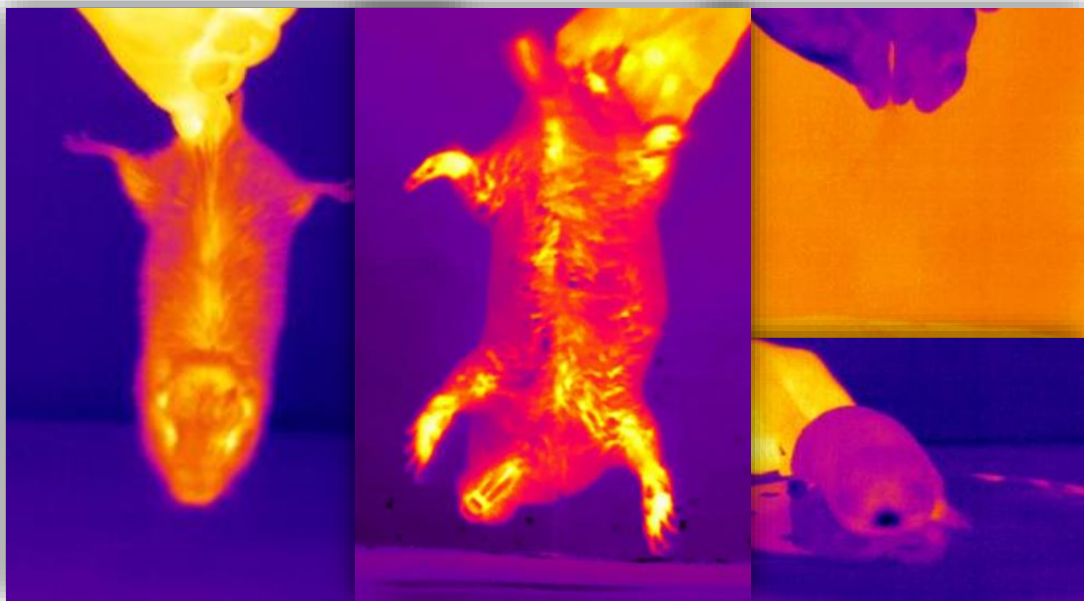


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The detection of thermal windows in fossorial rodents with varied sociality degree



Master's thesis

Bc. František Vejmělka

Supervisor: doc. Mgr. Radim Šumbera Ph.D.

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Annotation:

Eight rodent species with fossorial activity differing in a number of characteristics such as ecology, climatic conditions, geographical distribution, or kinship were studied using infrared thermography in order to describe their surface temperature and its patterns. An attempt to describe the relation between surface temperature and varied social organisation in burrowing rodents was made.

Declaration (in Czech):

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Podpis:

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1. Introduction

1.1. The role of fur in endothermy

The endothermic organisms are able to produce more metabolic heat compared to the ectotherms. Birds and mammals are known as “warm-blooded” vertebrates, having an insulative layer protecting them from the heat loss, which also leads to homoiothermy (homeothermy). Due to the capability of maintaining stable body temperature, the homoiothermic endotherms were able to inhabit almost all available habitats on the planet.

Body fat and fur are two most common ways how mammals protect their bodies from the undesirable heat loss. Terrestrial mammals possess rather thin skin and thin fat layer (fulfilling mainly energy storage function, if present) necessary for better movement abilities (Sokolov 1982).

The capability of air retaining in the fur and thus protecting skin against convection makes fur a good insulator (Sokolov 1982). Scholander et al. (1950) revealed positive relationship between fur thickness and its insulation ability. The longer the hairs are, the more air can be trapped within the fur layer. Reynolds (1993) demonstrated that due to the higher air retention of denser pelage, thermal loss of the Norway lemming (*Lemmus lemmus*) during winter decreased. Another thermal improvement of fur is air retention in hair medulla. Experimental substitution of the air in hair by Freon gas resulted in a decrease of thermal conductivity of the pelage (Hammel 1955 in Birkebak 1966). In addition, air cavities in the upper epidermis layer (*stratum corneum*) could contribute to insulation according to Sokolov (1982).

The importance of fur as a thermal insulation of mammals was confirmed repeatedly. The pelage removal caused increase of daily energy expense followed by rise in food consumption in different small mammal species such as the meadow vole (*Microtus pennsylvanicus*), the western harvest mouse (*Reithrodontomys megalotis*), the golden-mantled ground squirrel (*Spermophilus lateralis*), or laboratory mouse (Kenagy and Pearson 2000; Zhao and Cao 2009; Pearson 1960; Kauffman et al. 2004; Król et al. 2007).

1.2. Thermal windows

1.2.1. Heat Transfer

The heat exchange between organism and its environment is mediated via convection and evaporation, radiation, and conduction. A notably intensive heat transfer is enabled by so-called thermal windows. The mammalian thermal windows are sparsely furred

and therefore poorly insulated body parts. Together with behavioural control (see below), heat transfer in these tissues is regulated by vasodilatation and vasoconstriction (Zada and Jensen 2016; Buffenstein 2000). The presence of arteriovenous anastomoses in the thermal windows, controlling the blood supply of particular body parts, is not clear.

There are different strategies how the endotherms could minimise heat loss from their bodies to the surroundings at low ambient temperature (hereafter T_A). For example, an individual curled into a ball not only hides its ventral thermal window, but also reduces its surface-to-volume ratio, and thus decreases heat loss (Contreras 1986; Šumbera et al. 2007). Similarly, close animal aggregation for thermoregulatory purpose (social thermoregulation) decreases heat loss (e.g. Hayes et al. 1992; Kotze et al. 2008; Gilbert et al. 2010). Similar behaviour is known in birds as well, for example in mousebirds (Coliidae) or Chaetura swifts (Apodidae).

Next possibility is finding more appropriate microclimate. Mammals can orient themselves to the source of sunshine or heat, a behaviour known as basking. In small mammals, basking is advantageous especially in diurnal rodents experiencing cold nights. Surprisingly, poorer thermal insulation was found in couple of Afrotropical rodents (compared to their relatives from for example warm lowlands) - *Otomys sloggetti robertsi* (Rymer et al. 2007) or *Lophuromys melanonyx* (Ivlev and Lavrenchenko 2015). According to the authors, it probably enables them to gain more heat from solar radiation. Behavioural thermoregulation is important not only in small mammals. The guanaco (*Lama guanicoe*) can thus reach up to 67 % of energy saving thanks to appropriate body posture and thermal window alteration (“opening and closing”)(de Lamo et al. 1998). Yet when shaved, the llamas emitted heat with their whole body surface (Gerken 2010).

On the other hand, if there is high production of body heat, for example due to high physical activity, it is necessary to dissipate it from the body to avoid overheating. Therefore, the thermal windows are exposed to the environment (Atlee et al. 1997; Šumbera et al. 2007; Gerken 2010).

1.2.2. Location of the thermal windows

The thermal windows are often found at body extremities such as ear pinnae of the New Zealand rabbit (*Oryctolagus cuniculus*) and the African elephant (*Loxodonta africana*) (Mohler and Heath 1988; Phillips and Heath 1992); feet of the Eurasian otter (*Lutra lutra*) (Kuhn and Meyer 2009), the Pacific harbor and Northern elephant seals (*Phoca vitulina richardsi* and *Mirounga angustirostris*)(Khamas et al. 2012), and the woodchuck (*Marmota*

monax); as well as its snout (Phillips and Heath 2001). Williams et al. (1999) and Pabst (2002) argued that the dorsal fin of the bottlenose dolphin (*Tursiops truncatus*) serves as a thermal window. Another highly important area for heat dissipation is a tail. The giant otter (*Pteronura brasiliensis*), the muskrat (*Ondatra zibethicus*), or beavers (*Castor canadensis* and *C. fiber*) exemplify this case (reviewed in Kuhn and Meyer 2009). Further body region containing thermal windows is head, for instance in giraffe (*Giraffa camelopardalis*) (Mitchell and Skinner 2004), or foxes (*Vulpes vulpes*, *Alopex lagopus*, and *Vulpes macrotis*) (Klir and Heat 1992). In addition, the thermal windows are located on ventral part of a mammal – for example in the Talas tuco-tuco (*Ctenomys talarum*) (Cutrera and Antinuchi 2004), the giant mole-rat (*Fukomys mechowii*) (Šumbera et al. 2007), or the Brazilian free-tailed bat (*Tadarida brasiliensis*; together with flanks) (Reichard et al. 2010; 2012). Other areas of the animal's body taking part on the heat transfer include axillary and flank regions – e.g. in camels (Gerken 2010; Abdoun et al. 2012), or skin patches in giraffes (Mitchell and Skinner 2004). Interestingly, according to the Klir et al. (1990), the Mongolian gerbil (*Meriones unguiculatus*), possesses no thermoregulatory surface areas, it is supposed to use only behavioural and ecological adaptations for heat transfer.

Compared to the studies mentioned above using infrared thermography (IRT) to assess the areas of active heat transfer, thermal windows can be studied also by fur analysis. Underwood and Reynolds (1980), revealed the summer thermal window in the Arctic fox (*Vulpes lagopus*) studying pelage length. Šumbera et al. (2007) detected thinner ventral pelage in two species of African mole-rats. In my bachelor's study (Vejmělka 2016), I found different patterns in fur characteristics (length and density) in rodents with different sociality and the rate of underground activity. For more details, see the chapter The relationship of thermoregulation of chthonic mammals to their fur and social system.

1.2.3. Mammal thermal windows and environments

Conveniently distributed thermal windows enable mammals inhabit large number of environments. As mentioned above, aquatic mammals possess the thermal windows on poorly insulated extremities such as fins or feet. While using their feet to dissipate the surplus of body heat, the otters maintain the temperature in their pelage more than 10°C higher compared to the environment – both air and water (Kuhn and Meyer 2009). Mauck et al. (2003) were interested in a heat transfer mechanism of amphibiously adapted mammals when situated on the ground. The authors revealed “dynamical” thermal windows on the trunk of three seal species. In their wet fur, there were regions becoming dry faster (and thus seeming warmer

under IRT) than surrounding areas. These regions expanded dependently on T_A . Surprisingly, the authors found no special morphological adaptations, as for instance arteriovenous anastomoses, which were found not only in the flippers, but in whole skin of several other pinniped species (Bryden and Molyneux 1978). Khamas et al. (2012) found that while in otariids whole body skin is very emissive; in case of phocids, only the flippers act as a thermal window being the most emissive body region in hot and the least emissive region in cold.

In flying mammals, the patagium of the bats acts as a thermal window. In particular, the window is situated at the upside of the strongly pigmented and vasomoting membrane, while the underside is densely furred (Sokolov 1982). According to the author, denser pelage is supposed to be present at the ventral part of bat's trunk, which is windward. The thermal windows were found in flanks and body sides of the Brazilian free-tailed bat (Reichard et al. 2010; 2012). The authors state this feature (called "radiators" in that study) to be characteristic for the Molossidae, a warm-areas-inhabiting family containing long-distance migrating species, and thus requiring various adaptations for the long flights. However, in other long-distance migratory species of other bat families, these thermal windows were not found. Therefore, the pattern of its occurrence could be explained by a phylogenetic constraint (Reichard et al. 2010).

Arboreal mammals experience unexpectedly considerable thermal challenges as well, especially in warm regions. Thompson et al. (2016) used temperature loggers attached to the anklets of the mantled howling monkeys (*Alouatta palliata*) to examine thermal microenvironments the primates experience during the whole day. The authors ascertained significant rise in T_A connected with the monkey's move up. The rise is obvious even with the change by one meter (for example 0.5°C between five and six meters high). Briscoe et al. (2014) described koalas (*Phascolarctos cinereus*) resting against tree trunks in hot weather. Adpressing to the trunks or branches, cooler than the ambient air, leads to heat transfer via conduction (68% of the whole heat loss). The koalas adopted a posture called by authors as "tree-hugging" because the thermal window is probably located on their ventral side, which is less insulated (measured as fur depth). Interestingly, the difference compared to the dorsal pelage is more pronounced in southern populations facing greater T_A variations (Briscoe et al. 2015).

1.3. Mammals with underground activity

The most abundant mammal group with underground style of life are rodents (Nevo 1999). These belong to families Octodontidae, Ctenomyidae, and Echimyidae from South America; African Bathyergidae; Geomyidae and Aplodontidae from North America; old-world Spalacidae; or Cricetidae.

Mammals with underground activity differ in the degree of adaptations to subterranean life. Since the descriptive terms are loosely substitutable; here, I would like to define the terminology used in my study. For the rate of underground activity, I will use the word *chtonicity*, brought from ancient mythology. Considering the extremes of the chtonicity continuum (fig. 1), the terms *subterranean* and *fossorial* will be used in this work, following Šumbera (in press). Fossorial species are typical for surface foraging (for example the common vole *Microtus arvalis*); while the subterranean species forage underground (such as the naked mole-rat – *Heterocephalus glaber*), and do not leave their burrows unless necessary, for instance because of dispersion (Nevo 1999). Originally, fossorial means adapted to digging.

The underground ecotope on the one hand provides convenient microclimate, but on the other hand rather inhospitable habitat. McNab (1966) characterizes the burrows as dark and humid environment with low primary production and limited ventilation. The combination of high humidity and stable, relatively high temperature poses challenge for the thermoregulation of the chtonic mammals (see next chapter). Furthermore, adopting the underground niche brings the issue of food accessibility - it is necessary to dig it up which is energetically very demanding (McNab 1966; Luna and Antinuchi 2007b). Nonetheless, the mammal convergently adapted on many levels (Nevo 1999; Buffenstein 2000).

1.4. Thermoregulation of chtonic mammals

One of the characteristic issues for mammals inhabiting the subterranean burrows is poor heat transfer due to the high air humidity and the absence of air circulation (McNab 1966, Nevo 1999, Buffenstein 2000). Consequently, overheating might imperil the individual because burrowing produces high amount of heat that must be dissipated (Luna and Antinuchi 2007b; Zelová et al. 2010). In this situation, low thermal insulation and high thermal conductance would be thus expected to facilitate loss of heat. Surprisingly, despite whole life stay in this environment, quality of fur in subterranean mammals is considerably

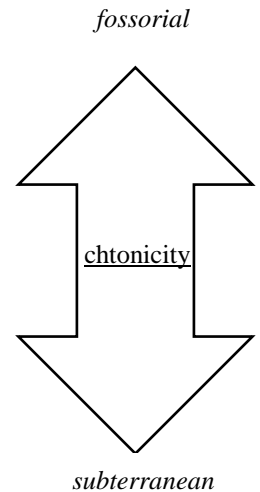


Figure 1: Defined terms of the chtonicity continuum.

high (e.g. 20 000 hairs/cm² in the European mole – *Talpa europea*, Sokolov 1982; or mole-rats – see Table 1).

The most crucial role in heat dissipation in chtonic mammals plays apparently conduction (McNab 1966; Buffenstein 2000). The most superficial layer of the (majority of mammals') body is pelage. Fur conduction conjoins with the microstructure of the hair (Birkebak 1966). The more air is trap in the fur (both within the pelage and inside the hairs), the better thermal insulation, i.e. the lower conduction. I summed up information regarding the hair microstructure of the chtonic mammals in my bachelor's thesis (Vejmělka 2016). The microstructure is connected for example with both phylogeny and ecology of certain species.

Thermal windows play a role in heat loss via conduction. As mentioned above, chtonic rodents possess their thermal windows situated mainly on the ventral side and feet (Cutrera and Antinuchi 2004; Šumbera et al. 2007; Vejmělka 2016). Okrouhlík et al. (2015) showed that burrowing giant mole-rat and silvery mole-rat (*Heliophobius argenteocinereus*) cooled themselves via the contact of their surface with the excavated substrate. The majority of the heat probably leave the body through their thermal windows on the ventre. In addition, differences were revealed in the distribution of thermal windows in respect to the social organisation of studied rodents (Šumbera et al. 2007; Vejmělka 2016).

Thermoregulation in chtonic mammals is species-specific. Boyles et al. (2012) found that the removal of the dorsal fur caused decrease in body temperature (T_B) of the highveld mole-rat (*Cryptomys hottentotus pretoriae*) while in the Mashona mole-rat (*Fukomys darlingi*) there was no effect on T_B . This might be a result of a different climate of the species' habitats.

1.5. The relationship of thermoregulation of chtonic mammals to their fur and social system

The characteristics of body insulation and the social organisation of the species may be interconnected. Šumbera et al. (2007) suggested that social system of chtonic mammals influences the characteristics of their thermal windows. The fur analysis of two mole-rat species in their study revealed longer and denser fur (except for the ventral side which is sparser) in the solitary silvery mole-rat, compared to the social giant mole-rat (Tab. 1); in spite of both species living in very similar climatic conditions and habitats. The social giant mole-rat possesses larger thermal window (on the most of its ventral region), whereas the solitary silvery mole-rat has smaller thermal window located on its chest. The worse pelage quality of social species improves heat dissipation, the social life style enables heat conservation thanks

to the huddling. The solitary species, on the other hand, are more resistant to lower T_A owing to more insulative fur with smaller thermal windows. That makes it better controllable, yet the heat is dissipated worse (Šumbera et al. 2007). Furthermore, the latter species is able to lower its surface temperature (hereafter T_S) after physically demanding activity better than the social mole-rat, even though its better insulation (Okrouhlík et al. 2015).

Table 1: Ecological and fur characteristics of selected chtonic rodents. Modified from Vejmlka (2016).

* Šumbera et al. (2007) used mole-rats from captivity, and divided their surface into ventral region and trunk.

Species and body region	Family	Social system	Chtonicity	Vejmlka (2016)		Šumbera et al. (2007) *	
				Length [mm]	Density [n/cm ²]	Length [mm]	Density [n/cm ²]
Dorsum							
<i>Fukomys anselli</i>	Bathyergidae	Social	Subterranean	6±0.6	12 187±2057		
<i>Fukomys mechowii</i>	Bathyergidae	Social	Subterranean	7.6±0.5	10 068±3210	7.1±0.8	11 154±538
<i>Heliophobius argenteocinereus</i>	Bathyergidae	Solitary	Subterranean	15±3	12 464±3923	17.1±2.1	16 460±2 767
<i>Nannospalax galili</i>	Spalacidae	Solitary	Subterranean	9.9±1.7	16 303±4154		
<i>Tachyoryctes macrocephalus</i>	Spalacidae	Solitary	Fossorial	12.5±1.6	10 373±1052		
<i>Tachyoryctes splendens</i>	Spalacidae	Solitary	Fossorial	13±0.7	12 884±3189		
Ventre							
<i>Fukomys anselli</i>	Bathyergidae	Social	Subterranean	6±0.6	7 386±1407		
<i>Fukomys mechowii</i>	Bathyergidae	Social	Subterranean	8.3±0.5	5 811±1949	7.5±0.8	2 753±110
<i>Heliophobius argenteocinereus</i>	Bathyergidae	Solitary	Subterranean	9.8±1.6	5 653±2559	11.0±1.5	1 778±263
<i>Nannospalax galili</i>	Spalacidae	Solitary	Subterranean	8.5±0.5	8 680±3235		
<i>Tachyoryctes macrocephalus</i>	Spalacidae	Solitary	Fossorial	11.6±1.3	5 292±137		
<i>Tachyoryctes splendens</i>	Spalacidae	Solitary	Fossorial	9.3±0.8	7 861±1453		

I tested the relation of social system and thermal insulation in my bachelor's work (Vejmlka 2016) using fur analysis in six rodent species differing in social organisation, chtonicity, and ecology (see Table 1). Ventral thermal windows were found – predominantly in case of hair length. To provide complex expression of the fur insulation, the parameter insulative volume combining both fur characteristics (length*density) was implemented. It states the amount of insulative medium for the volume unite of fur (see the thesis for details). Remarkable differences indicating the phenomenon of social thermoregulation were revealed in the insulative volume of the fur. Figure 2 illustrates high levels of insulative volume in solitary species, and low in social species (marked with asterisks). Interestingly, good insulation of the blind mole rat and the silvery mole-rat is achieved by the densest fur in the former, but the longest in the latter (Vejmlka 2016). The striking difference between the animals with different social system evinces the dorsal part of the animals, i.e. the one without thermal windows.

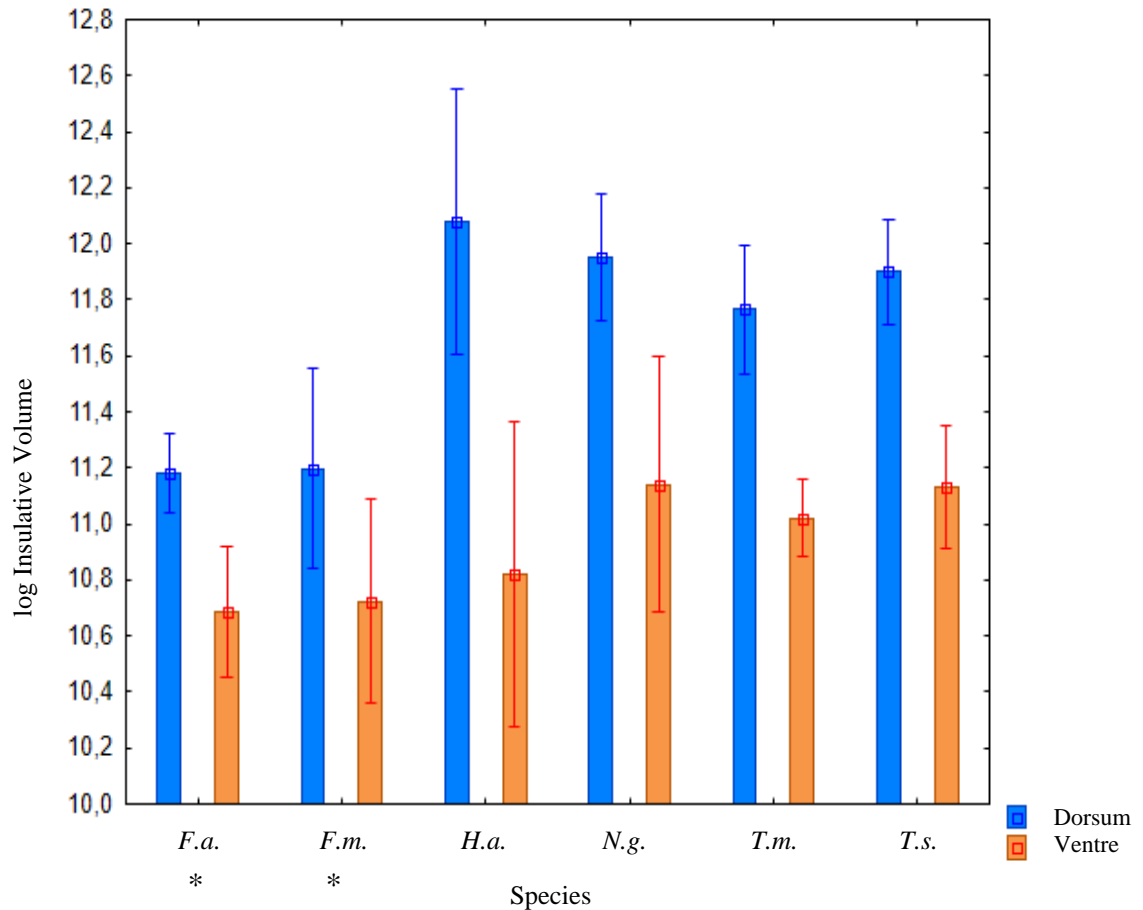


Figure 2: Log Insulative Volume of six studied rodent species with various social system and chthonicity rate (mean \pm s.d.)(Vejmělka 2016). *F.a.* = *Fukomys anelli* (social, subterranean); *F.m.* = *F. mechowii* (social, subterranean); *H. a.* = *H. argenteocinereus* (solitary, subterranean); *N.g.* = *Nannospalax galili* (solitary, subterranean); *T.m.* = *Tachyoryctes macrocephalus* (solitary, fossorial); *T.s.* = *T. splendens* (solitary, fossorial) – for details see Tab. 1. Social species are marked with an asterisk.

