) | 2.5% HPD | 97.5% HPD | pMCMC |
|-------------|--------------------------------|--------------|----------|-----------|-------|
| Dorsum      | Intercept                        | 15.237       | 12.534   | 17.958    |       |
|             | T_{a}                            | −0.394       | −0.437   | −0.349    | <0.0001|
|             | Social organisation (solitary)   | 6.358        | 3.664    | 8.995     | 0.001 |
|             | T_{a} × Social organisation      | −0.131       | −0.190   | −0.059    | <0.0001|
| Venter      | Intercept                        | 9.870        | 6.637    | 13.007    |       |
|             | T_{a}                            | −0.233       | −0.257   | −0.208    | <0.0001|
|             | Social organisation (solitary)   | 1.962        | −0.124   | 4.427     | 0.079 |
|             | T_{a} × Social organisation      | 0.004        | −0.046   | 0.053     | 0.884 |
| Feet        | Intercept                        | 22.6530      | 19.3105  | 26.4544   |       |
|             | T_{a}                            | −0.591       | −0.636   | −0.543    | <0.0001|
|             | Social organisation (solitary)   | −0.644       | −3.258   | 2.197     | 0.558 |
|             | T_{a} × Social organisation      | 0.005        | −0.092   | 0.093     | 0.902 |

Table 5. The results of GLS models comparing the difference between core body and surface temperature (T_{diff}) among the five ventral areas at ambient temperature (T_{a}) of 10, 30 and 35 °C in each of the seven subterranean rodent species. For each T_{a}, the venter was tested separately; n denotes to the number of individuals tested for each T_{a}; statistically significant results after Bonferroni correction α = 0.0024 applied are marked with an asterisk; post-hoc comparisons among the areas are depicted by letter combinations in Supplementary Fig. S1.

| Species | T_{a} (°C) (n) | Fixed term: ventral area | |
|---------|----------------|--------------------------|---|
| B. suillus | 10 (10) | F_{S,v}=0.7, p=0.616 | |
|          | 30 (9)    | F_{S,v}=1.3, p=0.302   | |
|          | 35 (10)   | F_{S,v}=0.4, p=0.817   | |
| G. capensis | 30 (7) | F_{S,v}=2.6, p=0.054   | |
|          | 35 (4)    | F_{S,v}=1.8, p=0.160   | |
| C. hottentotus | 30 (9) | F_{S,v}=0.8, p<0.001*  | |
|          | 35 (9)    | F_{S,v}=4.0, p=0.008   | |
| F. anselli | 10 (8)  | F_{S,v}=14.7, p<0.001* | |
|          | 30 (7)    | F_{S,v}=16.4, p<0.001* | |
|          | 35 (6)    | F_{S,v}=3.9, p=0.014   | |
| F. "Nsanje" | 10 (11) | F_{S,v}=39.5, p<0.001* | |
|          | 30 (8)    | F_{S,v}=11.3, p<0.001* | |
|          | 35 (6)    | F_{S,v}=0.4, p=0.814   | |
| S. cyanus | 10 (2)   | F_{S,v}=0.4, p=0.804   | |
|          | 30 (3)    | F_{S,v}=43.1, p<0.001* | |
|          | 35 (5)    | F_{S,v}=0.7, p=0.586   | |
| N. galili | 10 (17)  | F_{S,v}=6.1, p<0.001*  | |
|          | 30 (15)   | F_{S,v}=8.7, p<0.001*  | |
|          | 35 (17)   | F_{S,v}=1.4, p<0.239   | |
species at the lowest Ta of 10 °C (see Fig. 3). We may speculate that such difference can indicate better ventral fur insulation in these two species, as they occupy harsher environmental conditions compared to tropical habitats of both Fukomys species (see Table 1). Further studies that will focus on the fur quality including more species from various environmental conditions could help to better understand this concept.

Higher heat dissipation from the surface of social subterranean species is linked with lower insulative properties of their fur31,33. Dense heat conserving fur is probably not necessary in social species because they can take advantage of social thermoregulation at low Ta37,38. While individuals of social species are temporarily single such as during digging, burrow maintaining, and patrolling, metabolic heat produced by their activities could help to keep a stable Tb (c.f.36,78). On the contrary, solitary species cannot use huddling. Instead, solitary species can minimise body surfaces exposed to the environment solely by curling up during the rest, as observed in all solitary species at low Ta in the present study, and also during several radio-tracking studies under natural conditions79–81. Denser and thus well insulating fur across the dorsum and flanks of solitary species31,33 is important because this body region is always exposed to the environment when the animal is rolled into a ball. On the other hand, less insulating fur in social species is advantageous at high Ta, or whilst digging when it is necessary to dissipate surplus metabolic heat to avoid overheating. In this situation, better heat conserving fur of solitary species complicates heat dissipation as we observed higher Tdiff on the dorsum, and in some species also on the venter, compared to the feet at the highest studied Ta in solitary species only (see Supplementary Table S2). Thus, their feet likely play a crucial role in heat dissipation at high Ta and/or during digging in solitary species.

