FACULTY OF SCIENCE/UNIVERSITY OF SOUTH BOHEMIA
ČESKÉ BUDĚJOVICE
DEPARTMENT OF ZOOLOGY

Light perception in two mole-rat species, the silvery mole-rat (*Heliophobius argenteocinereus*) and the giant mole-rat (*Fukomys mechowii*)

Master thesis 2008

Bc.Ondřej Kott
Supervisor: Mgr.Radim Šumbera, PhD.

Kott O. (2008): Light perception in two mole-rat species, the silvery mole-rat
(*Heliophobius argenteocinereus*) and the giant mole-rat (*Fukomys mechowii*)
[MSc. thesis, in English] - pp.37, Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic

Annotation

Sight in subterranean mammals living in a dark ecotope has generally been assumed as not needed and therefore greatly diminished in its function. Recent neuroanatomical studies demonstrate unexpected preservation of the visual system of several African mole-rats (Bathyergidae, Rodentia). Only a few behavioural studies, testing visual abilities and discussing their adaptive significance in these rodents, have been published to date. A spontaneous preference to light stimuli of two mole-rat species, the silvery mole-rat (*Heliophobius argenteocinereus*) and the giant mole-rat (*Fukomys mechowii*), was tested in this study. Assessed results showed convincingly that both species are able to perceive light. The following experiments provided the first behavioural support to the perception of short-wavelengths in this intensively studied group of subterranean rodents.

Keywords: African mole-rats, sight, subterranean mammals, light perception, photoreceptors, retina

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Author: Bc.Ondřej Kott
Supervisor: Mgr.Radim Šumbera, PhD.

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This project was supported by grant SGA 2006/11 and (GACR) 206/04/P116

Acknowledgements:

My thanks belong to my supervisor Mgr.Radim Šumbera, PhD. and all who cooperated on this project, mainly to RNDr. Jiří Adamec, RNDr. Aleš „Žaba“Tomčala a Mgr. Jiří Kubásek. We are grateful for SGA 11/2006 and (GACR) 206/04/P116 for financial support.

Content:

1. Introduction

Sensory perception plays a crucial role in spatial and temporal orientation, foraging and communication with conspecifics. Like their surface dwelling counterparts, subterranean animals must find and recognize a mate, kin, intruders and danger. The subterranean environment restricts communicative signals and it is also deprived of most spatial and temporal orientation cues available aboveground. Since burrowing is energetically demanding, it is expected that energetically costly sensory organs and brain centres, which are useless underground, should regress (Nevo 1999, Burda 2003).

For a long time, sight in subterranean mammals has generally been assumed as completely reduced. However, recent neuroanatomical studies reporting a remarkable variability in visual systems cast doubt on the general expectation of sight uselessness in subterranean mammals (reviewed recently in Němec *et al*. 2007). Only a very few behavioural studies examined visual capacity/abilities in these animals (Rado *et al*. 1992, Werner *et al*. 2005, Wegner *et al*. 2006). This study provides results of a behavioural analysis of a light perception in two species of African mole-rats (Bathyergidae, Rodentia), the silvery mole-rat (*Heliophobius argenteocinereus*) and the giant mole-rat (*Fukomys mechowii*).

1.1. Sight

If we trace back through the fossil record, it appears that vision originated in the early Cambrian, some 530 million years ago (Land 2002). Based on paleontological evidence eyes are thought to have evolved independently in different organisms at least 40 times and possibly as many as 65 times (Salvini-Plawen and Mayr 1977). Despite the incredible diversity among extant eyes, the laws of physics constrain how light can be collected resulting in only eight known optical systems in animal eyes (Fernald 2004). All eye types share the same molecular strategy of absorbing photons. Across many species there is a notable continuity of the developmental genes that participate in the construction of similar - but not necessarily homologous - eyes (Fernald 2000). Seeing is important for most species and it has probably been a key selective advantage throughout the animal evolution. In some species, vision is the dominant sense while it is less important in others.