Although Sokolov (1982) claims that subterranean mammals usually have uniform fur all over their bodies, I found increasing insulation quality of ventral fur in the posterior direction in the solitary species of studied chthonic rodents (Vejmělka 2016; Fig. 3). In other words, the thermal window seems small, located on the chest (as described in Šumbera et al. 2007). A characteristic of the dorsal pelage is its uniformity.

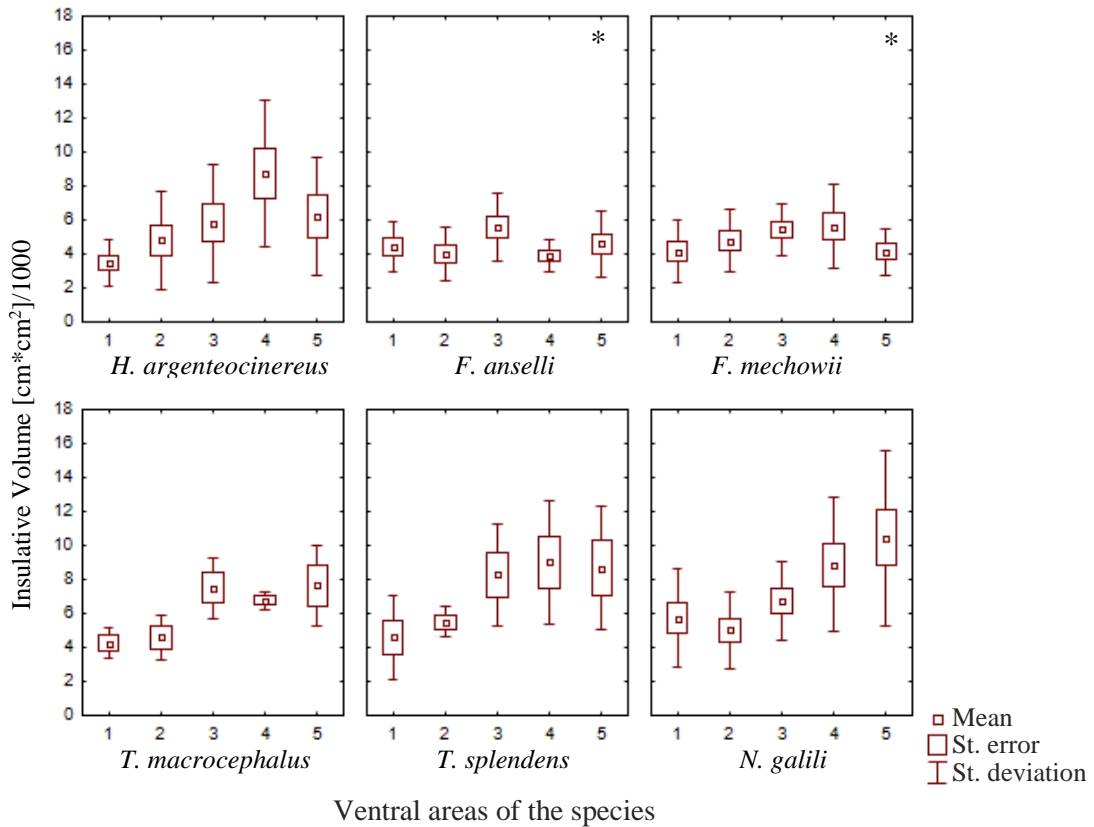


Figure 3: Insulative Volume of ventral fur in six rodent species with various social system and chtonicity rate (Vejmělka 2016) – for details see Tab. 1. Areas 1 – 5, anterior-posterior direction, respectively. Homogeneous fur can be seen only in social species (*Fukomys*) – marked with asterisks.

The IRT study of Šumbera et al. (2007) revealed interesting differences in T_s of two mole-rats with different social system. However, only two species are too little for the possibility of making any statement regarding the influence of social system on body heat dissipation in chthonic rodents, and it is necessary to enlarge the sample. To understand more the phenomenon of social thermoregulation with connection to thermal insulation, I analyzed here the surface temperatures of several chthonic rodent species with different level of sociality and from different ecological conditions in different ambient temperatures by using infrared thermography.

1.6. Tested hypotheses

- Main thermal window(s) is in all studied furred chronic species located on the ventral body region.
- Surface temperature will be generally higher on ventral and dorsal body region in social species.
- The main thermal window of the solitary species will be smaller and located on the chest compared to social species.
- Surface temperature across the whole body of the naked mole-rat is comparable without any indication of thermal windows.

2. Material and methods

2.1. Studied species

Eight species of chtonian rodents were analysed. The species differ in their social organisation, body mass, and level of underground activity (defined as chtonicity in the Introduction) (Tab. 2 in the Appendix). All measurements were conducted in two laboratories, in České Budějovice (University of South Bohemia; Czech Republic) and in Pretoria (University of Pretoria; Republic of South Africa). The species measured in České Budějovice were kept for at least three years in captivity and accustomed to handling. The South African species were captured about four months before the experiment and kept in the animal facility at the University. Further information about the animals used in this study are shown in Table 3 in the Appendix.

Altogether, 87 individuals were studied. Six species of African mole-rats (Bathyergidae, Phiomorpha, Hystricognatha) were analysed. Mole-rats are subterranean African endemic rodents differing in social organisation. The social Mashona mole-rat *Fukomys darlingi* (Thomas 1895) occupies mainly miombo woodlands of the Zimbabwean plateau. The individuals used in this study originated from two families. The social Ansell's mole-rat *Fukomys anselli* (Burda, Zima, Scharff, Macholan, and Kawalika 1999) lives in a small area in the miombo near Zambia's capital Lusaka. The studied animals originated from two families. The social naked mole-rat *Heterocephalus glaber* Rüppell 1842 inhabits semi-desert savannah areas of the Horn of Africa. All tested individuals lived in one family. The South African mole-rats occur syntopically at the original locality where they were captured. The solitary Cape dune mole-rat *Bathyergus suillus* (Schreber, 1782) inhabits sandy soils along the south-western coast of South Africa. The solitary Cape mole-rat *Georchus capensis* (Pallas, 1778) occupies mesic areas with sandy soils of the South Africa. The social common mole-rat *Cryptomys hottentotus hottentotus* (Lesson, 1826) lives in mesic and semi-arid regions of Southern Africa. The studied animals from later species originated from one family.

The coruro *Spalacopus cyanus* (Molina 1782); Octodontidae, Caviomorpha, Hystricognatha) is a social fossorial species occupying various habitats in Chile. Members of four families were measured.

The Upper Galilee Mountains blind mole rat (*Nannospalax galili* (Nevo, Ivanitskaya and Beiles 2001); Spalacidae, Myomorpha, Myodonta), is a solitarily subterranean species living in Mediterranean Israel.

Additional information about species, their ecology, and physiological parameters are shown in Table 2 in the Appendix. Each studied animal was actually nonbreeding adult.

In the animal facilities in České Budějovice, the stable room temperature is 25 (± 1) °C, and relative humidity 40-50% is maintained. The naked mole-rat live in a separate room in plexiglass maze consisting of boxes connected with tubes. Wood shavings are used as a bedding. One box (nest) is underlaid with a terrarium substrate heater (heating mat, about 29°C; Heat Wave Desert PT2030, Exo Terra, Rolf C. Hagen Inc.). The room in which the naked mole-rats live have temperature 25 (± 1) °C and relative humidity 29%. Other mole-rat species and coruros are kept in large terraria with peat as a substrate, with flowerpots as nests and plastic tubes provided. The blind mole rats are kept in terraria, standardised rodent cages Velaz T type, or in plexiglass maze connected with a box. The room temperature of the separated rooms with the blind mole rats and with the coruros is 22-23°C. The animals are fed with vegetables (such as carrots, potatoes, sweet potatoes, beetroot), apple, and chinchilla dry food mix (Tukan, Agrochovex s.r.o.; fruit, seeds, grains). Banana is added to the naked mole-rats' diet. Water is not provided.

In Pretoria, the studied animals were wild-captured, and kept in the laboratory animal facility for about four months. The temperature of the facility is 23°C. The animals were housed in plastic boxes with wood shavings used as a bedding. The common mole-rats and Cape mole-rats were fed with sweet potatoes and the Cape dune mole-rats with sweet potatoes, carrots and fresh grass.

2.2. Experimental design

The experiment was conducted in two periods. One was carried out on the 21st - 23rd February and 1st – 3rd March 2017 at the University of South Bohemia in České Budějovice, Czech Republic; the other on the 25th and 26th November 2017 at the University of Pretoria, Republic of South Africa. In České Budějovice, each species was examined during two days with one day off in-between to avoid exposing the animals to extreme temperatures in consecutive days, and not to separate the families for too long (in case of social species).

The studied species were tested in a broad range of ambient temperatures. Measurements started in 20°C or 25°C, and then moved towards extreme T_A (Tab. 4). The animals were weighted before and at the end of every experimental day.

Table 4: The succession of experimental days and temperatures for each of studied species.

1st = first day; 2nd = second day. Note that the days of each period do not correspond.

Species	Ambient temperature [°C]									
	10	15	20	25	27.5	30	32.5	35	37.5	40
<i>Nannospalax galili</i>	2 nd	2 nd	2 nd	1 st		1 st		1 st		
<i>Spalacopus cyanus</i>	2 nd	2 nd	2 nd	1 st		1 st		1 st		
<i>Fukomys darlingi</i>	2 nd	2 nd	2 nd	2 nd		1 st		1 st		
<i>Fukomys anselli</i>	2 nd	2 nd	2 nd	2 nd		1 st		1 st		
<i>Heterocephalus glaber</i>			2 nd	2 nd	1 st	1 st	1 st	1 st	1 st	1 st
<i>Bathyergus suillus</i>	2 nd	2 nd	2 nd	1 st		1 st		1 st		
<i>Georychus capensis</i>	2 nd	2 nd	2 nd	1 st		1 st		1 st		
<i>Cryptomys hottentotus h.</i>	2 nd	2 nd	2 nd	1 st		1 st		1 st		

In České Budějovice, each individual was kept separately in a plastic bucket with wood shavings during the experimental procedure. Over nights, the social species were kept with other family members in the buckets with perforated lids in T_A 25°C in a testing room. The bucket with the naked mole-rats was placed in the animal facilities on the heating mat. Figure 4 shows the diagram of the experimental procedure.

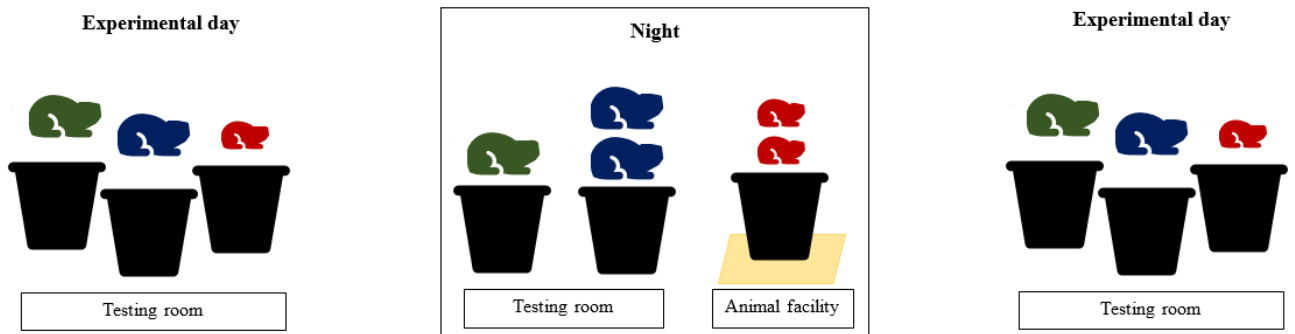


Figure 4: The diagram of the experimental procedure. Green colour represents solitary species; blue social species; red social *H. glaber*. Orange rhomboid symbolizes the heating mat in the animal facility.

In Pretoria, each individual was kept during the experimental procedure separately in a plastic bucket (the common mole-rats), or plastic box (high and open with the Cape dune mole-rats; closed with perforated lid in case of Cape mole-rats; see figure 5) with wood

shavings. Over the night, the social species was kept together with other family members in the bucket in the T_A of 25°C in the testing room.

In České Budějovice, the experiment was carried out in a room with controlled temperature at the Department of Zoology at the University of South Bohemia in České Budějovice.

In Pretoria, the experiment was conducted in a room with controlled temperature and humidity in the Small Animal Physiological Research Facility of the University of Pretoria.

Air temperature in experimental room was homogenised during the experiment. The ventilators were on only during the change of T_A (e.g. from 20°C to 15°C); and thermal acclimation of both animals and the camera. During the measurements and at night, the ventilators were switched off. The buckets containing animals were placed in the room at approximately the same height above ground (fig. 5).

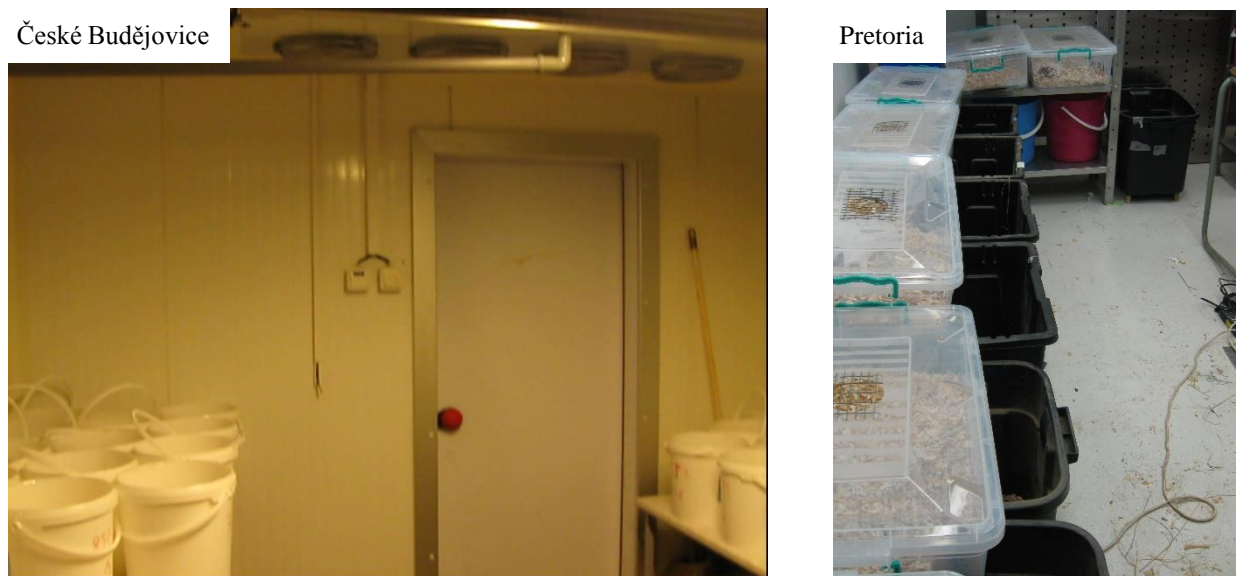


Figure 5: The experimental rooms with the containers with studied animals.

All species except for the naked mole-rat were tested in range of T_A from 10 to 35°C, that is in a broader range than they probably encounter in nature (Tab. 3 in the Appendix). The naked mole-rats were not exposed to T_A below 20°C, because they would quickly become lethargic (McNab 1966). Compared to the other species, finer scale of T_A was chosen for the naked mole-rat within and near its expected thermoneutral zone (see Table 2 in the Appendix) to recognize its thermoregulatory capabilities more specifically. Moreover, the naked mole-rat was the only species tested in $T_A > 35^\circ\text{C}$, i.e. 37.5°C and 40°C.

In České Budějovice, all tested individuals were fed with rodent dry food mix and a piece of carrot to ensure hydration the evening before the first experimental day (see Table 4). The African mole-rats were provided the dry mix the evening before the second

experimental day as well. In 20°C, they were fed with dry mix and carrots, and in lower T_A only with the dry food. The blind mole rats and the coruros were provided with carrots in T_A 30 and 35 °C, and after the end of the measurement in 10°C.

In Pretoria, the animals were fed with sweet potatoes (and carrots and hay in case of the Cape dune mole-rats) over the night and in the T_A 20 and 25 °C.

2.3. Measurements

To record the radiometric footage, Thermal imaging system Workswell WIRIS ver. 1.5.0 (long-wave IR, 7.5 – 13.5 μm , resolution 640p-45d, FOV 13 mm, accuracy 2°C or 2%) was used in České Budějovice. In Pretoria, Thermal Camera FLIR SC325 (long-wave IR, 7.5 – 13.0 μm , resolution 320x240, FOV 25° x 18.8°, accuracy 2°C or 2%) was used. Both devices (fig. 6), are hereafter referred as *the camera*. The principles and usage of the infrared thermography are briefly described in the chapter Infrared thermography in the Appendix.



Figure 6: The thermographic cameras used in the experiment.
From: WORKSWELLWIRIS, <https://workswell.cz>; and FLIR SC325 Thermal Camera, <https://www.instrumart.com>

The camera was left in the experimental room during the whole study to acclimate. The social species were divided into their buckets one by one an hour prior the beginning of the measurement. The measurement began after at least 30 minutes of animal habituation to particular T_A .

After the measurement of T_B , the surface temperature was measured immediately. In České Budějovice, T_B of each individual was assessed by inserting a probe of the thermometer (Thermalert TH-8; Physitemp Instruments Inc) into rectum. The depth depended on the species body size (0.5cm; 1cm; 3cm). In Pretoria, T_B was measured by chips in the abdominal cavity (except for one individual with its chip not working; its T_B was measured rectally) (Equine LifeChip[®]; Destron Fearing).

In České Budějovice, the studied animals were held 40 cm in front of the camera by tails (or the rear part of the dorsal skin in case of *coruro* to avoid the damage of the tail), and the lens was focused manually. In Pretoria, the distances were 89 cm, 66 cm, and 55 cm for the Cape dune mole-rat, Cape mole-rat, and common mole-rat, respectively. The lens of the FLIR camera focused automatically.

Each individual was filmed perpendicularly against thermally homogeneous background (filter paper in České Budějovice or white cloth in Pretoria). Before every measurement, the camera was calibrated. The recordings of each individual took two minutes on average.

Emittance was set to 0.97 for the furred species, and 0.98 for the naked mole-rat. Emittance 0.97 of the furred skin for long-wave infrared radiation was used for example in the eastern mole (*Scalopus aquaticus*) and rabbit (Birkebak 1966, Ludwig et al. 2006). The emittance of the human skin is 0.98 (Tattersall 2016). For more detailed discussion on emittance, see the chapter Infrared thermography in the Appendix.

In České Budějovice, the ambient temperature and humidity were recorded using two thermocouple data loggers (EL-USB-TC-LCD; EasyLog; Lascar Electronics); one placed in an empty bucket with wood shavings in the same height as the other buckets, the second one in front of the camera (with supplementary probe added). In Pretoria, the conditions of the testing room were set and controlled via custom-written software of the Small Animal Physiological Research Facility.

2.4. Analysis of the thermograms

The thermograms were selected from the thermographic footage (9 fps) in the software CorePlayer (ver. 1.7.70.320; Workswell s.r.o.), and subsequently enhanced by specifying the emittance, air humidity and ambient temperature, distance, and palette (FLIR iron) in the software ThermoFormat (Workswell s.r.o.). The air temperature and humidity for each experimental temperature were input as an average value of all measurements for the concrete species. Reflectance is negligible.

For each T_A , 13 areas of every individual were analysed, altogether (Tab. 5).

Table 5: The location of every studied area on the animal. See figure 8.

Area	Body region		
	Ventre	Dorsum	Foot
	<i>Whole</i>	<i>Whole</i>	
1	Between front legs	To the shoulders	
2	To the widest part of the chest	To the widest part of the chest	
3	To the end of the rib cage	To the end of the rib cage	
4	To the hips	To the hips	
5	Between hind legs	Caudally from the hips	

The analysed areas were manually marked out with a polygonal region of interest (ROI) (fig. 8). The mean of the values from every pixel of each studied ROI was the final output. Only parts orientated perpendicularly to the lens were analysed. The urinated spots, anus, and the open fur (i.e. visible skin due to hair shift) were not included. Only one foot was chosen for every animal, depending on the favourableness of its orientation. The ratio of the examined feet (front:hind) was 1:1.

