University of South Bohemia in České Budějovice
Faculty of Science
Department of Zoology

Ph.D. Thesis

Energetics of African mole-rats (Bathyergidae) from mesic tropics

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Annotation:

This Ph.D. thesis focuses on energetics of two bathyergid species from mesic Afrotropics, the solitary silvery mole-rat (*Heliophobius argenteocinereus*) and social giant mole-rat (*Fukomys mechowii*). Particularly, burrowing energetics and thermoregulatory abilities are presented and disscused in relation to the contrasting social organization of both species. Additionally, new data on resting and field metabolism in *H. argenteocinereus* are presented. These new findings are discussed in further detail and expand upon existing explanations for low resting metabolism in subterranean rodents and the differences in field metabolism in relation to seasonality of habitat. To test the hypothesis of mass independent metabolism in bathyergids, regression analysis was performed on all available published data relating to resting metabolism, including our data on *H. argenteocinereus.*

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Declaration of author:

I hereby declare that I worked out this Ph.D. thesis on my own, or in collaboration with the co-authors of the presented papers and manuscript, and only using the cited literature.

I declare that in accordance with the Czech legal code § 47b law no. 111/1998 in its valid version, I consent to the publication of my Ph.D. thesis (in an edition made by removing marked parts archived by the Faculty of Science) in an electronic way in the public access to the STAG database run by the University of South Bohemia in České Budějovice on its web pages.

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Co-authors agreements:

Jitka Zelová, the author of this Ph.D. thesis, is the first author of three papers (manuscripts). Major part of all laboratory measurements, fieldwork as well as analyses was performed by her. Jan Okrouhlík performed major part of isotope analyses and calculations. Manuscripts were prepared by the first author with the help of co-authors. She also participated in data collection and measurements as well as writing relevant part of the Paper 4. Contribution of other people is given in Acknowledgements.

All co-authors hereby consent to the publication of the papers in the Ph.D. thesis of Jitka Zelová and support it by their signatures:

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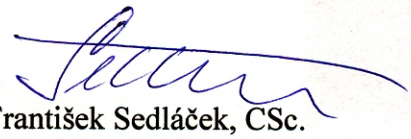

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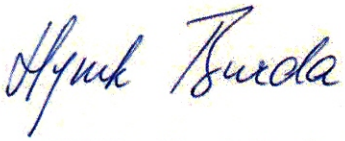

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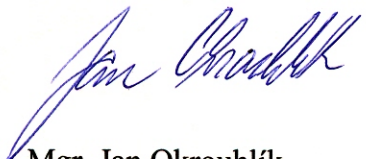

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Contents

Paper 1

ENERGETICS IN A SOLITARY SUBTERRANEAN RODENT, THE SILVERY MOLE-RAT, *HELIOPHOBIUS ARGENTEOCINEREUS*, AND ALLOMETRY OF RMR IN AFRICAN MOLE-RATS (BATHYERGIDAE)

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Energetics in a solitary subterranean rodent, the silvery mole-rat, *Heliophobius argenteocinereus*, and allometry of RMR in African mole-rats (Bathyergidae)

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Abstract

Low resting metabolic rate (RMR) in subterranean rodents used to be considered as a physiological adaptation to cope with stresses of the belowground environment. In African mole-rats (Bathyergidae, Rodentia), RMR was reported to be independent of body mass. This deviation from a general mammalian pattern was considered a precondition for evolution of eusociality, occurring in some bathyergids. We measured metabolic rate and thermoregulation in the silvery mole-rat, *Heliophobius argenteocinereus*, the only bathyergid genus for which well-supported, comparable data were still missing. Low RMR (154.04 mL O_2 h^{-1}, which is 82% of the value predicted for a rodent) corresponds to the value expected in a subterranean rodent. Broad range of the thermoneutral zone (25–33 °C) and only slightly higher conductance (17.3 mL O_2 h^{-1} $°C^{-1}$, i.e. 112.5% of that predicted for subterranean mammals) indicate that *H. argenteocinereus* is adapted to lower burrow temperatures rather than to high temperatures. Low RMR in this solitary species, as in other subterranean rodents in general, is probably associated particularly with high energetic cost of foraging. Our results combined with data on other mole-rats show clearly that RMR within the Bathyergidae is mass-dependent.