1.2. Eye structures and sight in mammals

1.2.1. Retina and photoreceptors

The retina is a structure involved in signal transduction. The projections from the retina to the brain are organized in parallel pathways, and the fibres of the tract terminate in five major subcortical visual centres called the suprachiasmatic nucleus (SCN), the lateral geniculate complex (LG), the pretectum, the superior colliculus (SC), and the accessory optic system (AOS) (Fig. 1). These areas receive input from different types of retinal ganglion cells (the output cells of the retina) and hence are provided with different types of visual information (Dusenbery 1992). Mammals possess a duplex retina containing rods and cones. These photoreceptors are the first step of visual processing, translating the light signal into neural signal. The rods are photoreceptors for low-light vision and the cone are photoreceptors for daylight and color vision. Rod and cone pathways are strictly separated in the outer retina; rods connect to rod bipolar cells and cones to cone bipolar cells. In the inner retina, cone bipolar cells form synapses with ganglion cells. Rod bipolar cells do not directly contact ganglion cells but feed into the cone bipolar cells via the specialized AII amacrine cell in the inner retina (Wässle 2004, Fig. 2). Rod-cone ratios differ considerably across mammals, roughly depending on their daily activity pattern. Only a few diurnal species are known to have more cones than rods. The strictly diurnal tree shrew (*Tupaia belangeri*) is exceptional in having about 95 % cones and only about 5 % rods (Müller & Peichl 1989). Nocturnal species have between 0,5 % and 3% cones among their photoreceptors, crepuscular and arrythmic species have between 2% and 10 % cones, and diurnal mammals have a wide range of cone proportions from 8% - 95% (for review see Anhelt & Kolb 2000, Peichl 2005).

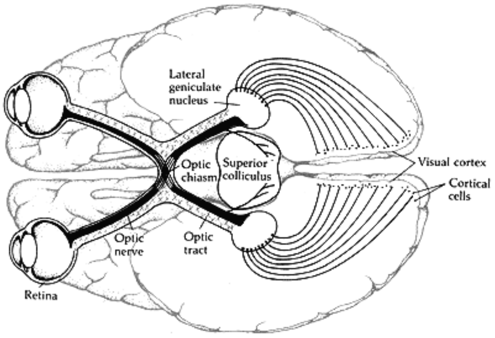

Fig. 1. Brain visual system architecture in mammals.
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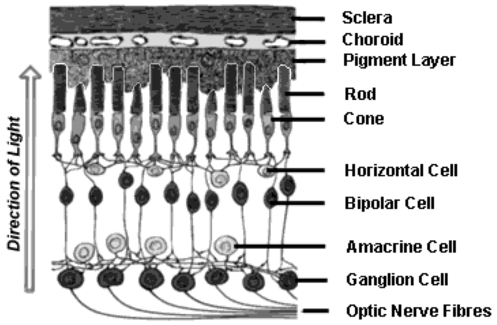

Fig. 2. Retina architecture in mammals.
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1.2.2. Cone types and color vision in mammals

Most nonprimate mammals possess dichromatic color vision based on two cone types with spectrally different visual pigments: a short-wavelength-sensitive (S-)cone and a long-wavelength-sensitive (L-)cone. Vertebrates possess one type of rhodopsin (visual pigment) located in the rods and four various opsin types located in four various cone spectral types. Four groups of vertebrate cone opsins are named according to their rough spectral sensitivity maxima: SWS1 (short-wavelength-sensitive 1, near UV and violet), SWS2 (short-wavelength-sensitive 2, violet and blue), RH2 (middle-wavelength-sensitive, green) a LWS (long-wavelength-sensitive, yellow and red). Rods contain opsin RH1, which is closely related to cone opsin RH2, indicating that the rod evolved out of a cone-like photoreceptor. Mammals have lost RH2 and SWS2 opsins and they possess only LWS and SWS1. Therefore, the most prevalent system of color vision in mammals is known as dichromacy (see Dusenbery 1992, Yokoyama 2000, Fernald 2000, 2004, Jacobs and Rowe 2004). This may hold true only for eutherian mammals. The presence of three cone types (SWS, MWS, LWS), and hence the potential for trichromatic color vision have been demonstrated in four marsupial species (Arrese *et al*. 2002, 2005a,b). Efficient trichromatic color vision re-evolved only in Old World primates and man by a duplication of the LWS opsin gene (reviewed in Jacobs 1993).