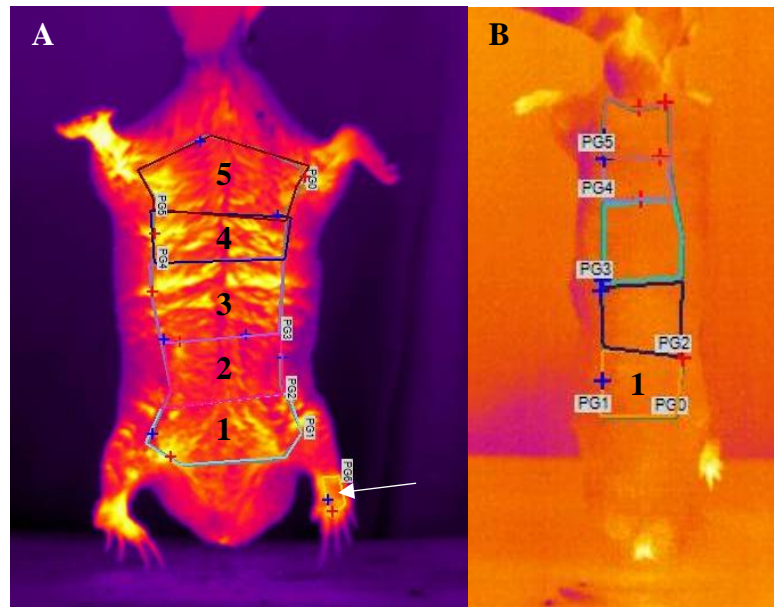


Figure 8: The situation of the studied areas on the animals. IR thermogram. A – ventre (*B. suillus*; 10°C), B – dorsum (*N. galili*; 35°C). Whole area = encircling 1+2+3+4+5. White arrow points at the front foot area.

In course of the analysis of the thermograms obtained in České Budějovice, an inaccuracy in measurement of the camera (WIRIS) was found, because surface temperature data were biased by a systematic error depending on the ambient temperature, the length of camera exposure to that temperature, and possibly other factors. Therefore, a correction for each picture was established. Before every measurement of each animal,

the background was measured using both infrared camera and thermocouple covered by filter paper placed in the centre of the camera's field of view. The temperature of the thermocouple was recorded by a certified temperature data logger (Lascar Electronics) every minute. Thus, it was possible to state a correction (i.e. the shift in measured T_S) for every single measurement (fig. 9).

For each individual thermogram sequence, a correction value (T_{Sc}) was obtained as follows:

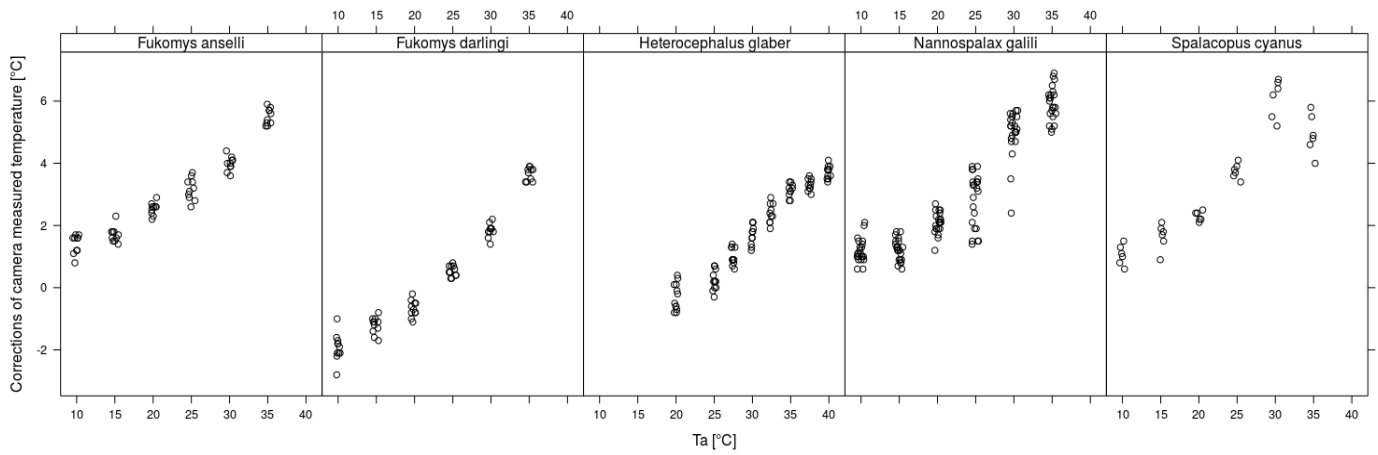


Figure 9: Correction (T_c) of every camera measurement for each studied individual from České Budějovice.

$$T_{Sc} = T_S - T_c$$

$$T_c = T_{St} - T_t$$

where T_S is the uncorrected thermogram surface temperature, T_c is the correction, T_{St} is surface temperature of the paper-cover thermocouple read by the camera, and T_t is temperature of the paper-cover thermocouple read by the temperature data logger. All subsequent assessments (Data analyses) were applied on the corrected data. In the rest of my work, the corrected value (T_{Sc}) is used; but for simplification, it is always (e.g. in figures) mentioned as T_S .

2.5. Data analyses

Principal component analysis (PCA) was used to explore interrelations between three different temperature variables (T_B , T_S , and their difference) measured for all furred species (the naked mole-rat was not used for its known extraordinariness); and their relations to T_A , focal body region, species, social system, and climatic parameters (passively projected to an ordination plot). The climatic parameters (downloaded for the original locality of each species from the Wordclim database; Tab. 3 in the Appendix) average annual rainfall

and minimal temperature were used for the visualisation, because they express the climatic characteristics cardinal for the chthonic rodent biology – precipitation and ambient temperature. Since body mass appeared to have various influence in different T_A , it was used as a covariable. Response variables entering the analysis were centred and standardized to have zero mean and unite variance. In addition, the PCA were conducted for every T_A separately for all studied furred species (with the data on the silvery mole-rat and giant mole-rat from Šumbera et al. 2007 added), for all bathyergids (incl. Šumbera et al. 2007), and for the bathyergids used solely in this study. The PCA plots were constructed with the CANOCO software package for Windows, version 5.11.

All data were analysed using R software (R Core Team 2016), extended with the *nlme* package designed for non-linear mixed effects models with nested random effects (Pinheiro et al. 2016). To test the differences in the temperature data obtained, generalized least-squares (GLS) marginal models in which individual identity was included to avoid pseudoreplications, as I tested different body regions of the same individual, were computed using the *gls* function. The response variable for every test was a newly created variable - the difference between T_B and T_S ($T_B - T_S$). This should express individual thermo-insulative ability (or the individual ability of body heat dissipation). The explanatory variables used in the models were body region, species, social system, area of the body region; in all models, body mass was treated as a covariate. For post hoc test of T_B among species, package *multcomp* was used (Hothorn et al. 2008). For comparing $T_B - T_S$ of the feet with other body regions, only hind feet were used, because front feet were often not in the contact with the ground (see figure 28 in the chapter Behavioural observation in the Appendix). To control familywise error, the Bonferroni correction was applied to adjust the significance level for the results of tests by dividing p-level of 0.05 by the number of tests (ambient temperatures; Tab. 4) performed (0.0083 in furred species and 0.00625 in the naked mole-rat). There was no effect of sex on any of tested variable in any of studied species ($p > 0.692$).

All graphs were constructed in the STATISTICA software (ver. 13, TIBCO Software Inc.). The plotted data are surface temperature, and $T_B - T_S$. For the visualisation of the pattern in ventral areas, the deviation from mean ventral surface temperature of each individual was used. All data are plotted as means \pm s.d. For simplification, only four T_A were chosen for visualisation – extremes (10°C and 35°C) and two T_A from within the range (20°C and 30°C). Moreover, comparing 30°C and 35°C shows how different the extreme temperature is.

3. Results

The PCA plot (fig. 10) shows the relations between the measured temperature variables, and how they are related to different T_A , measured body regions, and studied species. The first principal component (explaining 80.4% of the data variability) is strongly correlated with both T_S and $T_B - T_S$ that are negatively correlated to each other, with the gradient of T_A ranging from 10°C to 30°C, and to a lesser extent with the measured body regions. The second component (explaining 17.4% of the variability) is weakly related to T_B that is correlated with the highest T_A of 35°C. The studied species form a gradient along the second component by their increasing T_B . For similar PCA plot enriched by the two species of Šumbera et al. (2007) see figure 11 in the Appendix.

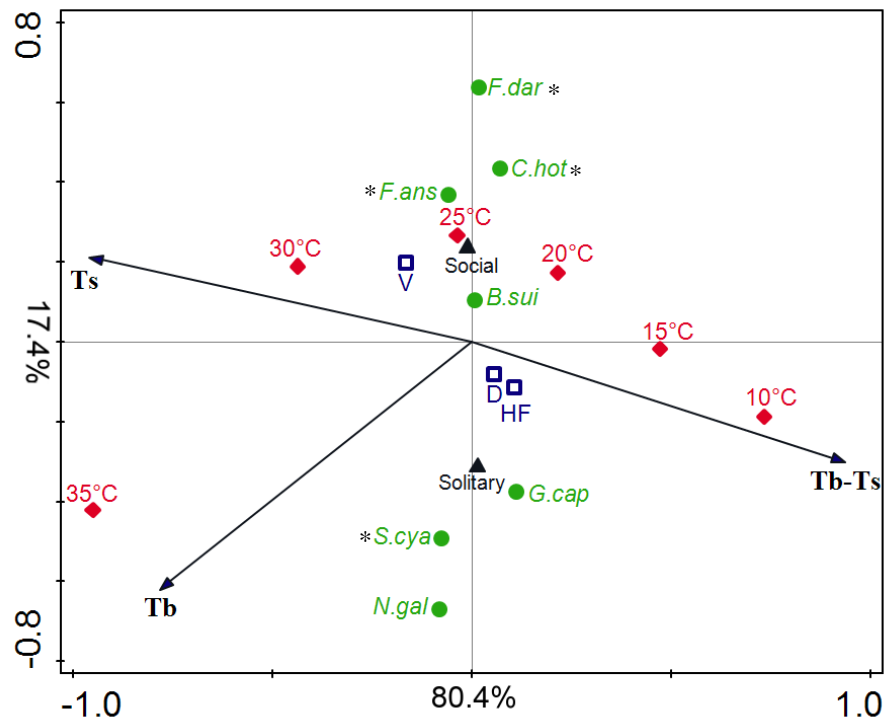


Figure 10: PCA visualisation of surface temperature (T_S), body core temperature (T_B), and their difference ($T_B - T_S$) (depicted as black arrows) of all studied furred species (green dots) in six ambient temperatures (red diamonds). Social species are marked with asterisks. Factors social system (black triangles) and body region (blue squares - Ventre, Dorsum and Hind Feet) are illustrated as well. All factors are passively projected. The eigenvalues of the first two axes are written in.

The summary of all the surface temperatures, body core temperatures, and their difference of all studied species in all T_A are shown in tables 6 and 7 in the Appendix; and in figures 12 and 13. Body core temperature differed markedly among the studied species (see table 6 in the Appendix, and figures 10 and 12). All the p values for interspecific T_B comparisons are shown in table 8 in the Appendix. The blind mole rat *Nannospalax galili*, the coruro

Spalacopus cyanus, and the Cape mole-rat *Georchus capensis* have comparable T_B , the highest among all of the studied species. The Cape dune mole-rat *Bathyergus suillus* has T_B between them and the rest of the mole-rats. The lowest T_B have the mole-rats of the genus *Fukomys*, especially the Mashona mole-rat *F. darlingi*. There is no difference between social mole-rats, except from significantly lower T_B of *F. darlingi* in 20°C and 25°C (fig. 12). Moreover, there is a rapid rise in T_B of *F. darlingi* from 25°C to the same levels as in most of the other species in 35°C. *B. suillus* did not differ in T_B from any bathyergid species.

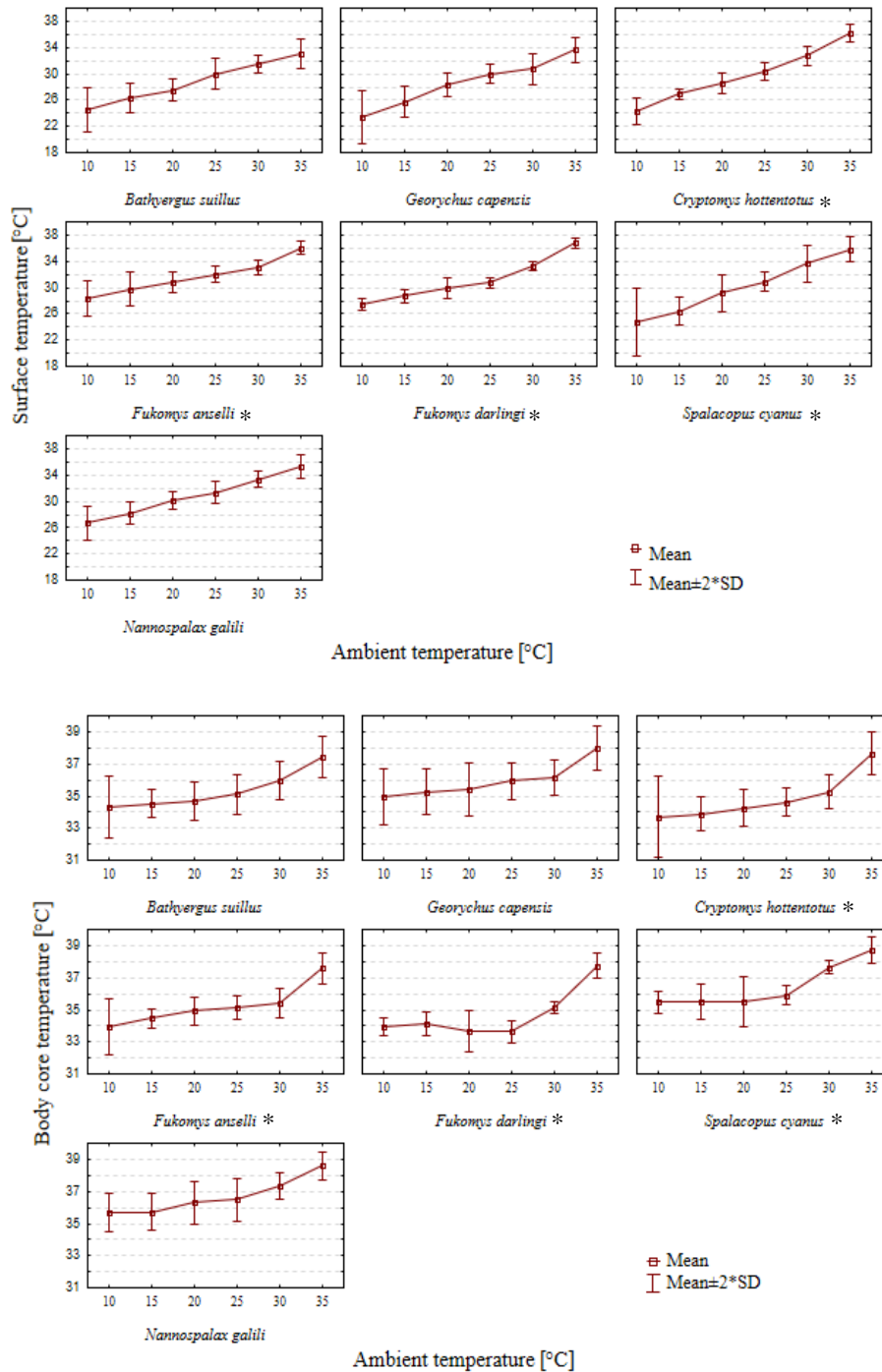


Figure 12: Ventral surface temperature and body core temperature of seven studied species in varied ambient temperature. Social species are marked with asterisks.

Figure 13 illustrates typical “endothermic poikilotherm” relationship of T_A and T_B , together with T_S in the naked mole-rat.

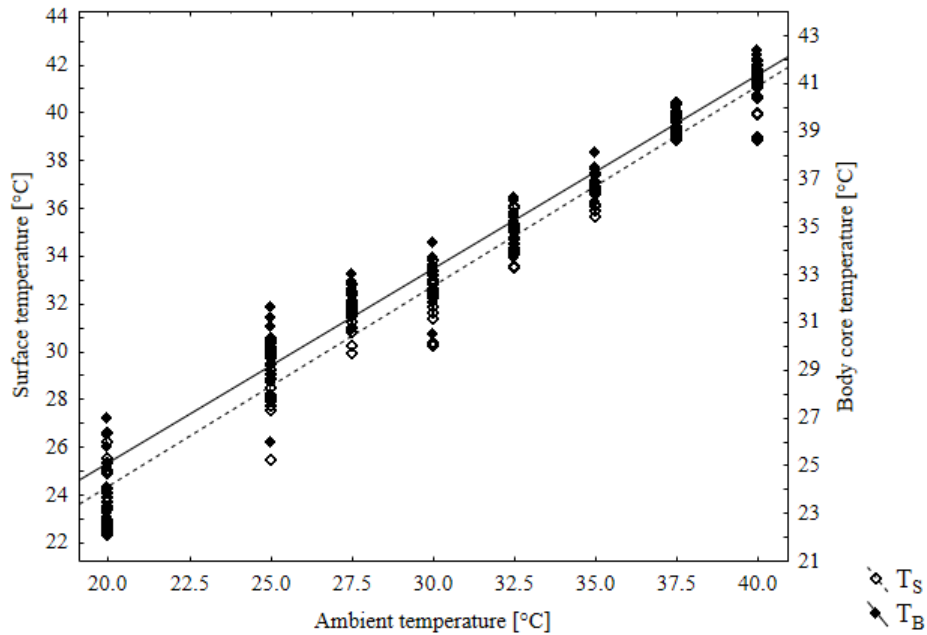


Figure 13: The dependence of T_S and T_B on T_A in the naked mole-rat. The solid line fits mean of measured surface temperatures; the dashed line fits mean of measured body core temperatures.

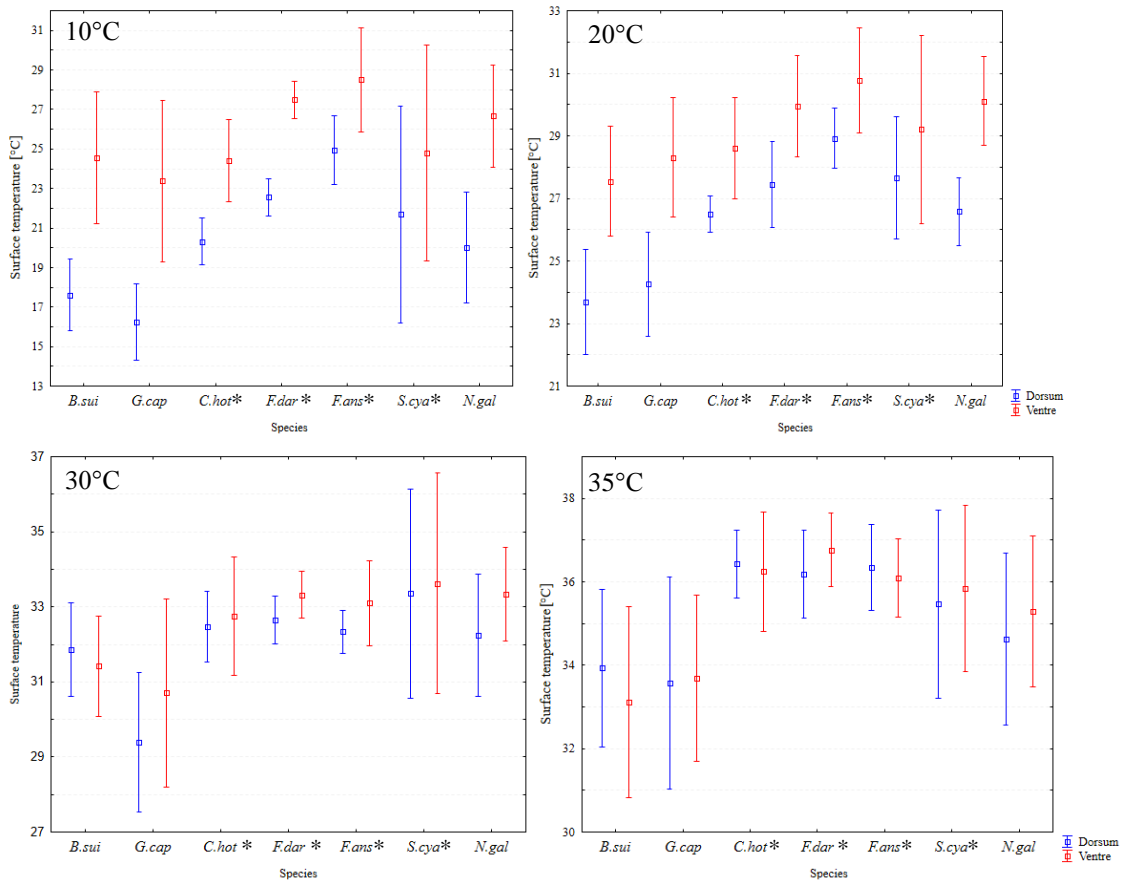


Figure 14: Dorsal and ventral surface temperature (mean \pm sd) of seven studied species in T_A 10°C, 20°C, 30°C, and 35°C.

Ventral surface temperature is significantly higher than dorsal in all species ($p < 0.0001$; Tab. 9) in the majority of T_A . However, in higher T_A (30°C and 35°C), the difference is not apparent (fig. 14). In 30°C, the dorsum is slightly warmer compared to ventre in *B. suillus*. In 35°C, dorsal T_S is subtly higher compared to ventral in all species except for *N. galili* (Tab. 6 in the Appendix).

Social species possess lower $T_B - T_S$ ($p < 0.0001$; fig. 15 in the Appendix; Tab. 9). In the naked mole-rat, there is a significant difference between body regions in 20°C, 25°C, and 30°C ($p < 0.0001$; Tab. 10 in the App). The difference did not exceed 1°C. Additionally, T_B is sometimes lower than T_S (fig. 15 in the Appendix).