Keywords: Allometry; Bathyergidae; *Heliophobius*; Resting metabolism; Thermoregulation

Abstrakt

Nízká úroveň klidového metabolismu (RMR) u podzemních hlodavců je považována za fyziologickou adaptaci na to, jak se vypořádat se stresovými faktory podzemního prostředí. U afrických rypošů (Bathyergidae, Hlodavci) bylo zjištěno, že RMR je na hmotnosti nezávislý. A tato mezi savci výjimečná vlastnost se stala předpokladem pro vznik eusociality, která se vyskytuje u některých druhů rypošů. Měřili jsme úroveň metabolismu a termoregulace u rypoše stříbřitého (*Heliophobius argenteocinereus*), zástupce jediného rodu rypošovitých, pro který relevantní údaje doposud chyběly. Nízká úroveň RMR (154.04 ml O_2 h^{-1}, což odpovídá 82% předpokládané hodnoty pro hlodavce) je srovnatelná s očekávanou hodnotou pro podzemní hlodavce. Široký rozsah termoneutrální zóny (25-33 °C) a jen nepatrně vyšší hodnota konduktance (17.3 ml O_2 h^{-1} ° C^{-1}, tj. 112.5% predikované hodnoty pro podzemní savce) nasvědčuje tomu, že *H. argenteocinereus* je spíš adaptován na nižší teploty podzemních nor než na teploty vyšší. Nízká úroveň RMR tohoto solitérního druhu, stejně jako u ostatních podzemních hlodavců, je zřejmě důsledkem vysokých energetických nákladů na hledání potravy v podzemí. Naše výsledky společně s hodnotami pro ostatní rypoše jasně prokazují, že RMR u čeledi Bathyergidae je na hmotnosti závislý.

Paper 2

A SEASONAL DIFFERENCE OF DAILY ENERGY EXPENDITURE IN A FREE-LIVING SUBTERRANEAN RODENT, THE SILVERY MOLE-RAT (*HELIOPHOBIUS ARGENTEOCINEREUS*; BATHYERGIDAE)

Zelová J., Šumbera R., Okrouhlík J., Šklíba J., Lövy M. & Burda H.

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A seasonal difference of daily energy expenditure in a free-living subterranean rodent, the silvery mole-rat (*Heliophobius argenteocinereus*; Bathyergidae)

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ABSTRACT

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

Keywords: doubly labelled water method, daily energy expenditure, *Heliophobius*, resting metabolic rate, seasonality, subterranean rodent

ABSTRAKT

V sezónních oblastech jsou zvířata vystavena pravidelným změnám podmínek prostředí. Dá se tedy předpokládat, že tyto změny budou příčinou změn v jejich celkovém energetickém metabolismu. Vztah mezi denním energetickým výdejem (DEE) a sezónně se měnícími podmínkami prostředí byl studován u mnoha volně žijících malých savců, avšak s rozporuplnými výsledky. Podzemní savci žijí v teplotně stálém prostředí a reprezentují tak vhodný model pro studium změn v DEE s ohledem na sezónní změny v tvrdosti půdy a dostupnosti potravy. Oba tyto faktory jsou pod přímým vlivem srážek a předpokládá se, že zásadním způsobem determinují aktivitu podzemních savců. Vliv srážek je zásadní především v některých tropických oblastech, kde se pravidelně střídají období sucha a dešťů. Abychom zjistili, jak takový savec reaguje na náhlé změny podmínek v tropech, měřili jsme DEE, klidový metabolismus (RMR) a energetický výdej za aktivitu (SusMS) u solitérního podzemního hlodavce, rypoše stříbřitého. Zaměřili jsme se na konec období sucha a na začátek období dešťů. Zatímco, hodnoty RMR se mezi oběma obdobími nelišily, hodnoty DEE a SusMS byly u rypošů 1.4 krát vyšší po prvních dešťových srážkách. Toto zjištění nás přesvědčuje o tom, že srážky jsou důležitým ekologickým faktorem zodpovědným za vyšší energetický výdej u rypošů, pravděpodobně z důvodu zvýšené aktivity.