1.2.3. Exceptions to the general pattern in mammals

Cone monochromacy, the possession of one cone type only, and, thus the absence of cone-based color vision, is rare among mammals. For example, some of terrestrial mammals have lost (S-)opsin expression and possess only (L-)cones. The absence of (S-)cones has previously been reported in a few nocturnal mammals, for example, in the family Procyonidae. The nocturnal racoons *Procyon lotor*, *Procyon cancrivorus*, and the nocturnal kinkajou (*Potos flavus*) completely lack (S-)cones and posses only (L-)cones (Jacobs & Deegan 1992). This is also the case for nocturnal primate species, such as the owl monkey (*Aotus trivirgatus*) and the greater bushbaby (*Galago garnetti*) (Wikler & Rakic 1990) and two species of African giant rats (*Cricetomys gambianus, C. emini*) (Peichl & Moutairou 1998). However, the absence of (S-)cones is not exclusively associated with nocturnality. It was also reported in two species of earless seals (*Phoca hispida, P. vitulina*) with diurnal and nocturnal activity (Peichl & Moutairou 1998). The same kind of deficit seems to be the rule among marine mammals. The pinnipeds and the cetaceans have lost their (S-)cones and became (L-)cones monochromats in the evolutionary process of adapting to marine environment (Griebel &

Peichl 2003, Peichl 2005). It has been suggested that blue cones were lost in the early ´coastal´ period of cetacean and pinniped evolution since many coastal waters preferentially absorb blue light and constitute a long-wavelength-dominated environment. On the other hand, other aquatic and semi aquatic mammals have retained two spectral cone types ((S-)cones and (L-)cones). In semi aquatic species terrestrial activities probably had some impact on keeping cone dichromacy. This was also reported for the fully aquatic manatee (*Trichechus manatus*) (Anhelt & Kolb 2000) or semi aquatic pygmy hippotamus (*Choreopsis liberiensis*) (Peichl *et al*. 2001). Modern mammals lost their ability to see ultraviolet in the course of evolution contrary to birds and lower vertebrates (Land 2002). However, in a few mammalian species we can find (S-)cones with maximal sensitivity in the near UV (around 360 nm). This spectral sensitivity shift possess, for example, different degus (*Octodon degus, O. bridgesi, O. lunatus*) (Chavéz *et al*. 2003), or cururo (*Spalacopus cyanus*) (Peichl *et al*. 2005). In these species it is used as an adaptation to visual demands during certain phases of surface activity. Fresh cururo and degu urine has a high UV reflectance, suggesting that scent marks may be visible to the UV-sensitive cones and could serve in a territorial behavior and spatial orientation (Chavéz *et al*. 2003, Peichl *et al*. 2005). On the other hand, no clear ecological value of UV sensitive cones was found in rat (*Rattus norvegicus*) having primarily a nocturnal activity (Jacobs *et al*. 2001). The same mechanism, but with a different morphological basis, evolved in the nectar feeding flower bat *Glossophaga soricina* of Central and South America. These bats pollinate rainforest plants, having a strong reflection of UV-spectrum light at night. *Glossophaga* lost the functional cones and retained only the rods as photoreceptors catching UV-photons. In these mammals only a single photoreceptor is responsible for the perception of light radiation over the whole wavelength spectrum, from about 310 nm to 600 nm (Winter *et al*. 2003).

1.3. Sight in subterranean mammals

1.3.1. An underground ecotope

The underground environment is generally characterized by predictable conditions with stable humidity and temperature, no light and air ventilation, and almost no predation (Nevo 1999, Lacey *et al*. 2000). On the other hand, subterranean mammals have to cope with low food productivity, high energetic costs of burrow building, and hypoxic (low O_2) and hypercapnic atmosphere (high CO_2). Hence, various morphological (external ear and tail reduction, shortened limbs or eye regression) and physiological adaptations (specific blood and tissue properties) evolved for life underground (Nevo 1999). The subterranean niche opened to mammals during the upper Eocene and then extended into the upper Tertiary and Quaternary when, in the course of global cooling and aridization, steppes, savannas, semi-deserts, and deserts expanded (Nevo 1999, Bennett & Faulkes 2000), and a high number of mammals (approximately 300 species) adapted to this unique habitat. Subterranean species have evolved independently among marsupials, insectivores, Afrotheria, and, most notably, rodents (Nevo 1999, Lacey *et al*. 2000).