Table 9: The results of GLS tests used to compare T_B - T_S values between dorsal and ventral body regions among species and between social and solitary systems across different T_A . Values lower than 0.0083 are shown in bolt. *H. glaber* was not included into the analyses.

value	factor	Ambient temperature [°C]					
		10	15	20	25	30	35
p	<i>species</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	body region	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0001
	interaction	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
F (df)	<i>species</i>	31.811 (6;253)	43.927 (6;259)	34.344 (6;255)	34.669 (6;261)	37.0855 (6;251)	28.586 (6;241)
	body region	4265.692 (1;253)	4186.307 (1;259)	2812.091 (1;255)	2218.987 (1;261)	431.876 (1;251)	16.9268 (1;241)
	interaction	52.281 (6;253)	55.899 (6;259)	40.933 (6;255)	51.081 (6;261)	30.2739 (6;251)	16.4506 (6;241)
p	<i>social system</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	body region	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0009
	interaction	<0.0001	<0.0001	<0.0001	<0.0001	0.0001	0.140
F (df)	<i>social system</i>	29.168 (1;263)	43.235 (1;269)	78.706 (1;265)	108.0077 (1;271)	95.8089 (1;261)	33.8918 (1;251)
	body region	3676.724 (1;263)	3294.039 (1;269)	2490.826 (1;265)	1595.8422 (1;271)	243.5059 (1;261)	93.042 (1;251)
	interaction	239.391 (1;263)	218.059 (1;269)	190.93 (1;265)	160.634 (1;271)	15.8328 (1;261)	11.3537 (1;251)

Table 11: The results of GLS tests used to compare T_B - T_S values of hind feet with ventral and dorsal body region among furred species and between social systems across different T_A . Values lower than 0.0083 are shown in bolt. *H. glaber* was not included into the analyses.

value	factor	Ambient temperature [°C]					
		10	15	20	25	30	35
p	<i>species</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	body region - <i>ventre</i>	<0.0001	<0.0001	<0.0001	<0.0001	0.9971	<0.0001
	interaction	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
F (df)	<i>species</i>	7.0748 (6;89)	8.088 (6;98)	6.9072 (6;87)	17.757 (6;94)	20.7379 (6;94)	20.3055 (6;94)
	body region - <i>ventre</i>	279.3384 (1;89)	334.745 (1;98)	162.231 (1;87)	176.272 (1;94)	0 (1;94)	84.0716 (1;94)
	interaction	6.2542 (6;89)	8.462 (6;98)	11.1823 (6;87)	11.938 (6;94)	15.2766 (6;94)	23.3104 (6;94)
p	<i>species</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	body region - <i>dorsum</i>	<0.0001	<0.0001	0.0012	0.0025	<0.0001	<0.0001
	interaction	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
F (df)	<i>species</i>	15.422 (6;89)	15.19 (6;98)	18.342 (6;87)	38.974 (6;94)	33.0901 (6;94)	23.072 (6;94)
	body region - <i>dorsum</i>	31.352 (1;89)	31.732 (1;98)	11.227 (1;87)	9.663 (1;94)	18.861 (1;94)	176.9215 (1;94)
	interaction	9.803 (6;89)	14.54 (6;98)	19.36 (6;87)	17.178 (6;94)	13.5578 (6;94)	19.9192 (6;94)
p	<i>social system</i>	0.0024	0.0050	<0.0001	<0.0001	<0.0001	<0.0001
	body region - <i>ventre</i>	<0.0001	<0.0001	<0.0001	<0.0001	0.9986	<0.0001
	interaction	ns	0.0044	0.0024	0.0005	<0.0001	<0.0001
F (df)	<i>social system</i>	9.7236 (1;100)	8.2041 (1;108)	21.5709 (1;97)	45.2839 (1;104)	42.9984 (1;104)	59.3175 (1;104)
	body region - <i>ventre</i>	173.0094 (1;100)	204.7469 (1;108)	98.6483 (1;97)	107.1664 (1;104)	0 (1;104)	30.3432 (1;104)
	interaction	ns	8.4734 (1;108)	9.7286 (1;97)	12.8749 (1;104)	32.0574 (1;104)	26.4809 (1;104)
p	<i>social system</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	body region - <i>dorsum</i>	0.0001	<0.0001	0.0124	0.013	0.0002	<0.0001
	interaction	0.0408	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
F (df)	<i>social system</i>	38.6754 (1;99)	36.204 (1;108)	67.283 (1;97)	117.427 (1;104)	84.7409 (1;102)	84.1317 (1;102)
	body region - <i>dorsum</i>	16.8601 (1;99)	19.248 (1;108)	6.486 (1;97)	6.393 (1;104)	14.5641 (1;102)	95.0743 (1;102)
	interaction	4.2965 (1;99)	28.941 (1;108)	28.398 (1;97)	39.916 (1;104)	53.9044 (1;102)	48.9413 (1;102)

There is a difference in T_B-T_S of the hind feet between the animals with different social system ($p \leq 0.005$; Tab. 11), with the solitary species having their feet warmer in the majority of T_A (15°C, 20°C, 25°C, 30°C) ($p \leq 0.0044$). It is reversely in 10°C and 35°C (fig. 16). Hind feet differ in T_B-T_S from ventre in all T_A ($p < 0.0001$), but 30°C; and from dorsum in all T_A ($p \leq 0.0002$), except for 20°C and 25°C (Tab. 11). Figure 16 illustrates the relationship of T_S of hind feet and other body regions in the animals of both solitary and social species. When tested interspecifically, no difference was found between hind feet and ventre in T_A 30°C (Tab. 11). In other ambient temperatures, all species differ in case of both ventre ($p < 0.0001$) and dorsum ($p \leq 0.0025$); and the interaction of both factors is significant as well ($p < 0.0001$) (Tab. 11). Figures 20-23 (in the Appendix) show the varying similarity of hind feet, ventral, and dorsal body region. In the naked mole-rat, the hind feet are colder from T_A 20°C to 32.5°C compared to the ventre ($p \leq 0.0012$; fig. 17; Tab. 12 in the App.) and do not differ in $T_A > 32.5^\circ\text{C}$. The thermal difference between the regions is considerably lower in comparison to the furred species (max. 6°C; fig. 17).

There is a difference between solitary and social species in the pattern of both ventral and dorsal surface temperature (Tab. 13). The difference between the areas is never more than 1°C, a value within the error range of the camera (fig. 18 in the Appendix); neither comparing animals with different social systems ($p \leq 0.004$), nor particular areas ($p < 0.0049$). Only in 35°C, ventral T_S is homogeneous. The dorsal areas differ between the social systems in T_A 15°C and 20°C ($p < 0.0001$ and $p = 0.0083$). The deviation from the mean of ventral T_S for each area is depicted in figure 18 in the Appendix. The same results for interspecific comparison are shown in figure 19 in the Appendix. Species differ in T_B-T_S of particular areas ($p \leq 0.0014$; Tab. 13), except for the thermally homogeneous dorsum in 20°C and ventre in 35°C. Thermal patterns are conspicuously alike in both tested species within the genus *Fukomys*. Generally, the highest T_S occur between V2 and V3 in social species (mostly due to the bathyergids), and areas V2 and V4 in solitary species (fig. 18 and 19 in the Appendix). The lowest T_S possesses the area V5 in the animals of both social systems. Correspondingly, both body regions of the naked mole-rat were found thermally inhomogeneous ($p \leq 0.001$; Tab. 14 in the Appendix), but the differences are only minor (fig. 19 in the Appendix).

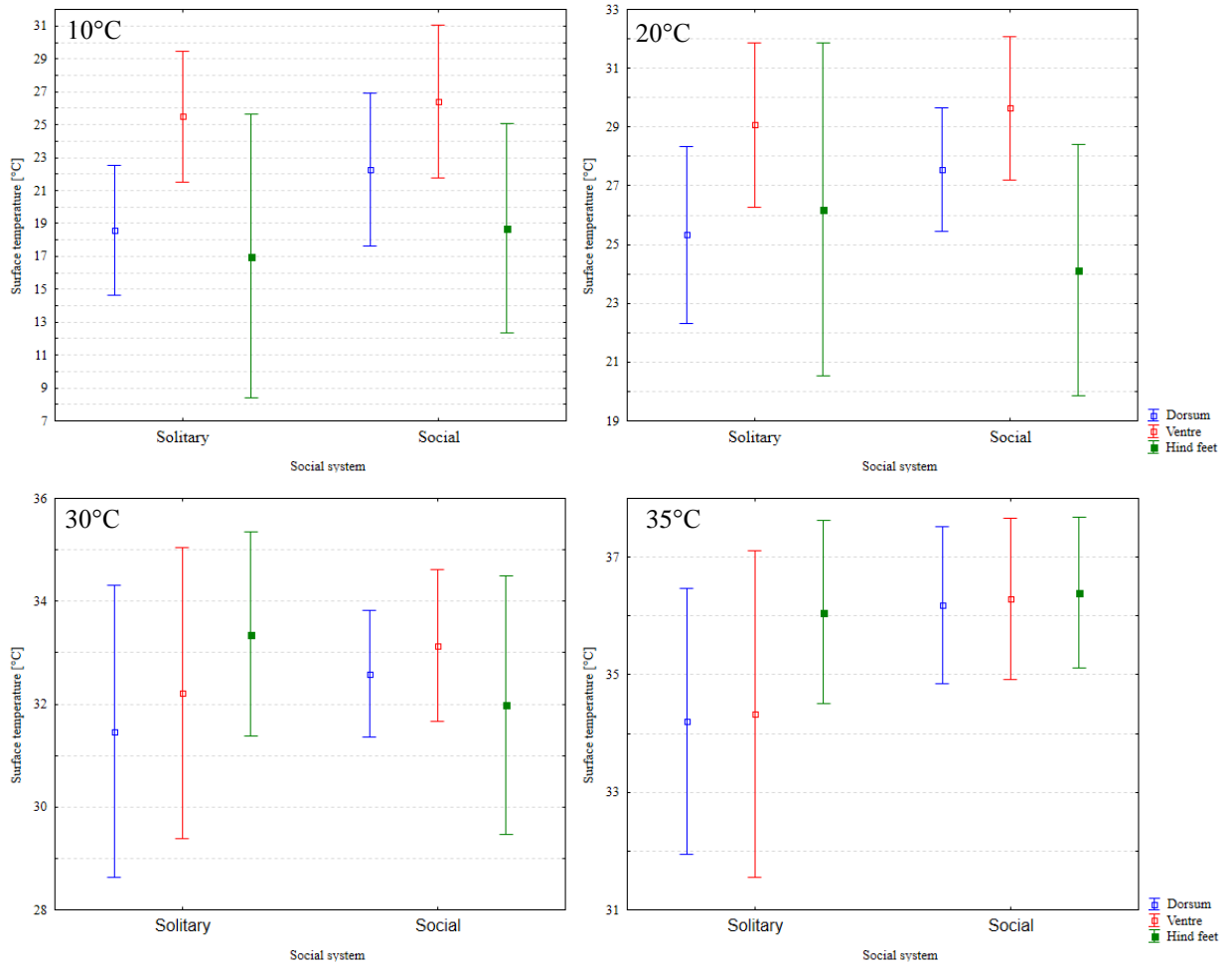


Figure 16: Surface temperatures (mean \pm sd) of three body regions in furred studied species with different social system in TA 10°C, 20°C, 30°C, and 35°C.

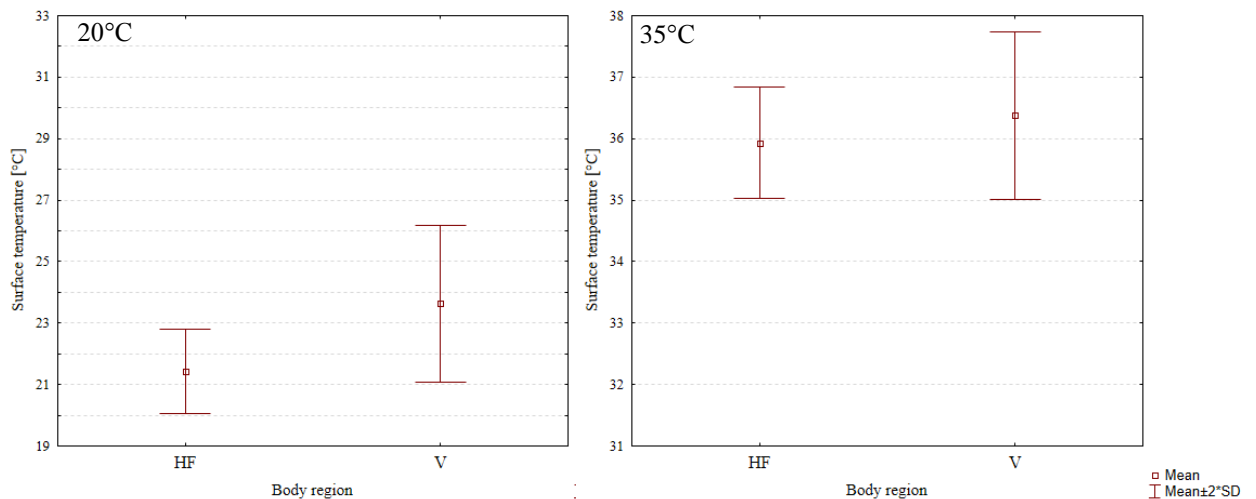


Figure 17: Surface temperatures (mean \pm sd) of hind feet (HF) and ventral region (V) of the naked mole-rat in TA 20°C and 35°C

Table 13: The results of GLS tests used to compare T_B - T_S values of ventral and dorsal areas among furred species and between social systems across different T_A . Areas were tested within ventral and dorsal body region, respectively. Values lower than 0.0083 are shown in bolt. *H. glaber* was not included into the analyses.

value	factor	Ambient temperature [°C]					
		10	15	20	25	30	35
p	<i>species</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	<i>ventral area</i>	<0.0001	<0.0001	<0.0001	<0.0001	0.0014	ns
	<i>interaction</i>	<0.0001	<0.0001	<0.0001	0.0014	<0.0001	ns
F (df)	<i>species</i>	19.1527 (6;334)	15.149 (6;334)	9.4122 (6;339)	18.5625 (6;339)	22.248 (6;334)	23.1141 (6;332)
	<i>ventral area</i>	6.5271 (4;334)	26.444 (4;334)	8.7019 (4;339)	12.7236 (4;339)	4.5552 (4;334)	ns
	<i>interaction</i>	4.6161 (24;334)	2.846 (24;334)	3.0688 (24;339)	2.1681 (24;339)	3.4387 (24;334)	ns
p	<i>species</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	<i>dorsal areas</i>	<0.0001	<0.0001	<i>0.0409</i>	<0.0001	<0.0001	<0.0001
	<i>interaction</i>	<0.0001	<0.0001	<i>0.0243</i>	<0.0001	<0.0001	<0.0001
F (df)	<i>species</i>	50.914 (6;299)	41.887 (6;289)	4.6331 (6;274)	38.966 (6;264)	27.431 (6;269)	15.8119 (6;279)
	<i>dorsal areas</i>	57.504 (4;299)	59.137 (4;289)	2.5302 (4;274)	8.759 (4;264)	15.7257 (4;269)	11.6043 (4;279)
	<i>interaction</i>	3.459 (24;299)	9.143 (24;289)	1.6975 (24;274)	3.414 (24;264)	3.9867 (24;269)	5.9664 (24;279)
p	<i>social system</i>	0.004	0.0002	<0.0001	<0.0001	<0.0001	<0.0001
	<i>ventral area</i>	0.0006	<0.0001	<0.0001	<0.0001	0.0049	ns
	<i>interaction</i>	ns	ns	ns	ns	ns	ns
F (df)	<i>social system</i>	8.3377 (1;363)	13.7618 (1;363)	18.11 (1;368)	52.7662 (1;368)	68.1832 (1;363)	59.0997 (1;337)
	<i>ventral area</i>	5.004 (4;363)	9.722 (4;363)	7.4519 (4;368)	11.6227 (4;368)	3.7946 (4;363)	ns
	<i>interaction</i>	ns	ns	ns	ns	ns	ns
p	<i>social system</i>	<0.0001	<0.0001	0.0955	<0.0001	<0.0001	<0.0001
	<i>dorsal areas</i>	<0.0001	<0.0001	<i>0.0452</i>	<0.0001	<0.0001	<0.0001
	<i>interaction</i>	ns	<0.0001	0.0083	ns	ns	<i>0.0190</i>
F (df)	<i>social system</i>	57.6701 (1;328)	63.1652 (1;375)	2.79726 (1;299)	135.0654 (1;293)	82.5741 (1;298)	60.9844 (1;304)
	<i>dorsal areas</i>	46.9991 (4;328)	37.4098 (5;375)	2.46488 (4;299)	7.0324 (4;293)	12.1091 (4;298)	8.2334 (4;304)
	<i>interaction</i>	ns	9.3405 (5;375)	3.50214 (4;299)	ns	ns	2.9949 (4;304)

The relationships among the three temperature variables and how they are related to different ambient temperatures, measured body regions, species studied and to two chosen climatic variables (minimal temperature and mean annual rainfall) for three different groups of furred chthonic rodents are shown in PCA plots (figures 20-23 in the Appendix; for simplification, only four T_A were chosen): A) only mole-rats used in this study (five species); B) mole-rats used in this study together with the solitary silvery mole-rat *H. argenteocinereus* and the social giant mole-rat *F. mechowii* analysed by Šumbera et al. 2007; and C) all furred species (nine species altogether). When visualised for each ambient temperature separately, the first principal component is correlated mainly with the measured body regions, with T_S being the highest in ventre and T_B-T_S being the highest in hind feet and less in dorsum in temperatures of 10°C and 20°C for all three groups (fig. 20 and 21). The second component is determined by the strong negative correlation of T_B with both climatic variables, i.e. T_B increases with decreasing both mean annual Rainfall and Minimal temperature. In 10°C, *B. suillus* is situated within the cluster of social mole-rats when comparing only mole-rats, but not in the case of non-bathyergids (fig 20. C). The correlation of climatic variables is more pronounced in the group B) and C), i.e. when non-bathyergid species were included. In 20°C, the Ansell's mole-rat *F. anselii* is less similar to other social bathyergids (fig. 21). In 30°C and 35°C, the first component is still determined by a negative correlation of T_S and T_B-T_S , but they do not differ substantially among the three different body regions (fig. 22 and 23). However, dorsum apparently differs from other two body regions in 30°C, and hind feet differs from dorsal and ventral body region in 35°C. The second component is again determined by the negative correlation of T_B and both climatic variables in 30°C and 35°C. In 35°C, *G. capensis* possesses markedly higher T_B than all other species of studied bathyergids (fig. 23 A and B), resembling thus more *N. galili* and *S. cyanus* (C). In 35°C, *F. anselii* is dissimilar to the other social mole-rats in case A), evincing the lowest T_B of all bathyergids used in this study.

Behavioural and thermographic observation are presented in the Appendix.

4. Discussion

Ventral thermal windows were found in all studied species, with no substantial difference between the species with different social systems in respect of surface temperature pattern. However, social species dissipate body heat better than solitary species do. Feet appeared to play an important role in the thermoregulation, too. Next, a pattern in body core temperature was ascertained among the studied species.

Chtonic rodents inhabit thermally challenging environment. On one hand, they usually face ambient temperatures 5-10°C below their thermoneutral zone (Šumbera in press), which is convenient, but on the other hand the heat dissipation via evaporation is not possible due to high air humidity, and absence of air circulation (McNab 1966, Nevo 1999, Buffenstein 2000). Thus, surplus of heat originated during heat producing activities such as digging must be dissipated via conduction with burrow walls. In this case, body regions with lower thermal insulation called thermal windows could be very effective.

Chtonic rodents may differ in their sociality rate. Among them, there are species with families/groups of about 10 individuals (genus *Fukomys*), but also species with families larger than 100 individuals (the naked mole-rat). Nevertheless, most of the chtonic rodents live solitary, namely *Bathyergus* and *Georychus* mole-rats, or *Nannospalax* blind mole rats. Since the differences in the group size are striking, there is a question of not only the location of the thermal windows of these rodents, but also of their pattern, i.e. spatial distribution across the body. Solitary species were supposed to have smaller, better controllable thermal window to prevent undesirable loss of body heat. Social species huddle with other group members in cold, and thus decrease the surface-to-volume-ratio. In this case, lower thermal insulation is advantageous, because heat generated by digging could be more easily dissipated. Lower insulative volume of dorsal fur was found in social chtonic rodent species (Vejmělka 2016).

4.1. Body core temperature

The studied chtonic rodent species form a gradient along the second principal component (17.4% of the variability explained) by their increasing body core temperature with no effect of their social system (fig. 10). The social coruro *Spalacopus cyanus*, and solitary blind mole rat *N. galili* and Cape mole-rat *G. capensis* evince the highest T_B in all T_A (Tab. 6 in the Appendix). The non-bathyergid species (the coruro and the blind mole rat) experience the lowest ambient temperatures of all studied species, as well as the broadest annual temperature range (Table 2 and 3 in the Appendix; figures 20-23 in the Appendix). The south

African bathyergid species inhabiting subtropical zone face milder temperatures in their habitats. However, the Cape mole-rat differs from its syntopical neighbours in its T_B remarkably. This discrepancy could be explained by different social organisation and body size. While the common mole-rat *Cryptomys hottentotus* lives socially and can thus take advantage of huddling, the Cape dune mole-rat *B. suillus* belongs to the largest of all chtonic rodents. Consequently, its surface-to-volume ratio is relatively smaller, and its heat loss lower. In addition, both species possess lower fur quality compared to the Cape mole-rat whose dorsal fur insulative volume is about one third larger (own unpublished data). The highest T_B in the thermoneutral zone (TNZ) of Cape mole-rat among all bathyergids was found also in other studies (Lovegrove 1987; Šumbera in press). Irvin and Krog (1954) in Schmidt-Nielsen (1997) state the cold-adapted mammals to have slightly higher T_B (mean value 38.6°C), yet this difference is considered insignificant (Arctic mammals compared to temperate). Additionally, populations of the Cape mole-rat can be found even in relatively high altitudes (Tab. 2; Okrouhlik pers. com.). The species with lowest T_B - Mashona mole-rat *F. darlingi*, originated from one of the warmest environments occupied by species under this study (average annual temperature similar to that of the naked mole-rat from arid climate; the lowest original altitude; Tab. 3) and correspondingly, they occur at the other end of the continuum.

Overall, the rise in T_B across the gradient of T_A did not exceed four °C in the furred species (maximally 3.9°C in the common mole-rat; tab. 6 in the Appendix). In case of the naked mole-rat, the “poikilothermic endotherm”, a strong dependence of T_B on T_A was observed (fig. 13). Body core temperature around 34°C is typical for the furred bathyergids (most placentals maintain their T_B around 38°C). There are some interesting interspecific differences in the dependence of T_B on T_A (fig. 12). The Mashona mole-rat and the coruro maintain their T_B relatively constant from 10°C to 25°C; and it begins to rise in $T_A > 25°C$. Furthermore, *F. darlingi* has the lowest T_B in 20°C and 25°C. In other species, there is more or less constant rise across all T_A , with steeper increase towards 35°C.

4.2. Thermographic measurements

Body regions with high T_s are clearly distinguishable on the thermograms (e.g. fig. 24; 25; 27 in the Appendix). Eyes and ears are observable best, having the highest temperature. However, these regions present only small surface to dissipate body heat. The larger the thermal window is, the more important role it plays. The most important way of body heat dissipation in chtonic rodents is probably conduction. Okrouhlik et al. (2015) found that the mole-rats are able to cool themselves down via contact with the colder substrate even during digging. Feet are quite

distinguishable in the thermograms as well, changing their surface temperature according to T_A (discussed below). All of these are the regions with no or only little thermal insulation by fur.