Klíčová slova: metoda dvojitě značené vody, denní energetický výdej, *Heliophobius*, klidový metabolismus, sezonalita, podzemní hlodavec

Paper 3

COST OF DIGGING IS DETERMINED BY INTRINSIC FACTORS RATHER THAN BY SUBSTRATE QUALITY IN TWO SUBTERRANEAN RODENT SPECIES

Zelová J., Šumbera R., Okrouhlík J. & Burda H.

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Cost of digging is determined by intrinsic factors rather than by substrate quality in two subterranean rodent species

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ABSTRACT

Searching for food by extensive digging is one of the most important aspects of life of subterranean rodents. We studied the effect of extrinsic (substrate quality) and intrinsic factors (sex and body mass) upon the cost of burrowing, expressed as digging metabolic rate (DMR) in two African mole-rat species (Bathyergidae, Rodentia) with distinct social structures. The sexually dimorphic giant mole-rat (*Fukomys mechowii*) is a highly social species, whereas the almost monomorphic silvery mole-rat (*Heliophobius argenteocinereus*) is a solitary bathyergid. Burrowing in *F. mechowii* was more costly (DMR was greater) than in *H. argenteocinereus*, but there was no difference in burrowing speed between both species. DMR within a particular species was dependent upon body mass, but independent of sex. Different substrate quality had no effect upon DMR in either species, yet it affected burrowing speed. We conclude that less effective digging in *F. mechowii* can be compensated by the joint workforce of other family members. Alternatively, *H. argenteocinereus*, being a more effective digger, can afford a solitary way of life.

Abstrakt

Hrabání nových chodeb za účelem získání potravy je jedním z nejdůležitějších aspektů života podzemních hlodavců. Studovali jsme vliv vnějších (kvalita substrátu) a vnitřních (pohlaví a hmotnost) faktorů na energetické náklady spojené s hloubením nových tunelů, vyjádřené jako pracovní metabolismus (DMR), u dvou afrických druhů rypošů (Bathyergidae, Rodentia) s rozdílným sociálním systémem. Pohlavně dimorfní rypoš obří (*Fukomys mechowii*) je vysoce sociální, zatímco téměř monomorfní rypoš stříbřitý (*Heliophobius argenteocinereus*) je solitérní. U sociálního *F. mechowii* bylo hrabání energeticky náročnější (DMR bylo vyšší) než u solitérního *H. argenteocinereus* a to bez rozdílu v rychlosti hrabání. DMR v rámci daného druhu byl závislý na hmotnosti těla, ale nezávislý na pohlaví. Rozdílná kvalita substrátu neměla žádný vliv na DMR ani u jednoho druhu. Rozdíl mezi substráty byl především v rychlosti hrabání. Domníváme se, že méně výkonné hrabání sociálního *F. mechowii* může být kompenzováno kooperativním hrabáním a aktivitou ostatních členů kolonie. Jinými slovy, *H. argenteocinereus* si zřejmě díky efektivnějšímu způsobu „tunelování“ může dovolit solitérní způsob života.

Paper 4

PATTERNS OF SURFACE TEMPERATURES IN TWO MOLE-RATS (BATHYERGIDAE) WITH DIFFERENT SOCIAL SYSTEMS AS REVEALED BY IR-THERMOGRAPHY

Šumbera R., Zelová J., Kunc P., Knížková I. & Burda H.

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PHYSIOLOGY & BEHAVIOR

Patterns of surface temperatures in two mole-rats (Bathyergidae) with different social systems as revealed by IR-thermography