1.3.2. Eye morphology and sight in Blind mole rat (Spalacidae, Rodentia)

Rodents are the most diverse mammalian order, therefore they are a suitable model group for the investigation of how the visual system adapts to various habitat conditions (Chavéz *et al*. 2003). Eurasian blind mole rat, superspecies *Spalax* (mainly *S. ehrenbergi*), has become a model species for studying regression, or rather adaptation, of the eye and retina in mammals in subterranean habitat. Blind mole rats possess the most rudimentary eyes (0.6 mm) of all mammals that have even regressed to a subcutaneous location. The number of ganglion cells and optic nerve fibers is low, indicating that little retinal information is transmitted to the brain. The retina is relatively normal but less organized than in sighted mammals. Rods are in dominance, cones are also present, but there is only one spectral type of cone visual pigment, the middle-to-long-wave-sensitive (L-)opsin, which is unusually red-shifted to 534 nm. This, and the lack of an (S-)opsin are interpreted as adaptations to the red-shifted spectrum of light reaching the *Spalax* eye after passing through the hemoglobin-rich skin (Bronchti *et al*. 1991, Cooper *et al*. 1993 a,b, Cooper *et al*. 1995, David-Gray *et al*. 1998, 2002, Janssen *et al*. 2000, Cernuda-cernuda *et al*. 2002). These studies also show that *Spalax* lacks all image-forming abilities. Various studies report that circadian activity of *Spalax* can be determined by light cycle changes under laboratory conditions (Rado *et al*. 1992, Ben-Shlomo *et al*. 1995, Goldman *et al*. 1997, Tobler *et al*. 1998). Circadian photopigment melanopsin, exprimed in the intrinsically photosensitive ganglion cells, is present and provides a major input to the central circadian pacemaker, the suprachiasmatic nucleus and the pretectum (Hanibal *et al*. 2002, Berson 2003). Discrimination between light and dark using a simple preference experiment was reported in the Blind mole rats (Rado *et al*. 1992). The authors of these studies proposed that regressed subcutaneous eye of *Spalax* may have been retained for photoperiodic perception. However, the adaptive value of a circadian clock in a constant darkness remains enigmatic.

1.3.3. Eye morphology and sight in the African mole-rats (Bathyergidae, Rodentia)

The African mole-rats are one of the most specialized groups of subterranean animals. Because of living in a monotonous dark environment, the African mole-rats were described as fully blind (Eloff 1951, 1958, Burda *et al*. 1990). However, recent morphological studies in three bathyergid species, *Fukomys anselli*, *F. Mechowii*, and *Heterocephalus glaber*, reported an unexpected conservation of the mole-rats visual apparatus (reviewed in Němec *et al*. 2007, 2008). The mole-rats possess microphthalmic eyes (2 mm diameter) superficially positioned and with normal ocular properties such as eyelids, clear cornea, lens, vitreous and iris with pupilary aperture (Cernuda-Cernuda *et al*. 2003, Peichl *et al*. 2004). Except for the naked mole-rat´s large lens, the lens size in other mole-rat species is surprisingly small in relation to their eye size (Nikitina *et al*. 2004, Peichl *et al*. 2004). This pattern is typical for diurnal mammals, in contrast to animals with nocturnal activity, which have larger lenses to collect light more effectively.

In three species of mole-rats, *F. mechowii*, *F. anselli*, and *H. glaber*, rod-dominated retina with unexpectedly high cone proportion (≈10 %, density 8000-15000/mm^2) was described. This cone/rod ratio in subterranean mammals is also more similar to diurnal than to nocturnal surface-dwellers. In *F. anselli* nearly all cones express the (S-)opsin in their outer segments. Many of these (S-)cones co-express small amounts of (L-)opsin, but there are only few pure (L-)cones expressing (L-)opsin exclusively. This (S-)opsin dominance and low levels of (L-)opsin were first described across the entire retina (Cernuda-Cernuda *et al*. 2003, Peichl *et al*. 2004). Another subterranean mammal, Chilean cururo (*Spalacopus cyanus*, Octodontidae), possesses the same proportion of cones among the photoreceptors as the mole-rats, but with higher density (10000-30000/mm^2). Here, majority of cones are pure (L-)cones, minority are pure (S-)cones, and no opsin co-expression occurs (Peichl *et al*. 2005). European mole (*Talpa europaea*) also possess approximately the same cone proportion, but there are two times more (L-)cones than (S-)cones in the dorsal retina and this ratio is reversed in the ventral retina (Glösmann *et al*. 1999).