Different social organisation and fur characteristics resulting in different body heat dissipation may have relevant ecological consequences. For the naked mole-rat Heterocephalus glaber, the combination of small body mass and hairless surface resulting together in very high heat losses limits its occurrence in lowland areas of East Africa because it is not able to disperse through the cooler highlands in the western and northern borders of its distribution82. We may assume that higher heat losses in social species may handicap them during dispersal and forming of new families especially in colder climate if they disperse singly. Although it is very difficult to collect such information in nature, it seems that dispersing individuals of social species can stay alone for long period of time, likely for weeks, months, or even years45–48 facing high thermal challenges during that time. In this regard, although anecdotal, the radio-tracking of F. mechwii revealed interesting finding related to this phenomenon47. Lövy et al.45 found that a solitarily living female had a different circadian activity pattern and resting position than conspecific mole-rats living in a group. This female was most active during the hottest part of day, and usually rested in the curled-up body position while mole-rats from the family were most active during the night, and rested communally outstretched in their nest as indicated by a signal of their collars. Both changing of resting position and activity pattern likely minimised her heat losses. Interestingly, the peak occurred during the hottest part of the day and the pattern of its activity was more similar to that of the activity of the solitary H. argenteocinereus and N. galili79,80 than to F. mechwii living in a family group67. Besides, less insulating fur of social species could explain why the social F. whytei does not colonise generally colder Afromontane grasslands from the lower altitudes of the Nyika Plateau where it is common in contrast to the solitary H. argenteocinereus, even though there is a higher food supply and more easily workable soil in grasslands44.

Finally, we analysed whether Tdiff differs along the venter, and if sociality influences the heterogeneity of ventral Tdiff distribution as suggested for two mole-rat species with contrasting sociality31. For this purpose,
we divided the venter into five areas (Fig. 1), and for each species, we analysed the pattern of T_{diff} at Ta below, within, and above TNZ (Table 5). Although there were some statistically significant differences in the pattern of T_{diff} among these ventral areas for particular species at Ta below and within TNZ (except for B. suillus and G. capensis; see Table 5 and Supplementary Fig. S1), the differences were usually small. Due to this and the absence of any consistent pattern within the tested species, we think that the differences have probably low biological importance. In C. hottentotus and S. cyanus, the differences were found only within TNZ, but not in the lowest Ta.

As expected, we found homogeneous pattern of T_{diff} at the highest Ta. Together with low values of T_{diff} at this Ta, it demonstrates that heat dissipation through the ventral surface is maximal. Similarly, no consistent differences in the pattern of the T_{diff} change across the five ventral areas between solitary and social species were detected in either of the three Ta (Table 5).

Nevertheless, limitations of the IRT approach should be considered when measuring T_c of restricted body areas in small mammals, such as those five ventral areas explored in our study. For instance, the analysis of the insulative quality of the fur might be a better approach to reveal potential differences if such heterogeneity exists. It should be noted that recent findings based on the histological analysis of small skin patches along the body in F. mechowii did not reveal any differences in the amount and structure of the adipose tissue and vascularisation along its venter43. This suggests fur having the main role in heat dissipation through the integument in mole-rats and subterranean rodents generally.

For future research on heat dissipation in subterranean rodents, histological analysis of the feet, analysis of T_s of the only hairless rodent H. glaber, experiments based on fur shaving, direct measurement of thermal insulation of fur, and/or measuring of skin temperature with thermocouples could bring valuable information on how subterranean rodents handle heat dissipation which is a crucial aspect for mammals who frequent burrows for their whole lives.