4.2.1. Difference between dorsal and ventral body region

Concerning large body regions of the studied animals, ventre dissipates significantly more heat than dorsum. For expressing individual body heat dissipation, the difference between T_B and T_S was used. The finding of lower ventral $T_B - T_S$ is consistent with the result of my bachelor's study (Vejmělka 2016) that the quality of pelage differs between body regions in chthonic rodent species, especially in the length of hairs. In addition, animal behaviour in extreme ambient temperatures clearly illustrates behavioural thermal window alternation – so called “opening and closing”. In lower T_A ($\leq 20^\circ\text{C}$) individuals curled into a ball, covering their ventre, with ruffled fur trapping more air inside, preventing front feet from contact with the floor preventing front feet from contact with the floor (chapter Behavioural observation in the Appendix). The question if the ruffled fur is an adaptation to low T_A , or only a by-product of curling up is worthy further research (compare the animal's posture in figures 28 and 29 in the Appendix). Furthermore, by rolling up their bodies, the surface-to-volume ratio is reduced. Contrarily, in high T_A ($\geq 30^\circ\text{C}$), they either exposed their ventre open (fig. 30 and 31 in the Appendix), or stretched on the ground addressing it to the floor (fig. 32 in the Appendix). Interestingly, similar behaviour (both curling up and ventre exposure; fig. 31) was observed even in the naked mole-rats with no obvious difference in thermal insulation between dorsum and ventre. In 35°C , dorsal T_S is subtly higher compared to ventral in all species except for the blind mole rat (tab. 6 in the Appendix). This might be explained by T_B notably increased in the highest T_A . In 35°C T_B is so closed to T_A that heat dissipation is slower and body heat is trapped for a longer time in dorsal fur with better thermal insulative properties.

The difference in insulative layer between ventral and dorsal body region is present in many terrestrial mammals. Dorsal fur is denser and longer, especially in case of overhairs, providing the protection against mechanical and radiation damage. The capability to curl enables mammals to cover their bellies. Exposed back must then be better protected. Till now, the presence of the ventral (+axillary) thermal window was explicitly proved by IRT in for instance camelids (Gerken 2010; Abdoun et al. 2012). Heath et al. (2001) cite Fowler's (1998) detection of thinner hair cover of ventral body region in alpacas (*Lama pacos*). Interestingly, the Arctic fox has shorter fur on ventre only in summer, while longer ventral fur (in comparison with dorsum) in winter (Underwood and Reynolds 1980). This is probably caused by the need for improving the thermal insulation when lying on the snow. As for rodents,

Knight (1986) measured fur length in newborn pups of the Gambian pouched rat (*Cricetomys gambianus*) and revealed the dorsal fur to grow faster and continually longer. Poorer furred bellies were found in six chthonic rodents in my bachelor's thesis (Vejmělka 2016). In this ecological group, the ventral thermal windows are of a particular interest for the apparent lack of other large thermal windows, such as those located on body extremities in other mammals.

4.2.2. Body heat dissipation between species with different social systems

Social species dissipate body heat better than solitary species, both in ventral and dorsal body region (fig. 15 in the Appendix), with the exception of 35°C. The fur is in this T_A so warmed through that there is no difference between the regions. Correspondingly, I revealed significantly different dorsal insulative volume between social and solitary subterranean rodents in my bachelor's work (Vejmělka 2016). Lower insulation quality enables social species to dissipate body heat better when overheating might be jeopardizing while huddling helps to conserve body heat within the group. Interestingly, Šumbera et al. (2007) did not find any difference in mean ventral temperature across all T_A between the solitary silvery mole-rat and social giant mole-rat. This might be because of “mosaic opening” of fur, discussed below.

The largest difference between T_B and T_S across studied T_A in furred species (Tab. 7 in the Appendix) was found in the solitary Cape mole-rat; the smallest in the social Ansell's mole-rat *F. anelli* in both body regions. In fact, of all the examined species, the Cape mole-rat seems to be the best thermally insulated subterranean rodent of tropical and subtropical climatic zone – its dorsal insulative volume substantially exceeds those of the silvery mole-rat and the Upper Galilee Mountains blind mole rat. Correspondingly, the Ansell's mole-rat possesses the worst thermal insulation of all the examined chthonic rodent species (see figure 2 in the Introduction).

4.2.3. Body heat dissipation via feet

Feet of chthonic rodents also take part in thermoregulation. The feet surface is in subterranean rodents not as negligible as for example eye or ear (due to their size). They clearly need large paws for sweeping the soil in their burrows; and compared to above-ground mammals, their feet are conspicuously larger. Moreover, the foot surface is bare, ideal for heat transfer. In low temperatures, feet are colder than ventre or dorsum. With rising temperature, the feet get warmer until they are as warm as dorsal (20°C and 25°C) or ventral (30°C) surface. Finally, the feet are warmer than both dorsal and ventral regions in 35°C (fig. 16) probably due to active vasomotion. Blood vessels are constricted in cold, allowing little blood to enter the peripheral

tissues and conserving the body heat; and *vice versa*, vasodilation helps to dissipate the surplus heat in high T_A . Feet thus behave like body-extremity-located thermal windows (e.g. Phillips and Heath 2001; Kuhn and Mayer 2009; Khamas et al. 2012). Similar results show the PCA figures (20-23 in the Appendix). Feet is situated close to dorsum in the multidimensional ordination space in low ambient temperatures (10°C and 20°C). In 30°C, T_S of the feet resembles T_S of the ventre. In the highest of used T_A (35°C), feet differ from both ventral and dorsal body region.

Studied solitary species have warmer feet in all but extreme T_A . Moreover, in 35°C, their feet are of similar temperature as those of social species, much higher than other body regions (fig. 16). This may serve as a mechanism to dissipate the excessive body heat conserved by means of better fur insulation (discussed above). Social species evince warmer feet in 10°C. Šumbera et al. (2007) found about 9-10°C higher T_S in small individuals of both social and solitary mole-rat species in low T_A (10°C and 15°C). They claim the shivering individuals of the solitary species might use their feet to dissipate sudden surplus of heat; which is reversely to my results. Interestingly, there are conspicuously high differences between T_B and T_S in the feet of the blind mole rat (table 7 in the Appendix) indicating its very good insulative value. For future research, both hind and front should be thermographically measured in all of the used T_A , and compared. To prevent the feet from moving (that makes exact measurement of T_S impossible), they should be leant against some LWIR-permeable material, such as thin plastic, or special “Infrared window glass” (normal glass is not LWIR-permeable). Front feet might appear to have higher T_S in lower ambient temperatures. By hiding them in ventral pelage, the animal prevents them thus from heat loss.

4.2.4. Ventral surface temperature pattern

There were significant differences in the pattern of surface temperatures among the five studied ventral areas between solitary and social species. However, the differences are so small that are probably of no biological sense, and stay within the camera’s error range ($\pm 2^\circ\text{C}$). Furthermore, similar deviation pattern was found even on dorsum which implies this small deviation to be normal. In 35°C, the ventre is homogeneous, showing total warming through of the fur in this extreme temperature again. In this respect, Šumbera et al. (2007) observed a specific pattern in ventral surface temperature of the solitary silvery mole-rat. There was a distinct “thermal window” located on the chest of studied individuals, and also a mosaic pattern of higher surface temperatures appearing as “many small thermal windows”. The authors discussed it as a possible consequence of ruffling (and thus opening) fur connected with moving

and bending of the measured individual. According to my experience with infrared imaging, the mosaic pattern certainly emerged this way. The longer the fur is, the easier it opens. The animals were held for their tails, and because the hairs grow cephalocaudally, even the effect of gravity might be responsible for easier fur opening. Since no anaesthesia was applied because it could change normal physiology (Bazin et al. 2004), the studied individuals could not be held head up. All the “opened spots” in the fur were avoid when analysing the thermograms. The chest area with distinguishably higher T_S might be of a different origin. The silvery mole-rats are kept in plexiglass mazes, so their chest areas might be of worse fur quality because of frequent contact with either burrow floor, or the excavated substrate. When considering the ruffling of its chest fur, no such pattern was observed in the Cape dune mole-rat with even longer fur (own unpublished data).

The species analysed in my study did not differ much in the pattern of their ventral surface temperatures, but some pattern could be observed. It should be mentioned, that the values in figure 19 (in the Appendix) are the deviations from mean ventral temperature (stated as $T_{S \text{ area}} - T_{S \text{ mean}}$). Therefore, the highest values represent the highest T_S measured in particular area, i.e. areas with the poorest thermal insulation. The figure looks then reversely to the figure 3 (in the Introduction) showing the insulative volume of ventral areas in chtonic rodents, with the highest values representing the areas with the best thermal insulation. The *Fukomys* mole-rats thus have the warmest areas (less insulated) on their chests, while the common mole-rat in the middle of its ventre. The Cape mole-rat dissipates the most heat from the area between its hind legs (especially notable in 10°C, and in 30°C - not shown; the pattern can be seen in both sexes). The coruro seems to have similar pattern to the Cape mole-rat. Comparing the insulative volume and the T_S deviations in case of the blind mole rat, the pattern is very alike – compare figure 3 and figure 19. I described the ventral pattern in fur insulative volume in my bachelor’s study (Vejmělka 2016). The species with different social systems differ similarly as described in Šumbera et al. (2007) by the use of IRT. Ventral insulative volume in front areas is smaller in four solitary species (fig. 3), while the social species have homogeneous ventral regions in term of hair length and density. However, the difference was not statistically tested due to low sample size. By now, the sample size has been far extended, so more thorough study can be conducted, and the question of ventral T_S pattern could be tested. Next possible study direction could also focus on lateral distribution of ventral thermal windows. By means of both fur analysis and IRT, its exact wide over the ventre shall be ascertained.

It should be mention that there are some shortcomings of my study considering the testing of relationship of surface temperature and sociality. Although I tested 8 species, three solitary and five social; regarding social species, one is without fur, two are members of the same genera, and there was only a few individuals of the last species (the coruro) analysed. Then, considering variously related species of different climatic conditions, multivariate ordination analysis appears to be more correct approach.

4.2.5. Thermal windows in the naked mole-rat

The naked mole-rat is an exceptional mammal in many aspects. From a thermoregulatory point of view, it not only lacks any insulative layer – possessing neither fur nor subcutaneous fat - but is also very small. Therefore, I expect no difference in surface temperatures between dorsal and ventral body region. The difference was found, but ranging only within few Celsius degree (within the camera accuracy range), having probably no biological importance (fig. 15 in the Appendix). Similarly, there are only small differences in its ventral (as well as dorsal) areas (fig. 19 in the Appendix). Compared to ventre, hind feet are colder in $T_A \leq 32.5^\circ\text{C}$ (Tab. 12 in the Appendix), but in higher T_A , there is no difference. Still, the difference between the regions is lower compared to the furred species. T_B was sometimes found lower than T_S (see figure 15 in the Appendix). Unfortunately, two individuals died in 40°C probably as a consequence of lung collapse as suggested by autopsy. Although higher T_A was measured in its tunnels (table 2 in the Appendix; Holtze et al. 2018), the naked mole-rats probably do not face it, and rather seek for a convenient T_A in deeper burrows.

4.2.6. Other thermographic observation

In the ventral area “V2” of the Upper Galilee Mountains blind mole rat, two less insulated spots were found in all females, both via IRT and visually (figure 24). Every such spot contains a nipple. For more detailed discussion of discrepancy in mammary formula of *Nannospalax* see the chapter Thermographic observation (in the Appendix).

The Ansell’s mole-rat possesses considerably lower temperature of its nose’s skin compared to the rest of its body, especially in higher T_A (fig. 25 in the Appendix). This may indicate the presence of another area taking part in active heat exchange. A countercurrent heat exchanger might be present here. This feature can be found for instance in gazelles (Schmidt-Nielsen 1997), but was hypothesized even in the golden hamster (*Mesocricetus auratus*)(neck region; Gordon et al. 1981); often connected with panting. Using this cooling system, brain is prevented from overheating. In the case of mole-rats, the surface of the nasal

cavity would more actively dissipate the heat to the damper cavity, which leads to higher evaporation and thus cooling down. T_B of the mole-rat is always higher than T_A and thus the cooling might be effective (Tab. 6 in the Appendix). Similar feature was found in the naked mole-rat (see figure 26). On the other hand, this phenomenon is subtle in the common mole-rat and the Mashona mole-rats, especially towards extreme temperatures. The noses of the blind mole rats seem to lose heat only closely above rhinarium (in both low and high T_A ; fig. 8) and above. The fossorial coruros do not seem to use their noses in thermoregulation. Its nose (rhinarium) is relatively small compared to the subterranean species. To conclude, there is an indication of thermal-window-like region located on the head in chthonic mammals, but further research is requested to better understand the topic. When investigated using IRT, proper orientation of the particular region to the camera (i.e. perpendicular) is extremely essential.

4.3. Behavioural observation and the influence of captivity

Studied animals were observed to curl not only in low T_A ($\leq 20^\circ\text{C}$), but some individuals in high T_A (30°C and 35°C) as well (Tab. 17 in the Appendix). Since species observed to curl in high T_A (the common mole-rat and the blind mole rat) possess similarly short, but quite dense dorsal fur (notably denser than other social mole-rats; own unpublished data), this behaviour could help them to dissipate the surplus heat via “opened spots” in the short fur (see *N. galili* in the figure 28, or *G. capensis* in the figure 32 in the Appendix). Interestingly, some of blind mole rats and coruros were observed to address their bellies to provided carrot pieces in high temperatures. Since the carrot was stored outside the testing room, it had different temperature, and the animals could thus cool themselves down via conduction (fig. 33 in the Appendix).

All of the examined animals were held at least four months in captivity. Thus, the emotional fewer should be lowered (see the chapter Infrared thermography in the Appendix). However, there is a question of the influence of captivity on the thermoregulation of chthonic mammals. The south African mole-rats used in this study were wild-captured, while the rest was bred in captivity. Concerning the fur density, my results (Vejmělka 2016) on the individuals from the wild differ from those of Šumbera et al. (2007) - the mole-rats bred in captivity (higher temperature) possess 2-3 times sparser ventral fur (Table 1 in the Introduction). This study may thus further serve as a base for further comparisons with the IRT studies on chthonic rodents from various conditions.

4.4. Thermoregulation in relation with sympatry

Differences in thermal insulation may help animals to coinhabit the same habitats. In this study, three mole-rats occurring syntopically around south African Darling were studied (Bennett and Faulkes 2000). Several factors may enable coexistence in quite heterogeneous environment: social way of life in the common mole-rat may allow them to occupy very hard soils, and socially thermoregulate; large body mass in the Cape dune mole-rat and claw-digging may enable survival in this cold environment in sandy soil; or thermally well insulated body in the Cape mole-rat allow them to stay in hard soils and survive in quite cold environment. There are other examples of chtonian rodent sympatric occurrence possibly explained by thermoregulatory differences. Two tuco-tuco species inhabiting coastal grasslands of Argentina, *Ctenomys talarum* and *Ctenomys australis*, may be able to cooccur due to thermal restrictions, with *C. talarum* restricted in high T_A (Luna and Antinuchi 2007a). Indeed, my unpublished results on fur characteristics indicate notably denser fur in *C. talarum* compared to its larger neighbor. Finally, Nyika Plateau in Malawi is inhabited by the silvery mole-rat and the Whyte's mole-rat (*Fukomys whytei*), a social species. Lövy et al. (2012) mentions that one possible explanation of the absence of the social species from higher altitudes is its less effective thermoregulation in colder environment.

Higher body core temperature appears to be an important factor unifying three unrelated species (the Cape mole-rat, the blind mole rat, and the coruro), and setting them apart from other studied chtonian rodents, however related, syntopic, or sharing the same social organization; possibly due to the fact of having in common the presence in relatively severe climatic conditions. As evident from the results, T_A 35°C is too high for the thermoregulation of all the studied species except for the naked mole-rat that differs from them considerably. Ventral thermal window was clearly observable in all species in all T_A . Its pattern does, however, not differ markedly between the social systems. The important thermal window found on the chest of the silvery mole-rat (Šumbera et al. 2007) might be localized on (hind) feet in other solitary species, enabling them to dissipate the surplus heat from their well thermally insulated bodies in high ambient temperatures. The occurrence of arteriovenous anastomoses in the regions functioning as thermal windows in chtonian rodents is still disputable. Therefore, as a logical consequence of the study concerning the thermal windows in chtonian rodents, additional histological research comparing the body regions is desirable. Finally, IRT of shaved animals would surely bring answers to the questions of the detection of chtonian rodent thermal windows.

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6. Appendix

6.1. Infrared Thermography

6.1.1. Basic Principles

From all of the possibilities of heat (energy) exchange, infrared thermography (IRT) occupies itself with radiation, that is to say transmitting energy by means of electromagnetic waves. Thermography is a technique transferring the emitted, transmitted, and reflected energy of the object to the visible spectrum (regarding human eyesight). Every “warm” object (i.e. object possessing true heat – above zero Kelvin) emits electromagnetic radiation (due to the kinetic motion of the particles).

For the needs of IRT, a small portion of the radiation is used. The infrared spectrum extends from the wavelengths of 700 nm (visible “white” light lies between 390-700 nm) up to 1 mm (10^6 nm; lower limit of the microwaves) (Fig. 7).

Temperature, in comparison, expresses a measure of the thermal energy contained in certain object. It can be delineated in relative scales. Using IRT, it is thus possible to measure the energy, visualise it, and convert to temperature scales.

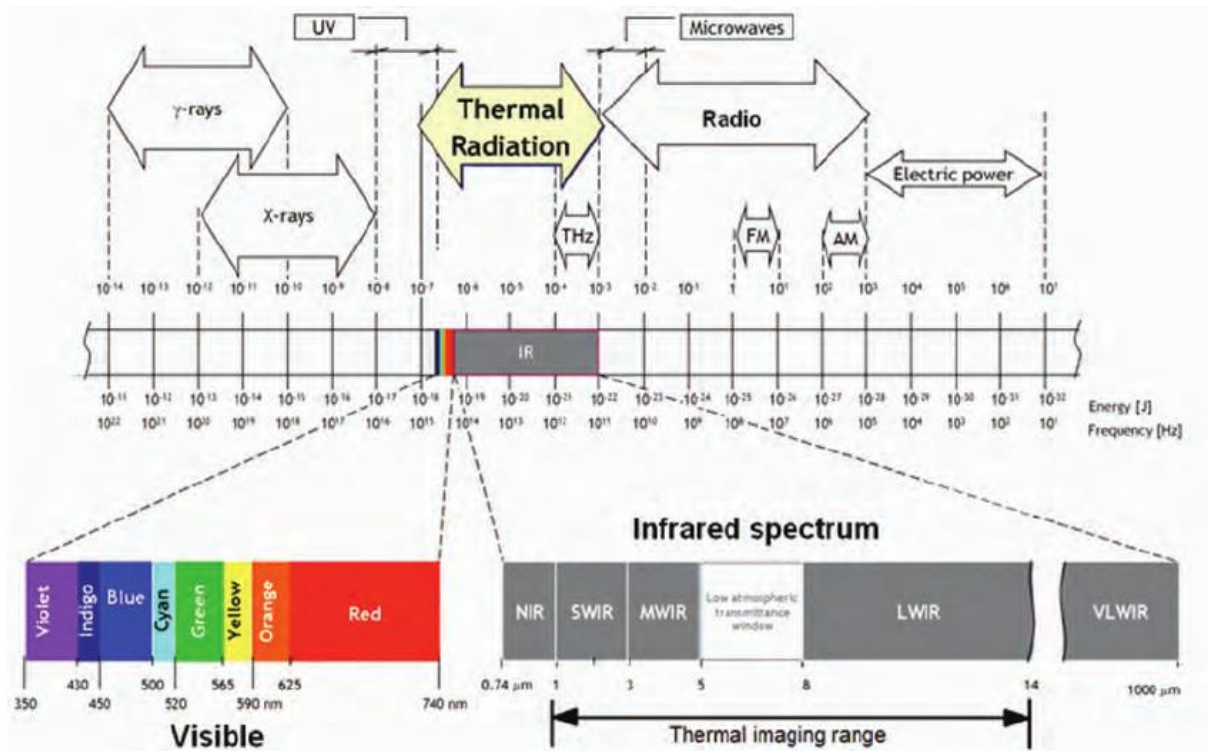


Figure 7: The illustration of the electromagnetic spectrum with the emphasis put on visible and infrared part of the spectrum. LWIR = long-wave infrared radiation.
Abbas et al. 2011 (modified from Infrared vision, <http://mivim.gel.ulaval.ca>).

6.1.2. Infrared thermography in biology

IRT application in biology requires realisation of a couple of facts. Firstly, long-wave infrared radiation (LWIR) is the only part of the spectrum relevant for biological applications (Tattersall 2016). The narrow extent of the spectre is called infrared thermal range, occurring within 8 and 15 μm (8,000–15,000 nm; Fig. 7). Body heat, for instance, is emitted to the environment in this form. Secondly, concerning terrestrial mammals, the measured materials are entirely solid (skin, fur), and air is the only environment, through which the energy is passing. Thirdly, it is important to realise that IRT measures only T_s , not the whole temperature of the object (such as core temperature of the animal).

Next, no biological material is a blackbody, every object emits energy and simultaneously receives it from other objects. An ideal grey body, in contrast, emits energy constantly, independently of the wavelength. This is the state the majority of real matters matches more.

With energy reaching the surface, there are two possible ways to continue. One part is reflected back to the environment. The rest of the waves is absorbed. Since there is no transmittance (τ) through biological objects, the relationship of the energy reaching the surface can be described in a following equation where ρ stands for reflectance, and α for absorptance:

$$\rho + \alpha = 1$$

As mentioned above, biological objects can be perceived as grey bodies. In that case, Kirchhoff's law of thermal radiation can be applied (Birkebak 1966; Tattersall 2016), claiming that absorptance equals emittance (ϵ) (not to be confused with *emissivity* used for ideal materials). Then:

$$\rho + \epsilon = 1$$

Emittance values for biological tissues (consisting mostly of water and organic matter) range from 0.95 to 0.98 (Hammel 1956 in Tattersall 2016). With the knowledge of the previous equation, the reflectance can be considered very poor. Similarly, the reflectance of other objects in the vicinity is negligible, compared to the high emittance.

Since organisms do not live in the vacuum, air gases (as well as wind convective cooling if measured outside) need to be taken into account when assessing T_s of the focus object. The most important radiation absorber is water vapour. This issue is the more pronounced, the longer the distance from the object is. For this reason, both air humidity and the distance must be taken into consideration. The observer should not be more than 100 meters away from the measured object (Tattersall 2016). For the distances exceeding 20 meters, see Faye et al.