The optic nerve is thin and macroscopically barely visible in bathyergids. The very low number of optic nerve fibers and hence retinal ganglion cells indicates poor visual resolution (Cernuda-Cernuda *et al*. 2003, Němec *et al*. 2004).

In the African mole-rats all subcortical visual centres are cytoarchitectually poorly developed and reduced in size, while degree of reduction differs between nuclei. The lateral geniculate complex and the pretectal nuclei are moderately reduced (Němec *et al*. 2004).

Nuclear expression of transcriptional regulatory protein (c-Fos) as a marker of cell activity was examined immunohistochemically in *F. anselli* (Oelschläger *et al*. 2000). The olivary pretectal nucleus, which in mammals is involved in light/dark discrimination, as well as, the dorsal lateral geniculate body as part of the image-forming visual system, were consistently labeled by c-Fos after light stimulation, indicating that vision in *Fukomys anselli* plays more significant role than previously assumed (Oelschläger *et al*. 2000). Another laboratory study reported c-Fos expresion in the suprachiasmatic nucleus which is synchronized according to the phase of the circadian clock in solitary *Georychus capensis* (Oosthuzien *et al*. 2005).

On the other hand, the accessory optic system, responsible for mediation of optokinetic response in reaction to a slow motion of large visual stimuli across the retina, is vestigial and incomplete in mole-rats (Němec *et al*. 2004, Crish *et al*. 2006). Also the superficial layers of superior colliculs, a brain structure involved in the detection of, and orientation toward objects in the peripheral visual field, allowing approach or avoidance decisions, are extremely reduced (Němec *et al*. 2004). These morphological findings indicate that visual signals cannot be effectively processed by the brain structures and thus used in a surface spatial orientation. In contrast, subsystems involved in a photoperiod perception, form and brightness discrimination are anatomically rather well developed, and, therefore, may still play an important role.

Besides neuroanatomical studies, light perception in animals can be also tested by simple behavioral experiments under laboratory conditions. Surprisingly, light perception ability in subterranean rodents, and in mole-rats particularly, has been rarely tested. The first study in the African mole-rats, i.e. intensively studied group of subterranean rodents, has not been published until quite recently. It was reported that the social Zambian mole-rats (*F. anselli*, *F. kafuensis* and their hybrids) are able to discriminate between light and dark boxes in a standard preference test (Wegner *et al*. 2006).

2. Goals of the study

Main goals of the study were:

a) To test if both studied bathyergids are able to discriminate between light and dark (Experiment 1).

b) In case of positive results, to test what parts of the light spectrum the mole-rats perceive and if they avoid the part of light corresponding with (S-)cones dominance in retina.
(Experiment 2).

c) To test if a light stimulus invokes a plugging behavior in mole-rats (Experiment 3).

3. Materials and methods

3.1. Study animals (Bathyergidae)

The African mole-rats are endemic rodents to Sub-Saharan Africa. Members of genera *Bathyergus, Georychus*, and *Heliophobius* are solitary, whereas other three genera *Heterocephalus, Fukomys* (this genus has recently been emancipated from genus *Cryptomys*, see Kock *et al*. 2006), and *Cryptomys* are highly social or even eusocial. They are food specialist on geophytes – plants with subterranean storage organs (Shermann *et al*.1991, Bennett & Faulkes 2000, Burda 2001).

The silvery mole-rat (*Heliophobius argenteocinereus*, Peters 1846) inhabiting Tanzania, Malawi, southern Kenya, southeast D.R. Congo, eastern Zambia, and northern Mozambique, has the largest distribution among bathyergids (Šumbera *et al*. 2007). It possesses long, dense hair of greyish color sometimes with a white head spot (Nowak 2001). Males weigh on the average 190 g, females around 162 g (Šumbera *et al*. 2003a). In general they live in mesic areas (> 900 mm annual rainfall) and in elevations of up to 2000 m a.s.l., but they can also be found in arid areas (for example in Kenya) (Šumbera *et al*. 2007). The silvery mole-rats live in various types of habitat, but mostly in hard soils of woodlands dominated by *Brachystegia* or *Combretum* trees (miombo woodland) (Šumbera *et al*. 2007). They build long, highly branched burrow systems, and they change its architecture seasonally (Šumbera *et al*. 2003b) and have low population densities (Šumbera *et al*. 2007).