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Abstract

Furred subterranean mammals face the problem of dissipating heat to the environment because high humidity and absence of air flow in sealed belowground tunnels constrain heat loss from body by convection and evaporation. In order to detect body areas responsible for heat loss, surface temperatures in two species of African mole-rats were measured at different ambient air temperatures by infrared thermography. Fur characteristics were also evaluated. Thinner pelage of the ventrum, its moderate temperature and large size suggest that ventral side of the body is the main thermal avenue for heat loss in both species. Interspecific differences could be explained by different fur characteristics connected with social thermoregulation. Compared to the social *Fukomys mechowii*, the solitary *Heliophobius argenteocinereus* has denser and longer fur on most of its body; its surface temperature was thus lower than in *F. mechowii* at lowered ambient temperatures. On the other hand, the denser and longer hair cover in *H. argenteocinereus* impedes heat dissipation at highest ambient temperatures (and probably also during digging activity) resulting in increase of core body temperature. *H. argenteocinereus* seems to be more sensitive to overheating than *F. mechowii*. At lower air temperatures, the social species may uses huddling to combat hypothermia.

Keywords: Surface temperature; *Fukomys mechowii*; *Heliophobius*; Bathyergidae; Subterranean rodent; Sociality; Heat dissipation, Thermoregulation; IR-thermography; Fur; Insulation

Abstrakt

Osrstění podzemní savci čelí problému, jak efektivně odvádět teplo z těla do prostředí, protože vysoká vzdušná vlhkost a absence proudění vzduchu v uzavřených podzemních tunelech znemožňuje zbavit se přebytečného tepla konvekcí a evaporací. Abychom identifikovali tělní okrsky, přes které by mohla probíhat výměna tepla, měřili jsme povrchovou teplotu různých částí těla dvou druhů afrických rypošů infračervenou kamerou v gradientu okolních. Zároveň byla měřena délka a hustota osrstění. Řidší osrstění ventrální části těla, její mírnější teplota a větší rozměr ukazuje, že především ventrální část těla je zodpovědná za tepelnou výměnu u obou druhů. Solitérní *Heliophobius argenteocinereus* má, při porovnání se sociálním *Fukomys mechowii*, hustější a delší srst na většině těla, a proto byla jeho povrchová teplota nižší při nižších teplotách okolí. Na druhou stranu, hustší a delší srst u *H. argenteocinereus* brání disipaci tepla při vyšších teplotách (a pravděpodobně také během hrabání) a tak dochází k přehřívání. *H. argenteocinereus* se zdá být více citlivý na přehřátí než je tomu u *F. mechowii*. Nižším okolním teplotám může sociální druh čelit sociální termoregulací.

Conclusion

This thesis presents and discusses data on energetics and the thermoregulatory abilities of strictly subterranean rodents, the African mole-rats (Bathyergidae) from mesic Afrotropics. Our results have important implications towards understanding bathyergids ecophysiology and behavioral ecology.

The following is a list of our major findings:

A detailed study on the physiological parameters in *H. argenteocinereus* shows that this species follows the trend of low RMR and body temperature found in subterranean rodents. Low RMR is probably associated with high cost of burrowing and low habitat productivity. Slightly higher thermal conductance indicates that this species is adapted to lower burrow temperatures. Meta-analysis of our results, combined with data on other mole-rats, shows clearly that metabolism within Bathyergidae is mass-dependent.

Investigation of overal energy demands found seasonal differences in energy expenditure within free-living individuals with significantly higher values after rain compared to the end of dry season. We can only speculate that the higher energy demands are due to enhanced digging activity after rain, when soil becomes softer and more workable; or mole-rats reduce energy expenditure in the drought and wait for more favorable conditions.

Quantification of digging energetics revealed that different substrate quality (hardness and moisture content) has no effect on digging expenditure in two mole-rat species. However, burrowing in damp softer substrate was significantly faster for both species. In addition, data show that social *F. mechowii* pays a higher energy cost per unit of burrowed distance than solitary *H. argenteocinereus*, suggesting the solitary species is a more efficient digger than the social species.

Finally, surface temperature measurements by infrared thermography revealed that the ventral side of the body, which contains thinner, shorter fur, serves as the main conductive heat loss portal. Additionally interspecific differences in fur characteristics were found, which is likely the primary reason for differences in surface temperatures between species, suggesting a relation to each's distinct social lifestyle. For example, solitary *H. argenteocinereus* is dependent upon longer, denser fur in the cold, whereas social *F. mechowii* may use huddling in the nest to conserve heat and thus afford shorter, thinner fur.