(2016). For the mistakes, biologists do when using IRT, see Harrap et al. (2018)(a review of works from 2007-2017).

Last but surely not least matter is the angle of the incidence. If the lens is situated within 60° and 120° (i.e. less than 30° from the perpendicular), no undesirable effects emerge.

For biological material, the most convenient lenses of the infrared cameras are made of germanium or zinc sulphide. These materials possess ideal transmissivity for the aim part of the spectrum (compared to glass for instance that is impenetrable for the radiation).

6.1.3. Advantages and usage

Infrared thermography is, especially in biology, quite a modern method. Except for medicine (both human and veterinary), IRT is very useful in thermal physiology, too. The infrared thermography is capable of showing the relationship between surface and subcutaneous temperature on the basis of the temperature gradient in fur (Thompson et al. 2017). Recently, there is a distinct increase in the use of IRT not only studying endotherms (see the chapter Thermal windows), but also ectotherms (for example Tattersall et al. 2004; Skandalis et al. 2006b; Cadena et al. 2013).

The most often stressed advantage is the noninvasiveness of IRT. For apparent reasons, the animal can be observed from distance. Therefore, the measurements are considered as objective, as never before. Measuring the temperature using thermometers and rectal thermocouples rises the stress level of the individual. Even the iButton temperature loggers must be applied first and removed afterwards.

Infrared thermography, on the other hand, enables to measure T_s without disturbing the animal, also in its natural environment. Cilulko et al. (2013) mention some studies engaged in wild mammals' reproduction control (the Asian elephant *Elephas maximus* – increased temperature of reproductive organs; the black rhinoceros *Diceros bicornis* and the giant panda *Ailuropoda melanoleuca* – pregnancy detection), as well as behavioural analyses (the rhesus monkey *Macaca mulatta* – decreased nasal temperature when scared). Another possibility is the detection of the endotherms in the wilderness and estimation of their population size (see Cilulko et al. 2013). Moreover, Boonstra et al. (1994) report high success in detecting rodent and lagomorph nests and burrows with decreased success rate with increasing insulation properties of fur or the nest. Moreover, the thickness of the vegetation cover needs to be considered because of its radiation-absorptive properties.

6.1.4. Emotional fever

Measuring of body surface temperature with the aid of IRT is important especially regarding so-called emotional fever (or stress-induced hyperthermia, SIH). Some authors discovered a rise (up to 2°C) of T_B following handling in the rat, the Eastern chipmunk (*Tamias striatus*), domestic fowl, the common eider (*Somateria mollissima*), the zebrafish (*Danio rerio*; up to 4°C), and human (academic examination of medical students) (Thompson et al. 2003, Vianna and Carrive 2005; Careau et al. 2012; Cabanac and Aizawa 2000; Cabanac and Guillemette 2001; Rey et al. 2015; Briese 1995).

SIH is connected with considerable vasoconstriction in skin arteries of body extremities (Cabanac and Aizawa 2000; Vianna and Carrive 2005). This adaptation is advantageous in the event of injury, the blood loss of such body part would be reduced. Lower blood provision leads to lower heat supply, which results in lower surface temperature of that particular body part showed by infrared thermography.

Thompson et al. 2003 claim that emotional fever disappears after repeated handling (about 10 weeks for their rats). However, it appears again as soon as another stressing stimulus emerges. To sum up, if the studied animal is thermographically measured without any intervention, or if it is used to the particular handling, emotional fever will not occur and the IRT results can be considered reliable.

6.1.5. Emissivity inconsistency

Results of infrared thermography extensively depend on the settings of the infrared camera, with emissivity being the most crucial (e.g. Harrap et al. 2018). Surveying the furred species of his study, emittance was set to 0.97, a value that fits in the range of 0.95-0.99, used in a number of infrared studies on mammals, yet originating from a single study (Hammel 1956; cited from Tattersall 2016). Regarding all works conducting IRT of mammals (excluding human) between 2007-2017, the mean of their reported emittance values is 0.977 (Harrap et al. 2018). However, during the year 2018 a work of McGowan et al. was published (i.e. after the measurements in this study were finished), lowering the emittance of mammal fur (called emissivity therein). For the new emittance rates of the mole-rats used in the study, the Damaraland mole-rat (*Fukomys damarensis*), Highveld mole-rat (*Cryptomys hottentotus pretoriae*), and Natal mole-rat (*C. hottentotus natalensis*), see Table 15.

Table 15: The emittance (ϵ) values (Error = 95% CI) in three mole-rats measured by McGowan et al. (2018).

Species	N of pelage samples	ϵ
<i>Fukomys damarensis</i>	2	0.79 ± 0.04
<i>Cryptomys hottentotus pretoriae</i>	1	0.84 ± 0.02
<i>Cryptomys hottentotus natalensis</i>	1	0.86 ± 0.07

To examine possible impact of this inconsistency on the results, I adjusted the emittance in my thermograms of the common mole-rat *Cryptomys hottentotus hottentotus* according to McGowan et al. (2018) from 0.97 to 0.84 and obtained the results shown in Table 16. The differences do not exceed the range stated by the camera manufacturers (accuracy 2°C or 2%) in higher temperatures. In lower T_A (<20°C), there is a slightly higher difference that will probably rise with declining temperature. That is given by greater difference of temperature of the measured object (animal) and reflected/atmospheric temperature.

Table 16: The difference of the surface temperatures (ΔT_s) after the change of emittance (ϵ) in all studied T_A for *C.hottentotus h..*

T_A [°C]	T_s by $\epsilon = 0.97$ [°C]	T_s by $\epsilon = 0.84$ [°C]	ΔT_s [°C]
10	21.9	23.6	1.7
15	25.5	27	1.5
20	26.9	27.9	1
25	29.7	30.4	0.7
30	32.5	32.8	0.3
35	35.8	35.9	0.1

6.2. Tables and figures

(next pages)

Table 2: Additional information about studied species, their ecology and physiological parameters.

Species	Family	Social system	Chtonicity	Thermo neutral zone [°C]	Burrow temperature [°C]	Altitude [m a.s.l.] ^{t,u}	Climatic zone	Geographical distribution
<i>Bathyergus suillus</i>	Bathyergidae	Solitary	Subterranean	25 – 31 ^a	12.4 - 31.6 ^k	10 - 300	Subtropics	South Africa
<i>Georchus capensis</i>	Bathyergidae	Solitary	Subterranean	26.3-34 ^b	12.0 – 30,7 ^k 9.8 – 36.3 ^m 10.2 – 29.7 ⁿ	0 – 1300 ^v	Subtropics	South Africa
<i>Cryptomys hottentotus h.</i>	Bathyergidae	Social	Subterranean	27 – 30 ^c	15.9 – 27.8 ⁿ	-	Subtropics	Lesotho; Malawi; Mozambique; South Africa; Swaziland; Zimbabwe
<i>Fukomys darlingi</i>	Bathyergidae	Social	Subterranean	28–31.5 ^d 27-34 ^e	-	up to 1524	Tropics	Malawi; Mozambique; Zimbabwe
<i>Fukomys anselii</i>	Bathyergidae	Eusocial	Subterranean	28-32 ^f	18-26 ^p	ca. 1250	Tropics	Zambia
<i>Heterocephalus glaber</i>	Bathyergidae	Eusocial	Subterranean	31-37 ^g 31-34 ^h	29.1 – 30.6 ^g 29 – 32 ⁿ 24.6 – 48.8 ^q	400 - 1500	Tropics	Ethiopia; Kenya; Somalia
<i>Spalacopus cyanus</i>	Octodontidae	Social	Fossorial	10-32 ⁱ	8-32.1 ^r	0 - 3400	Subtropics / Temperate	Chile
<i>Nannospalax galili</i>	Spalacidae	Solitary	Subterranean	26,4-? ^j	6-8 ^{p,s}	ca. 770	Subtropics	Israel

a = Lovegrove 1986; b = Lovegrove 1987; c = Bennett et al. 1992; d = Bennett et al. 1993; e = Zemanová et al. 2012; f = Marhold and Nagel 1995 (in Begall et al. 2015); g = McNab 1966; h = Buffenstein and Yahav 1991; i = Contreras 1983; j = Haim and Izhaki 1993 (in Šklíba et al. 2014); k = Okrouhlik (unpubl.), soil temperature 30cm deep; m = Okrouhlik (unpubl.), soil temperature 10cm deep; n = Bennett et al. 1988; p = Šklíba et al. 2014, winter; q = Holtze et al. 2018; r = Begall and Gallardo 2000; s = Šklíba et al. 2016; t = [IUCN 2018](#); u = Wilson et al. 2016; v = Okrouhlik (pers. com.).

Table 3: Information about tested individuals of each species. Body mass stated as range; mean \pm s.d.. Climatic characteristics were downloaded from the Wordclim database (<http://worldclim.org>). For species with original locality not known, data from the whole range of species' occurrence were used.

Species	Number of individuals of each sex *	Body mass [g]	Approximate original altitude [m a.s.l.]	Original locality; GPS	Average annual rainfall [mm]	Average annual temperature [°C]	Minimal temperature [°C]	Annual temperature range [°C]
<i>Bathyergus suillus</i>	♀ 4:6 ♂	495-915; 694 \pm 146	252	Darling, South Africa; 33°22'S 18°25'E	435	17.6	6.7	20.8
<i>Georychus capensis</i>	♀ 5:4 ♂	101-264; 148 \pm 48	252	Darling, South Africa; 33°22'S 18°25'E	435	17.6	6.7	20.8
<i>Cryptomys hottentotus h.</i>	♀ 4:6 ♂	46-101; 71 \pm 13	252	Darling, South Africa; 33°22'S 18°25'E	435	17.6	6.7	20.8
<i>Fukomys darlingi</i>	♀ 6:5 ♂	93-188; 139 \pm 27	53	Nsanje, Malawi; 16°55'S, 35°16'E	842	25.7	14	21.8
<i>Fukomys anselli</i>	♀ 5:4 ♂	63-105; 80 \pm 11	1320	Lusaka, Zambia; 15°28'S, 28°25'E	824	19.9	7.7	22.2
<i>Heterocephalus glaber</i>	♀ 6:6 ♂	28-49; 37 \pm 6	-	Not known	374	25.8	17.6	16
<i>Spalacopus cyanus</i>	♀ 2:3 ♂	60-124; 101 \pm 19	-	Not known	377	13.1	1.9	22
<i>Nannospalax galili</i>	♀ 10:11 ♂	119-243; 171 \pm 32	770	Gush Halav, Israel; 33°02'N, 35°27'E	791	16.7	1.3	28.2

* Different numbers entered different statistical analyses.

Table 6: Body core and surface temperatures (mean \pm s.d.) of seven studied species in different ambient temperatures.

Species	Body region	Ambient temperature [$^{\circ}$ C]					
		10	15	20	25	30	35
<i>Bathyergus suillus</i>	Body core	34.3 \pm 1.0	34.5 \pm 0.4	34.7 \pm 0.6	35.1 \pm 0.6	35.9 \pm 0.6	37.4 \pm 0.6
<i>Georychus capensis</i>	Body core	35.0 \pm 0.9	35.3 \pm 0.7	35.4 \pm 0.9	35.9 \pm 0.6	36.1 \pm 0.6	37.9 \pm 0.7
<i>Cryptomys hottentotus h.</i>	Body core	33.7 \pm 1.2	33.9 \pm 0.5	34.3 \pm 0.6	34.6 \pm 0.4	35.3 \pm 0.5	37.6 \pm 0.7
<i>Fukomys darlingi</i>	Body core	34.0 \pm 0.3	34.1 \pm 0.4	33.7 \pm 0.7	33.6 \pm 0.4	35.1 \pm 0.2	37.7 \pm 0.4
<i>Fukomys anselli</i>	Body core	33.9 \pm 0.8	34.5 \pm 0.3	34.9 \pm 0.4	35.2 \pm 0.4	35.4 \pm 0.5	37.6 \pm 0.5
<i>Spalacopus cyanus</i>	Body core	35.5 \pm 0.4	35.5 \pm 0.6	35.5 \pm 0.8	36.0 \pm 0.3	37.6 \pm 0.2	38.7 \pm 0.4
<i>Nannospalax galili</i>	Body core	35.7 \pm 0.6	35.7 \pm 0.6	36.3 \pm 0.7	36.5 \pm 0.7	37.4 \pm 0.4	38.7 \pm 0.4
<i>Bathyergus suillus</i>	Dorsum	17.6 \pm 0.9	21.3 \pm 0.9	23.7 \pm 0.8	27.9 \pm 1.1	31.9 \pm 0.6	33.9 \pm 0.9
<i>Georychus capensis</i>	Dorsum	16.2 \pm 1.0	20.2 \pm 0.7	24.3 \pm 0.8	26.6 \pm 0.8	29.4 \pm 0.9	33.8 \pm 1.4
<i>Cryptomys hottentotus h.</i>	Dorsum	20.3 \pm 0.6	24.1 \pm 0.5	26.5 \pm 0.3	29.3 \pm 0.5	32.5 \pm 0.4	36.4 \pm 0.4
<i>Fukomys darlingi</i>	Dorsum	22.6 \pm 0.5	24.9 \pm 0.7	27.5 \pm 0.7	29.2 \pm 0.3	32.6 \pm 0.3	36.2 \pm 0.5
<i>Fukomys anselli</i>	Dorsum	24.9 \pm 0.8	26.9 \pm 0.8	28.9 \pm 0.5	30.4 \pm 0.6	32.3 \pm 0.3	36.3 \pm 0.5
<i>Spalacopus cyanus</i>	Dorsum	21.7 \pm 2.7	24.5 \pm 0.8	27.7 \pm 1.0	30.1 \pm 0.4	33.2 \pm 1.3	35.5 \pm 1.1
<i>Nannospalax galili</i>	Dorsum	20.0 \pm 1.4	23.2 \pm 1.1	26.6 \pm 0.5	28.9 \pm 0.9	32.2 \pm 0.8	34.6 \pm 1.0
<i>Bathyergus suillus</i>	Ventre	24.6 \pm 1.7	26.3 \pm 1.1	27.6 \pm 0.9	30.2 \pm 1.3	31.4 \pm 0.7	33.1 \pm 1.1
<i>Georychus capensis</i>	Ventre	23.4 \pm 2.0	25.8 \pm 1.2	28.3 \pm 1.0	30.0 \pm 0.7	30.7 \pm 1.3	33.7 \pm 0.9
<i>Cryptomys hottentotus h.</i>	Ventre	24.4 \pm 1.0	26.9 \pm 0.4	28.6 \pm 0.8	30.4 \pm 0.7	32.7 \pm 0.7	36.2 \pm 0.7
<i>Fukomys darlingi</i>	Ventre	27.5 \pm 0.5	28.7 \pm 0.5	30.0 \pm 0.8	30.7 \pm 0.4	33.3 \pm 0.3	36.8 \pm 0.4
<i>Fukomys anselli</i>	Ventre	28.6 \pm 1.3	29.8 \pm 1.3	30.7 \pm 0.8	32.1 \pm 0.7	33.1 \pm 0.6	36.1 \pm 0.5
<i>Spalacopus cyanus</i>	Ventre	24.8 \pm 2.7	26.4 \pm 1.1	29.2 \pm 1.5	30.9 \pm 0.7	33.6 \pm 1.3	35.8 \pm 1.0
<i>Nannospalax galili</i>	Ventre	26.7 \pm 1.3	28.2 \pm 0.9	30.1 \pm 0.7	31.3 \pm 0.9	33.3 \pm 0.6	35.3 \pm 0.8
<i>Bathyergus suillus</i>	Feet	18.5 \pm 5.5	25.8 \pm 3.9	28.9 \pm 3.8	30.6 \pm 1.9	34.1 \pm 0.8	36.5 \pm 0.6
<i>Georychus capensis</i>	Feet	17.9 \pm 3.7	21.1 \pm 3.0	24.1 \pm 2.3	27.4 \pm 2.5	32.2 \pm 1.0	36.1 \pm 0.6
<i>Cryptomys hottentotus h.</i>	Feet	17.2 \pm 5.2	20.7 \pm 4.3	23.9 \pm 3.6	27.7 \pm 2.6	32.4 \pm 1.4	36.6 \pm 0.6
<i>Fukomys darlingi</i>	Feet	17.7 \pm 2.7	22.1 \pm 3.6	23.0 \pm 1.9	27.1 \pm 1.2	32.3 \pm 0.8	36.4 \pm 0.6
<i>Fukomys anselli</i>	Feet	18.8 \pm 0.9	21.1 \pm 1.1	23.2 \pm 1.2	27.1 \pm 0.6	31.2 \pm 0.8	36.2 \pm 0.6
<i>Spalacopus cyanus</i>	Feet	18.5 \pm 3.9	21.1 \pm 2.5	26.5 \pm 0.9	29.0 \pm 1.8	34.0 \pm 1.3	36.8 \pm 1.1
<i>Nannospalax galili</i>	Feet	17.5 \pm 3.7	22.5 \pm 2.9	24.7 \pm 1.4	28.7 \pm 1.1	33.6 \pm 0.5	35.9 \pm 0.8

Table 7: T_B-T_S (mean \pm s.d.) in different body regions of seven studied species in different ambient temperatures.

Species	Body region	Ambient temperature [°C]					
		10	15	20	25	30	35
<i>Bathyergus suillus</i>	Dorsum	16.7 \pm 1.1	13.3 \pm 0.8	11.0 \pm 0.7	7.2 \pm 0.9	4.1 \pm 0.9	3.5 \pm 0.8
<i>Georchus capensis</i>	Dorsum	18.7 \pm 1.7	15.0 \pm 1.4	11.1 \pm 1.4	9.3 \pm 1.1	6.7 \pm 1.1	4.1 \pm 1.4
<i>Cryptomys hottentotus h.</i>	Dorsum	13.4 \pm 1.5	9.8 \pm 0.8	7.8 \pm 0.6	5.3 \pm 0.6	2.8 \pm 0.5	1.2 \pm 0.5
<i>Fukomys darlingi</i>	Dorsum	11.4 \pm 0.5	9.2 \pm 0.7	6.3 \pm 0.4	4.4 \pm 0.4	2.5 \pm 0.3	1.5 \pm 0.5
<i>Fukomys anselii</i>	Dorsum	8.9 \pm 0.9	7.5 \pm 0.6	6.0 \pm 0.7	4.7 \pm 0.7	3.1 \pm 0.5	1.2 \pm 0.4
<i>Spalacopus cyanus</i>	Dorsum	13.8 \pm 2.6	11.0 \pm 0.4	7.9 \pm 0.2	5.9 \pm 0.3	4.5 \pm 1.1	3.3 \pm 1.0
<i>Nannospalax galili</i>	Dorsum	15.7 \pm 1.4	12.6 \pm 1.3	9.7 \pm 0.8	7.6 \pm 0.9	5.1 \pm 0.7	4.0 \pm 1.0
<i>Bathyergus suillus</i>	Ventre	9.8 \pm 2.1	8.3 \pm 1.0	7.1 \pm 1.0	4.9 \pm 1.2	4.5 \pm 0.9	4.3 \pm 0.9
<i>Georchus capensis</i>	Ventre	11.6 \pm 2.0	9.5 \pm 1.5	7.1 \pm 1.5	5.9 \pm 1.1	5.4 \pm 1.3	4.3 \pm 1.3
<i>Cryptomys hottentotus h.</i>	Ventre	9.2 \pm 1.6	7.0 \pm 0.8	5.7 \pm 0.9	4.2 \pm 0.7	2.5 \pm 0.7	1.4 \pm 0.7
<i>Fukomys darlingi</i>	Ventre	6.5 \pm 0.3	5.4 \pm 0.5	3.8 \pm 0.6	2.9 \pm 0.4	1.8 \pm 0.3	1.0 \pm 0.4
<i>Fukomys anselii</i>	Ventre	5.3 \pm 1.6	4.7 \pm 1.3	4.1 \pm 1.1	3.0 \pm 0.8	2.3 \pm 0.6	1.5 \pm 0.4
<i>Spalacopus cyanus</i>	Ventre	10.7 \pm 2.5	9.1 \pm 0.9	6.3 \pm 0.8	5.0 \pm 0.5	4.0 \pm 1.1	2.9 \pm 0.8
<i>Nannospalax galili</i>	Ventre	9.0 \pm 1.3	7.5 \pm 1.0	6.2 \pm 0.8	5.1 \pm 0.9	4.0 \pm 0.5	3.3 \pm 0.7
<i>Bathyergus suillus</i>	Feet	15.8 \pm 5.7	8.8 \pm 3.7	5.8 \pm 3.6	4.5 \pm 1.7	1.9 \pm 0.7	1.0 \pm 0.3
<i>Georchus capensis</i>	Feet	17.1 \pm 4.0	14.1 \pm 3.2	11.3 \pm 2.6	8.5 \pm 2.7	3.9 \pm 1.2	1.9 \pm 0.7
<i>Cryptomys hottentotus h.</i>	Feet	16.4 \pm 4.8	13.2 \pm 4.2	10.4 \pm 3.4	6.9 \pm 2.7	2.8 \pm 1.5	1.0 \pm 0.5
<i>Fukomys darlingi</i>	Feet	16.4 \pm 2.6	12.0 \pm 3.6	10.6 \pm 1.8	6.6 \pm 1.2	2.8 \pm 0.7	1.3 \pm 0.6
<i>Fukomys anselii</i>	Feet	15.1 \pm 0.9	13.4 \pm 1.1	11.9 \pm 0.9	8.1 \pm 0.8	4.2 \pm 0.8	1.5 \pm 0.4
<i>Spalacopus cyanus</i>	Feet	17.0 \pm 4.1	14.4 \pm 3.0	9.0 \pm 0.5	6.9 \pm 1.8	3.7 \pm 1.1	1.9 \pm 0.9
<i>Nannospalax galili</i>	Feet	18.2 \pm 3.8	13.3 \pm 2.9	11.7 \pm 1.6	8.0 \pm 0.9	3.8 \pm 0.4	2.7 \pm 0.6

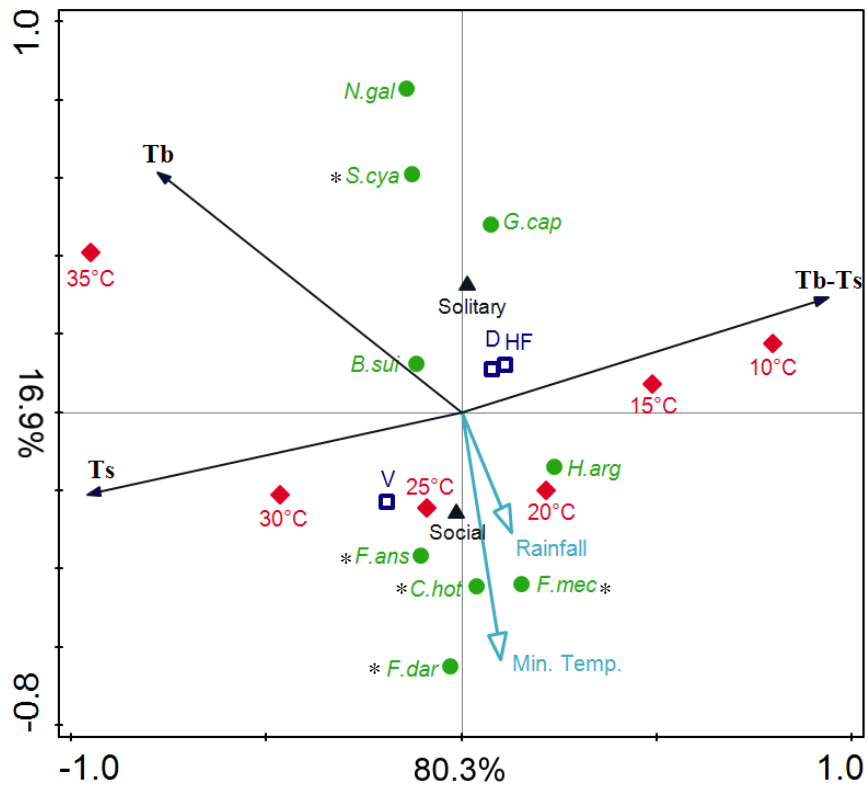


Figure 11: PCA visualisation of surface temperature (Ts), body core temperature (Tb), and their difference (Tb-Ts) (depicted as black arrows) of all studied furred species (green dots) with two mole-rat species from Šumbera et al. 2007 (*F. mechowii*, *H. argenteocinereus*) added in six ambient temperatures (red diamonds). Social species are marked with asterisks. Factors social system (black triangles) and body region (blue squares - Ventre, Dorsum and Hind Feet) are illustrated as well. All factors are passively projected, as well as two climatic variables (azure arrows). The eigenvalues of the first two axes are written in.