The giant-mole rats (*Fukomys mechowii*, Peters 1881) live in northern Zambia, south D.R.Congo, and Angola. They also occur in habitats and soils with annual rainfall of around 1100 mm (Kawalika *et al*. 2007). They possess beige or light brown pelage. Males weigh 250-600g and females 200-355g (Scharff *et al*. 1999). They are highly social, probably eusocial, and they form groups of up to 40 members (Scharff *et al*. 2001). They construct large burrow systems with seasonal architectural changes (Sichilima *et al*. 2008 in press).

All the silvery mole-rats were caught in Malawi Mpalanganga estate, Zomba (15º 27´S, 35º 15´E), Zomba plateau (15º 20´S, 35º 16´E), and Mulanje-Chitakali (16º 02´S, 35º 30´E) in 2000 and 2005. Some of the giant-mole rats were caught in 1999 in Ndola, Zambia, and the rest of them came from our breeding stock.

3.2. Laboratory conditions

The study animals were maintained in a room with moderate temperature (25±1°C) and an artificial light regime 12L/12D in the Department of Zoology, University of South Bohemia. The silvery mole-rats were housed individually in Plexiglass mazes and the families of the giant mole-rats in terrariums filled with horticultural peat. The mole-rats were fed carrots, potatoes, lettuce, apples, and rodent-pellets.

Animals at least one year old were tested. Each mole-rat was tested once in each experiment. There was a break of at least one week between each trial. The social giant mole-rats were tested in pairs (or threesomes) to avoid social stress.

3.3. Experiment 1 (spontaneous preference in nest building - dark/light)

Fig. 3. Two-arm maze for spontaneous preferences testing

The maze was located in the experiment room next to the place the animals were housed in to avoid various types of disturbances. Spontaneous preference to build a nest was tested using a two-arm maze. The binary choice apparatus (Fig. 3), made from plastic (0.5 cm thickness), composed of a cylindrical centre (diameter 22 cm, height 35 cm), an inner cylinder (diameter 20 cm, height 30 cm, made from a metal plate providing opening and closing of the tunnels), two opposite tunnels (15 x 8 x 8 cm) with two boxes (20 x 20 x 20 cm), was used (sensu Wegner *et al*. 2006). The boxes could be covered with an opaque plastic lid or a translucent Plexiglass lid. Two fluorescent tubes (OSRAM L 58 W/31- 380) illuminated the nest boxes at a distance of 130 cm. In each trial one box was closed with the opaque lid, and the other one with the translucent lid. The cylindrical centre was closed with a round translucent lid. Light intensities on the bottom of the illuminated sites were measured by a data logger (Minikon QT, EMS, Czech Republic). They varied between 10 (the box) to 12 μmol photons/m^2 per s (the cylinder). The position of each lid was swapped after each trial and the whole apparatus was cleaned using ethanol.

Animals were placed into the closed cylindrical centre. Three pieces of carrot, pellets and a nesting material (8 strips 25 x 5 cm of filter paper) were provided. Then the inner cylinder was rotated and animals could explore the maze. We checked if nest construction was done after 60 minutes. If it had not been built after 60 minutes, we waited 30 minutes more to let the animals make the nest. A result was recorded when all nesting material was found in one box.

3.4. Experiment 2 (spontaneous preference in nest building - color preference)

The same apparatus as in Experiment 1 was used. It differed only in lids with a central opening (5 cm diameter) in which a special filter was inserted. Color filters (diameter 50 mm, thickness 5 mm, Chroma Technology Corp., Rockingham, USA) representing a specific parts of the light spectrum were used (Tab. 1, Fig. 5).

We used 40 W lamps to illuminate the boxes. The position of the lamp was set according to the type of filter in order to have light intensity of app. 5 μmol photons/m^2 per s in each box. Preferences for building of nests in boxes illuminated by different color of light were tested (Tab. 2). A glass dish (diameter 20 cm, height 3 cm) filled with cold water (6°C, 400 ml) was placed above each lid to absorb heat radiation from the lamps. Temperature in each box was measured after each trial using a probe thermometer (TESTO 425). No difference in temperature was found between boxes. The rest of the protocol was the same as in Experiment 1.

Table 1. Coloured filter types (Chroma Tech. Corp.).

COLOR	WAVE-LENGTH RANGE
BLUE	420-490 nm
GREEN	470-550 nm
GREEN+YELLOW	495-590 nm
RED	665-735 nm

Table 2. Filter combinations in Experiment 2.