### Table 6. Relationships between the difference between core body and surface temperature (T_{diff}), ventral area (five ventral areas, for details see Fig. 1) and social organisation (solitary vs. social) in seven species of subterranean rodents. 2.5% HPD and 97.5% HPD represent lower and upper highest posterior density intervals; pMCMC denotes to the p value obtained from MCMCglmm; ventral area × social organisation = interaction between ventral area and social organisation.

| Ta (°C) | Fixed terms | Estimate (β) | 2.5% HPD | 77.5% HPD | pMCMC |
|---------|-------------|--------------|----------|-----------|--------|
| 10      | (Intercept) | 7.828        | 1.728    | 13.867    | 0.026  |
|         | Ventral area 2 | −0.275      | −1.111   | 0.456     | 0.481  |
|         | Ventral area 3 | −0.099      | −0.899   | 0.668     | 0.817  |
|         | Ventral area 4 | 0.134       | −0.679   | 0.889     | 0.743  |
|         | Ventral area 5 | 0.478       | −0.311   | 1.253     | 0.225  |
|         | Social organisation (solitary) | 2.712      | −2.031   | 6.858     | 0.187  |
|         | Ventral area 2 × social organisation (solitary) | 0.122      | −1.109   | 1.290     | 0.848  |
|         | Ventral area 3 × social organisation (solitary) | 0.044      | −1.113   | 1.141     | 0.938  |
|         | Ventral area 5 × social organisation (solitary) | −0.355     | −1.526   | 0.857     | 0.356  |

| Ta (°C) | Fixed terms | Estimate (β) | 2.5% HPD | 77.5% HPD | pMCMC |
|---------|-------------|--------------|----------|-----------|--------|
| 30      | (Intercept) | 2.603        | 0.647    | 4.388     | 0.017  |
|         | Ventral area 2 | −0.111      | −0.421   | 0.181     | 0.461  |
|         | Ventral area 3 | −0.119      | −0.415   | 0.195     | 0.427  |
|         | Ventral area 4 | −0.030      | −0.351   | 0.253     | 0.846  |
|         | Ventral area 5 | −0.003      | −0.325   | 0.256     | 0.980  |
|         | Social organisation (solitary) | 2.053      | 0.444    | 3.786     | 0.034  |
|         | Ventral area 2 × social organisation (solitary) | 0.097      | −0.352   | 0.559     | 0.657  |
|         | Ventral area 3 × social organisation (solitary) | 0.049      | −0.390   | 0.494     | 0.834  |
|         | Ventral area 4 × social organisation (solitary) | −0.181     | −0.637   | 0.253     | 0.409  |
|         | Ventral area 5 × social organisation (solitary) | 0.092      | −0.340   | 0.526     | 0.683  |

| Ta (°C) | Fixed terms | Estimate (β) | 2.5% HPD | 77.5% HPD | pMCMC |
|---------|-------------|--------------|----------|-----------|--------|
| 35      | (Intercept) | 1.441        | −0.949   | 3.734     | 0.137  |
|         | Ventral area 2 | −0.051      | −0.225   | 0.103     | 0.506  |
|         | Ventral area 3 | −0.037      | −0.188   | 0.122     | 0.641  |
|         | Ventral area 4 | 0.046       | −0.127   | 0.187     | 0.543  |
|         | Ventral area 5 | 0.026       | −0.116   | 0.202     | 0.728  |
|         | Social organisation (solitary) | 2.967      | 1.097    | 4.553     | 0.008  |
|         | Ventral area 2 × social organisation (solitary) | −0.048     | −0.275   | 0.196     | 0.677  |
|         | Ventral area 3 × social organisation (solitary) | −0.063     | −0.287   | 0.187     | 0.585  |
|         | Ventral area 4 × social organisation (solitary) | −0.239     | −0.443   | 0.016     | 0.041  |
|         | Ventral area 5 × social organisation (solitary) | −0.166     | −0.406   | 0.049     | 0.153  |
Data availability

The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

Received: 1 February 2020; Accepted: 30 December 2020
Published online: 21 January 2021

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Acknowledgements
We thank to K. Hrubá, J. Řihánková, and K. Schoeman for their assistance during data collection and processing and P. Duda for help with phylogenetic analyses. Our thanks are due to R. Pešková for her care of analysed rodents, to prof. C. Pirk for lending us an IRT camera, to prof. A. McKechnie for letting us to use the experimental room, and to two anonymous reviewers for their constructive comments. This study was supported by the Czech Science Foundation (GACR 17-19896S to R.S.), Faculty of Science, University of South Bohemia in České Budějovice (Junior Premium Scholarship for talented applicants to F.V.), South Bohemia university Grant (GAU No. 048/2019/P to F.V.), and South African Research Chair (SARChI chair, GUN Number 64756 to N.C.B.; Chair Postdoctoral Fellowship to J.O.).

Author contributions
R.S., F.V., J.O., and M.L. conceived and designed the conceptual framework of the study. F.V., M.L., and J.O. collected data. F.V., M. L., G.S. and J.O. analysed data. E.N. and N.C.B. contributed with experimental animals. R.S. and N.C.B. provided funding for research. F.V and R.S. wrote the text with assistance of all co-authors.

Competing interests
The authors declare no competing interests.

Additional information
Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-021-81404-3.

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