Table 8: Significance levels in post-hoc interspecies (furred) comparison of T_B across T_A . Values lower than 0.0083 are shown in bold.

Compared species	Ambient temperature [°C]					
	10	15	20	25	30	35
<i>C.hot</i> - <i>B.sui</i>	1.000	0.999	0.999	0.991	0.787	0.725
<i>F.ans</i> - <i>B.sui</i>	1.000	0.784	0.898	0.774	0.650	0.769
<i>F.dar</i> - <i>B.sui</i>	1.000	0.989	1.000	0.970	0.954	0.622
<i>G.cap</i> - <i>B.sui</i>	0.744	0.106	0.495	0.127	0.057	0.378
<i>N.gal</i> - <i>B.sui</i>	0.216	0.005	0.022	0.006	<0.001	0.025
<i>S.cya</i> - <i>B.sui</i>	0.445	0.048	0.453	0.192	<0.001	0.036
<i>F.ans</i> - <i>C.hot</i>	0.999	0.090	0.460	0.316	0.998	1.000
<i>F.dar</i> - <i>C.hot</i>	0.998	0.997	0.305	<0.001	0.743	1.000
<i>G.cap</i> - <i>C.hot</i>	0.032	<0.001	0.014	<0.001	0.016	0.946
<i>N.gal</i> - <i>C.hot</i>	<0.001	<0.001	<0.001	<0.001	<0.001	0.012
<i>S.cya</i> - <i>C.hot</i>	0.002	<0.001	0.016	0.003	<0.001	0.010
<i>F.dar</i> - <i>F.ans</i>	1.000	0.335	0.002	<0.001	0.342	1.000
<i>G.cap</i> - <i>F.ans</i>	0.103	0.070	0.787	0.082	0.058	0.833
<i>N.gal</i> - <i>F.ans</i>	<0.001	<0.001	<0.001	<0.001	<0.001	0.002
<i>S.cya</i> - <i>F.ans</i>	0.007	0.007	0.647	0.268	<0.001	0.003
<i>G.cap</i> - <i>F.dar</i>	0.072	<0.001	<0.001	<0.001	<0.001	0.924
<i>N.gal</i> - <i>F.dar</i>	<0.001	<0.001	<0.001	<0.001	<0.001	0.002
<i>S.cya</i> - <i>F.dar</i>	0.006	<0.001	<0.001	<0.001	<0.001	0.007
<i>N.gal</i> - <i>G.cap</i>	0.382	0.441	0.020	0.244	<0.001	0.187
<i>S.cya</i> - <i>G.cap</i>	0.861	0.938	1.000	1.000	<0.001	0.141
<i>S.cya</i> - <i>N.gal</i>	1.000	0.999	0.332	0.647	0.493	0.985

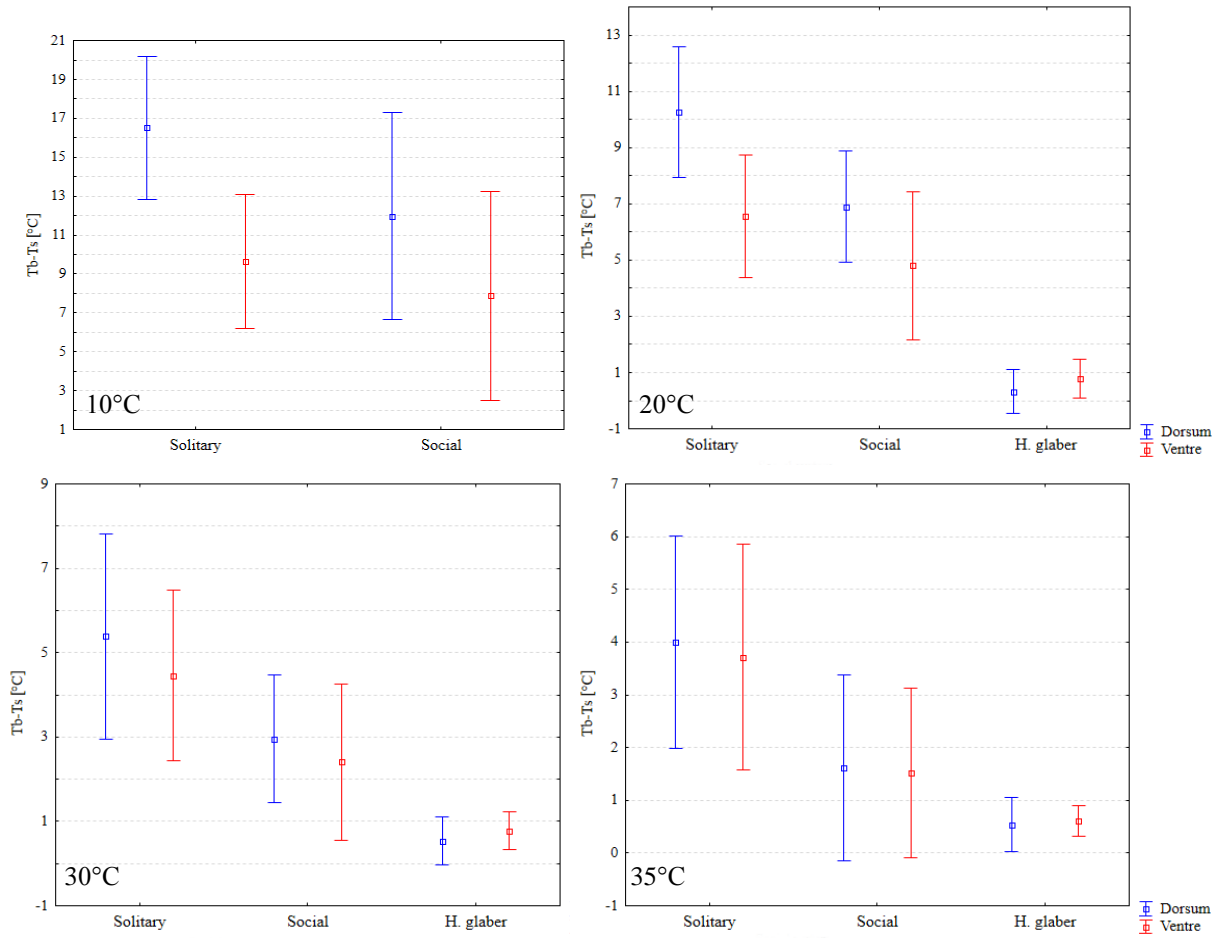


Figure 15: Difference between body core temperature and surface temperature of dorsum and ventre (mean \pm sd) in furred studied species with different social system, and in the naked mole-rat in T_A 10°C, 20°C, 30°C, and 35°C.

Table 10: The results of GLS tests used to compare T_B - T_S values between dorsal and ventral body regions of the naked mole-rat across different T_A . Values lower than 0.00625 are shown in bolt.

value	factor	Ambient temperature [°C]							
		20	25	27.5	30	32.5	35	37.5	40
p	body region	<0.0001	<0.0001	0.029	<0.0001	0.0063	0.0442	0.0596	0.3963
F (df)	body region	74.9589 (1;19)	33.35294 (1;21)	5.563718 (1;19)	41.87917 (1;19)	9.71429 (1;17)	4.72222 (1;17)	4.073965 (1;17)	0.757426 (1;17)

Table 12: The results of GLS tests used to compare T_B - T_S values of hind feet with ventral body region in the naked mole-rat across different T_A . Values lower than 0.00625 are shown in bolt.

value	factor	Ambient temperature [°C]							
		20	25	27.5	30	32.5	35	37.5	40
p	<i>hind feet - ventre</i>	0.0004	<0.0001	<0.0001	<0.0001	0.0012	0.0369	0.1946	0.0405
F (df)	<i>hind feet - ventre</i>	39.21296 (1;7)	135.2422 (1;9)	255.2302 (1;5)	79.33449 (1;13)	21.7742 (1;9)	6.61719 (1;7)	1.90786 (1;11)	12 (1;93)

Table 14: The results of GLS tests used to compare T_B - T_S values of ventral and dorsal areas among furred species and between social systems across different T_A . Areas were tested within ventral and dorsal body region, respectively. Values lower than 0.00625 are shown in bolt.

value	factor	Ambient temperature [°C]							
		20	25	27.5	30	32.5	35	37.5	40
p	<i>ventral areas</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
F (df)	<i>ventral areas</i>	170.61751 (4;49)	97.89104 (4;54)	152.2234 (4;49)	47.21724 (4;49)	36.10131 (4;44)	29.38305 (4;44)	25.257143 (4;44)	34.3022 (4;34)
p	<i>dorsal areas</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.001	<0.0001
F (df)	<i>dorsal areas</i>	84.30336 (4;44)	60.3469 (4;54)	73.25046 (4;39)	30.979504 (4;39)	41.68062 (4;44)	12.45994 (4;44)	5.74252 (4;39)	9.033673 (4;39)

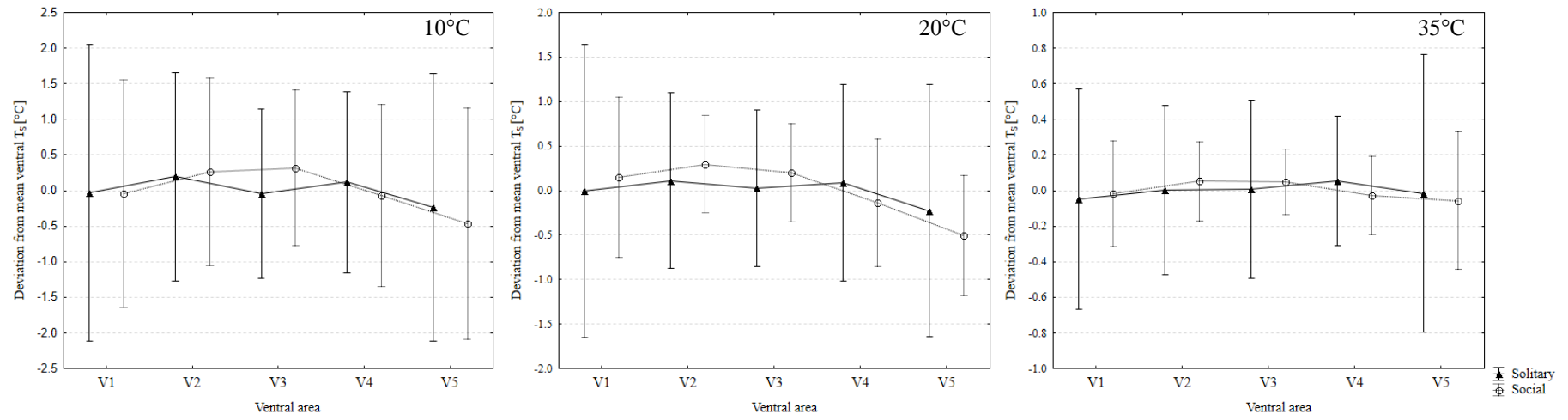


Figure 18: Deviation from mean ventral T_S (mean \pm sd) for ventral areas in furred studied species with different social system in T_A 10°C, 20°C, and 35°C.

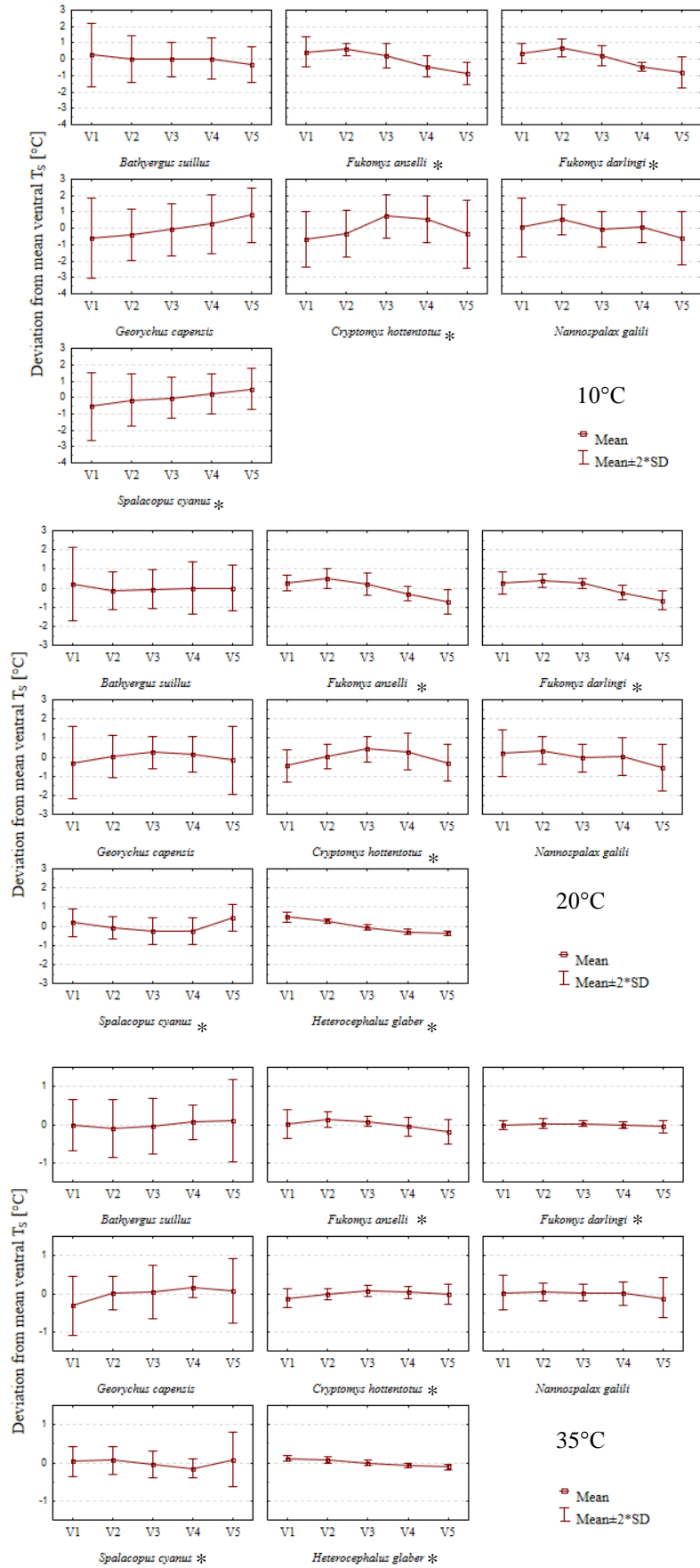


Figure 19: Deviation from mean ventral T_S for ventral areas in all studied species in T_A 10°C, 20°C, and 35°C. Social species are marked with asterisk.

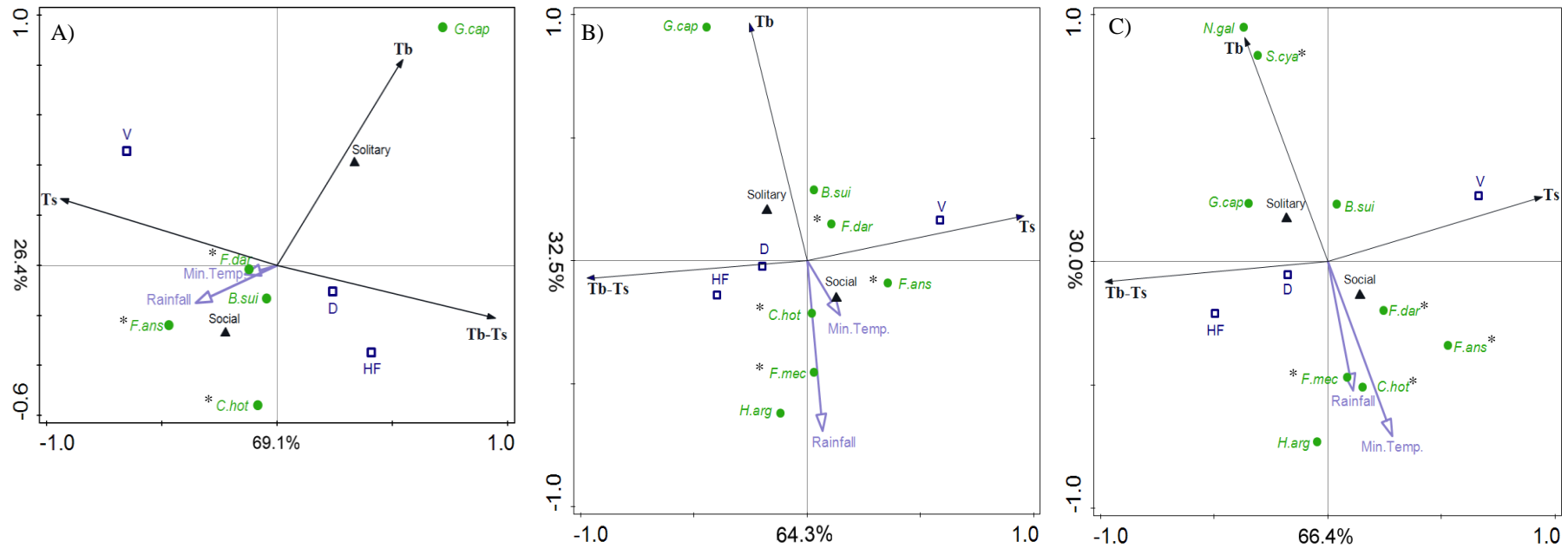


Figure 20: PCA visualisation of surface temperature (Ts), body core temperature (Tb), and their difference (Tb-Ts) (depicted as black arrows) of all studied furred species (green dots; A) mole-rats used in this study, B) *A* with *H. argenteocinereus* and *F. mechowii* from Šumbera et al. 2007 added, C) *B* with studied non-bathyergids added) in 10°C . Social species are marked with asterisks. Factors social system (black triangles) and body region (blue squares - Ventre, Dorsum and Hind Feet) are illustrated as well. All factors are passively projected, as well as two climatic variables (azure arrows). The eigenvalues of the first two axes are written in.

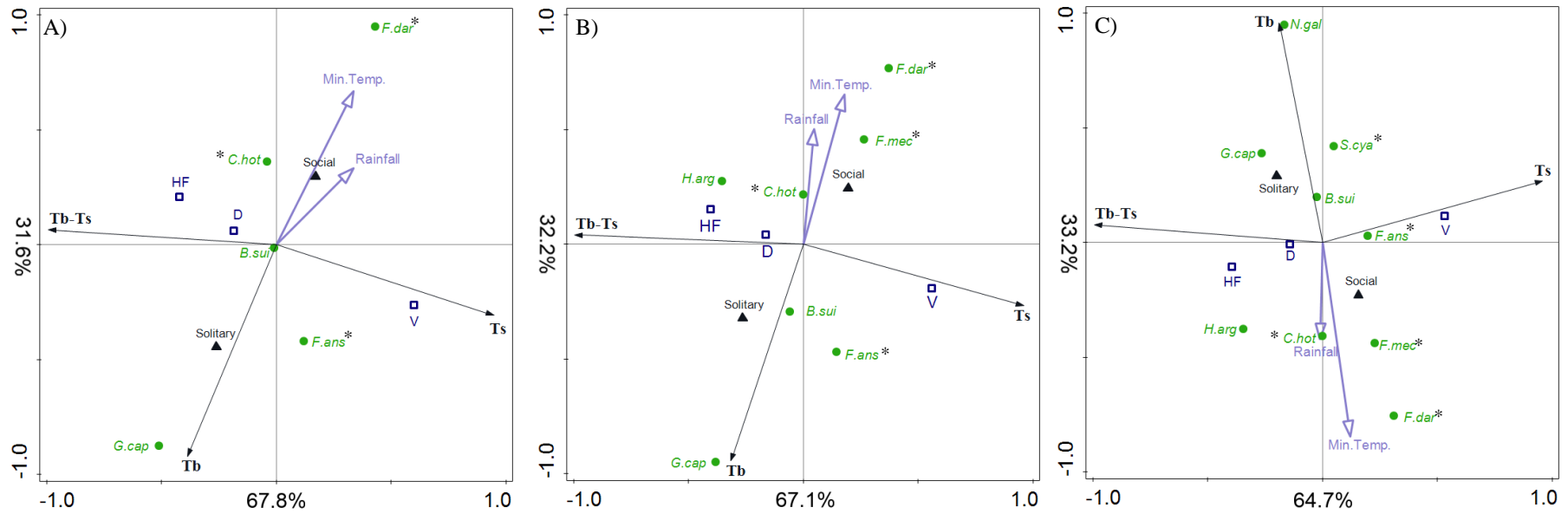


Figure 21: PCA visualisation of surface temperature (Ts), body core temperature (Tb), and their difference (Tb-Ts) (depicted as black arrows) of all studied furred species (green dots; A) mole-rats used in this study, B) A with *H. argenteocinereus* and *F. mechowii* from Šumbera et al. 2007 added, C) B with studied non-bathyergids added) in 20°C. Social species are marked with asterisks. Factors social system (black triangles) and body region (blue squares - Ventre, Dorsum and Hind Feet) are illustrated as well. All factors are passively projected, as well as two climatic variables (azure arrows). The eigenvalues of the first two axes are written in.

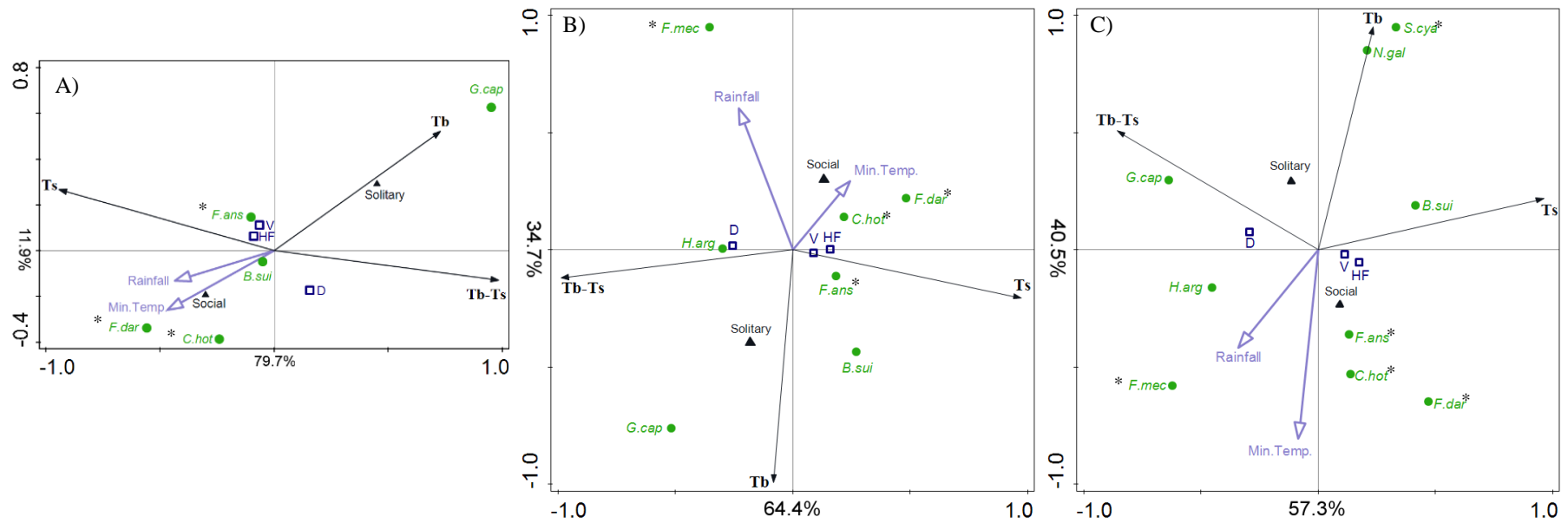


Figure 22: PCA visualisation of surface temperature (Ts), body core temperature (Tb), and their difference (Tb-Ts) (depicted as black arrows) of all studied furred species (green dots; A) mole-rats used in this study, B) A with *H. argenteocinereus* and *F. mechowii* from Šumbera et al. 2007 added, C) B with studied non-bathyergids added) in 30°C. Social species are marked with asterisks. Factors social system (black triangles) and body region (blue squares - Ventre, Dorsum and Hind Feet) are illustrated as well. All factors are passively projected, as well as two climatic variables (azure arrows). The eigenvalues of the first two axes are written in.

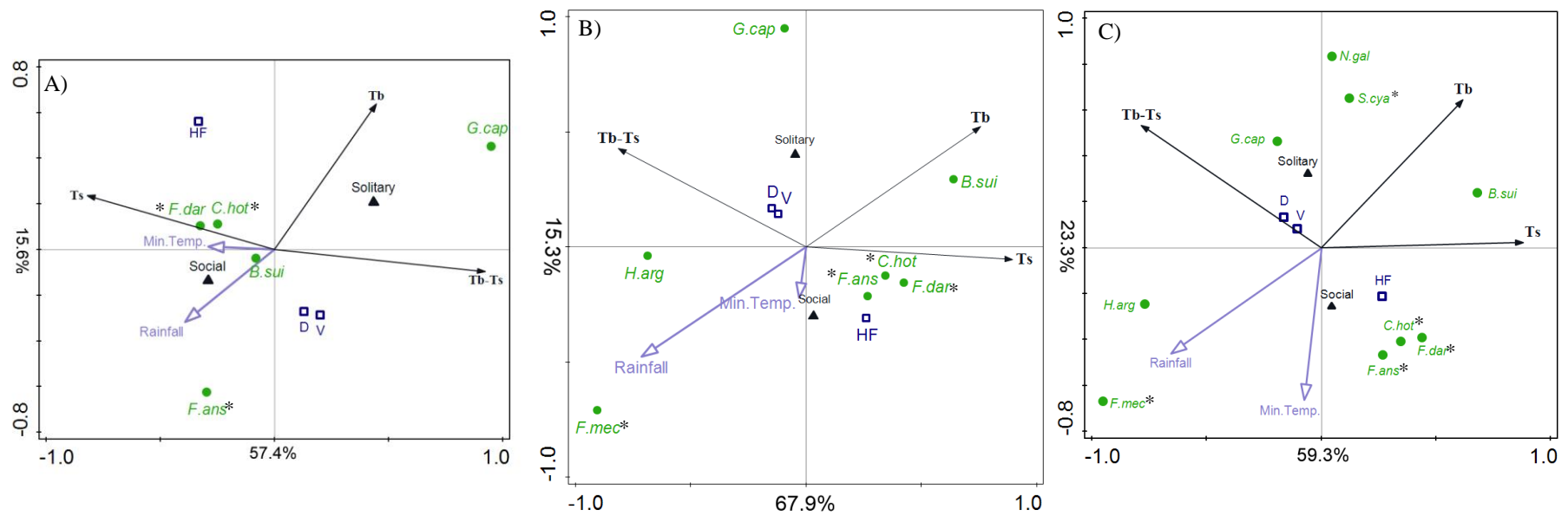


Figure 23: PCA visualisation of surface temperature (Ts), body core temperature (Tb), and their difference (Tb-Ts) (depicted as black arrows) of all studied furred species (green dots; A) mole-rats used in this study, B) A with *H. argenteocinereus* and *F. mechowii* from Šumbera et al. 2007 added, C) B with studied non-bathyergids added) in 35°C. Social species are marked with asterisks. Factors social system (black triangles) and body region (blue squares - Ventre, Dorsum and Hind Feet) are illustrated as well. All factors are passively projected, as well as two climatic variables (azure arrows). The eigenvalues of the first two axes are written in.

6.3. Thermographic observation

Body regions with the highest surface temperature are eyes and ears, followed by feet (in high T_A). Furthermore, the inner sides of thighs and upperarms show similar surface temperature, as the ventral region of the animals. The same feature can be seen on figures of Šumbera et al. (2007) on the giant mole-rat and the silvery mole-rat.

On the ventral region of the Upper Galilee Mountains blind mole rat, several of distinctive characteristics were found. In some individuals of both sexes, larger naked parts can be found round their *umbilici*. Additionally, colder spots (better fur insulation) are apparent on both sides of their genital region and in front axillary regions (fig. 24). Regarding the circum-genitalia region, the same feature can be seen in the common mole-rat and the Cape dune mole-rat.

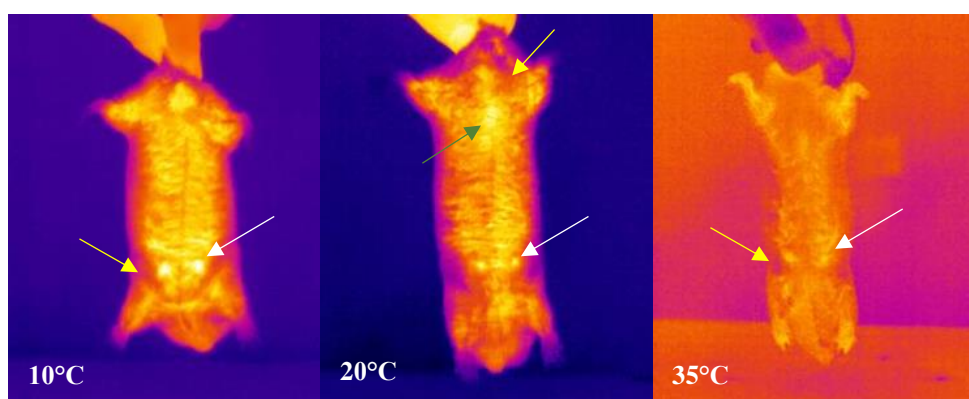


Figure 24: Thermograms of three *N. galili* females in T_A 10°C, 20°C, and 35°C. Two spots with lower fur insulation visible in the area V2 of the ventre (white arrows), as well as better furred spots (yellow arrows). Naked spot round *umbilicus* is marked with a green arrow.

There are two less insulated spots visible in the area V2 of all females. The same feature can be seen on thermograms (fig. 24). Every such spot contains a nipple. Since all of the animals were kept solitary in the laboratory, none of them had surely pups in last three years, and most of them probably never, so this represents the normal state of its appearance. The (super)species *Nannospalax ehrenbergi* is stated to have the mammary formula as following:

$$0 + 2 = 4$$

that is, all four nipples occurring only in the inguinal group (Norris 2017). However, my results demonstrate the presence of two nipples in pectoral group in the species *Nannospalax galili*, one of four species appertaining to the (super)species *N. ehrenbergi*. The species has up to four pups. Other *Nannospalax* (super)species (*leucodon* and *xanthodon*) possess one pair of pectoral, and two pairs of inguinal nipples (Norris 2017).

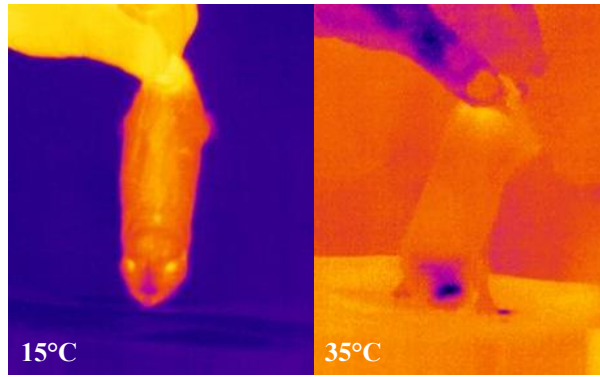


Figure 25: Changes in the nose surface temperature of *F. anselli* in 15°C and 35°C.

The Ansell's mole-rat possesses considerably lower temperature of its nose's skin compared to the rest of its body. Moving from high T_A to lower, the cooler surface seems to continuously lessen in its upper part (more posterior; between the eyes), i.e. changes to the triangular shape (fig. 25).

Similarly, the naked mole-rat has different nose temperature compared to the rest of its body. The higher T_A , the larger part of its face shows lower surface temperature (up to nearly whole head in 40°C) (fig. 26).

In all the T_A , the coruro show conspicuous stripes with notably high T_s running from its eyes to ears (fig. 27). The fur is obviously shorter in these stripes of facial area. The coruro is the only fossorial species used in this study.

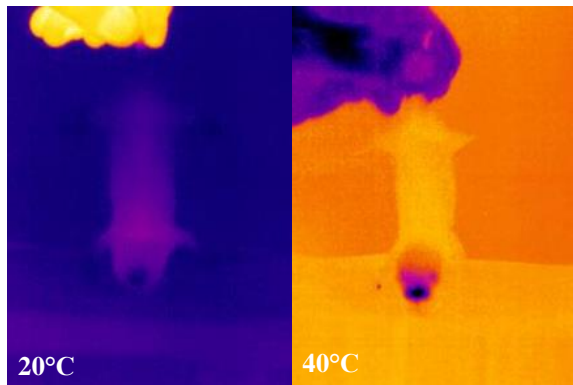


Figure 26: *H. glaber* in its extreme studied ambient temperatures. Note the cool nose surroundings in high T_A .

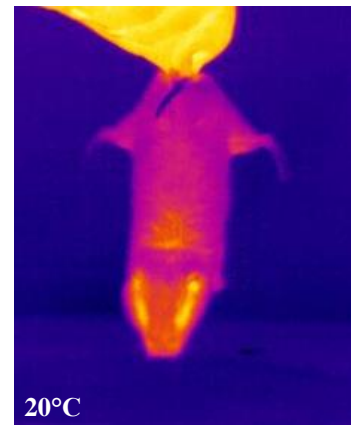


Figure 27: *S. cyanus* with notably warm stripes on its face.

Some individuals of the naked mole-rats possessed very similar (sometimes the same) surface temperature as the T_A was (fig. 26). Higher temperatures occurred in dorsal area D1.

6.4. Behavioural observation

In the course of the experiment, noticeable behavioural features were observed in the studied species (Table 17 and following figures, non-identical scales) .

Table 17: Behaviour noticed in the studied rodents under different ambient temperatures.

Species	Ambient temperature [°C]							
	10	15	20	25	30	33	35	40
<i>Bathyergus suillus</i>	C	C					E	
<i>Georchus capensis</i>	C E R	C					E V	
<i>Cryptomys hottentotus h.</i>	C	C					C E	
<i>Fukomys darlingi</i>	E S	C O R S	C		F	D	D V	
<i>Fukomys anelli</i>	E S	C O R	E		E		B	
<i>Heterocephalus glaber</i>			C S					D
<i>Spalacopus cyanus</i>		R		R	F		E D F V	
<i>Nannospalax galili</i>	C R	C S			C D		B V	

C = curled / hunched (fig. 28)

D = lying on dorsum (fig. 31)

O = often scratching

B = buried under wood shavings

F = lying on side (fig. 30)

R = ruffled fur (fig. 28; 29)

E = exposed bucket bottom (fig. 30; 32)

V = lying on ventre (fig. 32)

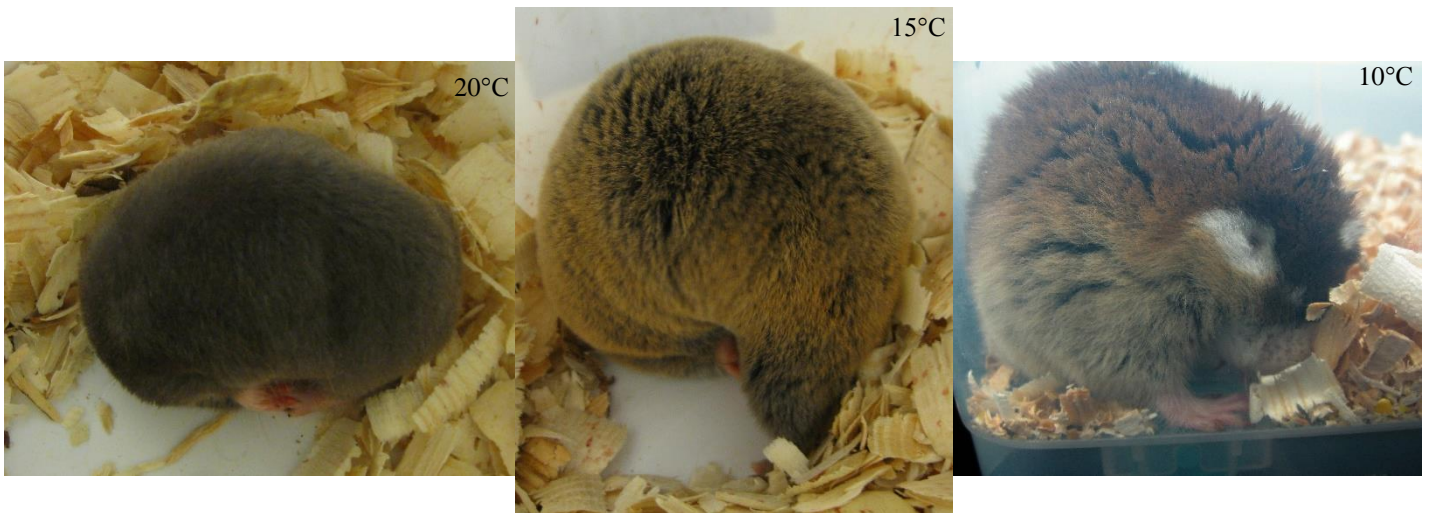


Figure 28: *F. darlingi*, *N. galili* and *G. capensis* curled / hunched with ruffled fur and front feet hidden.



Figure 29: *S. cyanus* with ruffled fur.

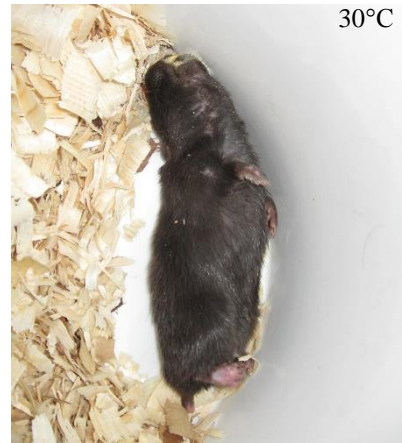


Figure 30: *S. cyanus* lying on its side on the exposed bucket bottom.

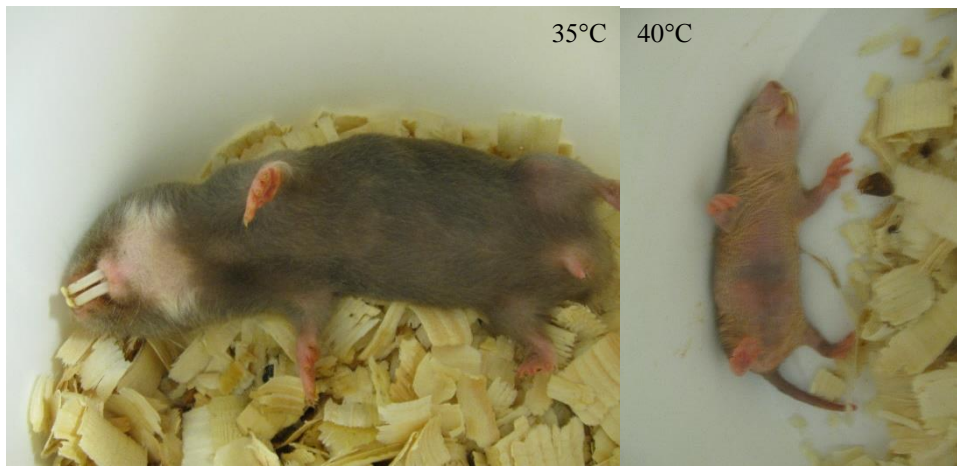


Figure 31: *F. darlingi* and *H. glaber* lying on dorsum.

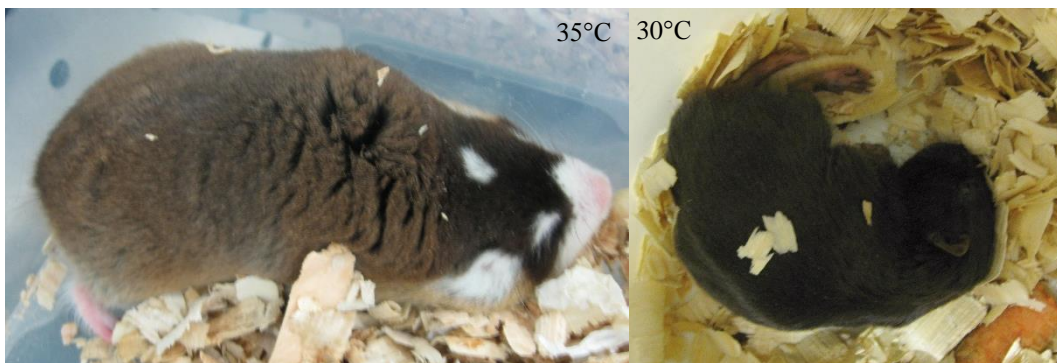


Figure 32: *G. capensis* and *S. cyanus* adpressing their ventral region to the bucket bottom.

The majority of the studied animals hunched, or even curled in a ball under low temperatures. The front feet were hidden, so that they were not in contact with the floor. Some individuals leaned against the ground with their heads (fig. 28).

The blind mole rats and the coruros adressed their ventral regions to carrot pieces (fig. 33).

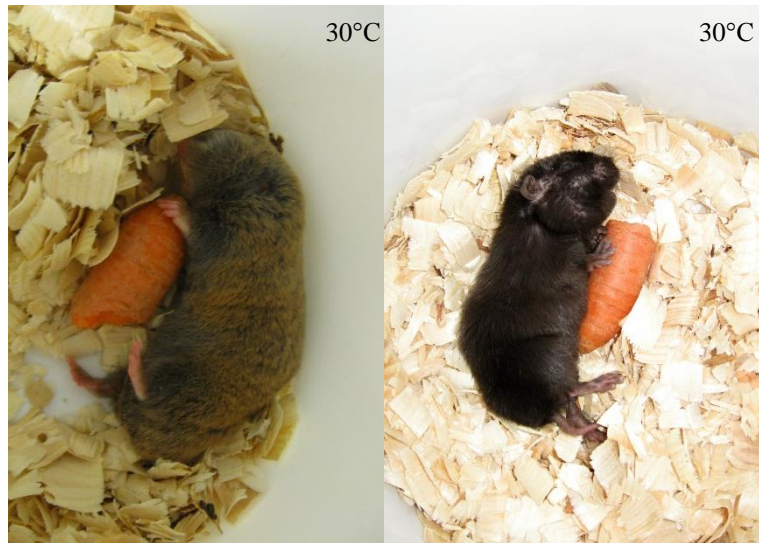


Figure 33: *N. galili* and *S. cyanus* nestling up to a carrot in high T_A .

6.5. Anecdotal notes

Cold thumbs of hind feet were found in one individual of the Mashona mole-rat and one naked mole-rat in high temperatures.

Of all the tested species, the coruros were the calmest in all the T_A . As for the mole-rats, the least active were the Ansell's mole-rats. In the genus *Fukomys*, frequent scratching was observed in 15°C. During the measurements of the surface temperatures, the blind mole rats opened their mouths in the direction of the IR camera.