TRIAL	WAVE-LENGTH RANGE
DARK/RED	0 nm/665-735 nm
DARK/BLUE	0 nm/420-490 nm
BLUE / RED	420-490 nm /665-735 nm
BLUE / GREEN	420-490 nm /470-550 nm
BLUE / GREEN+YELLOW	420-490 nm / 495-590 nm

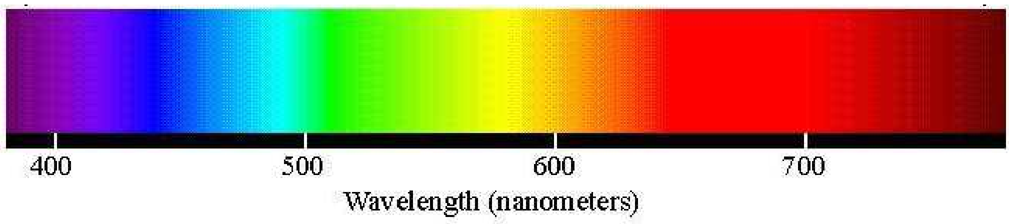

Fig. 4. Light color spectrum.
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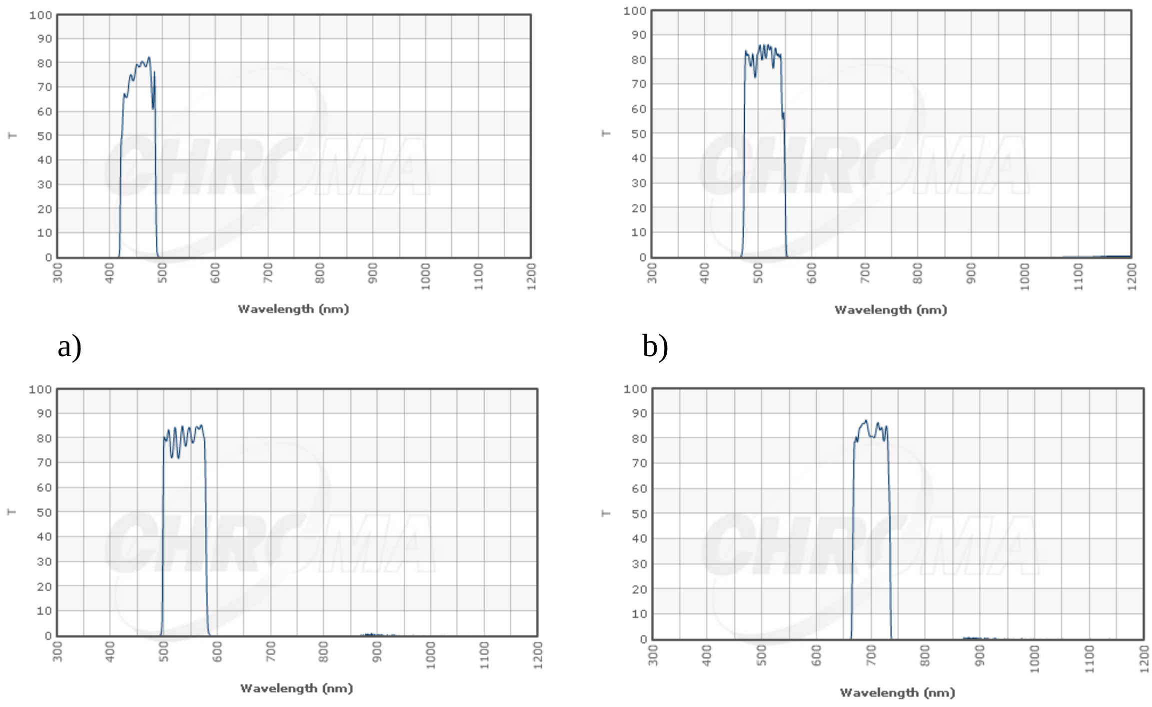

a)

b)

c)

d)

Fig. 5. Filter walength-range (Chroma Tech., Corp., Rockingham, USA); a) short-wavelength filter (420-490 nm), b) middle-wavelength filter (470-550 nm), c) middle-wavelength filter (495-590 nm), d) long-wavelength filter (665-735 nm).

3.5. Experiment 3 (light localization)

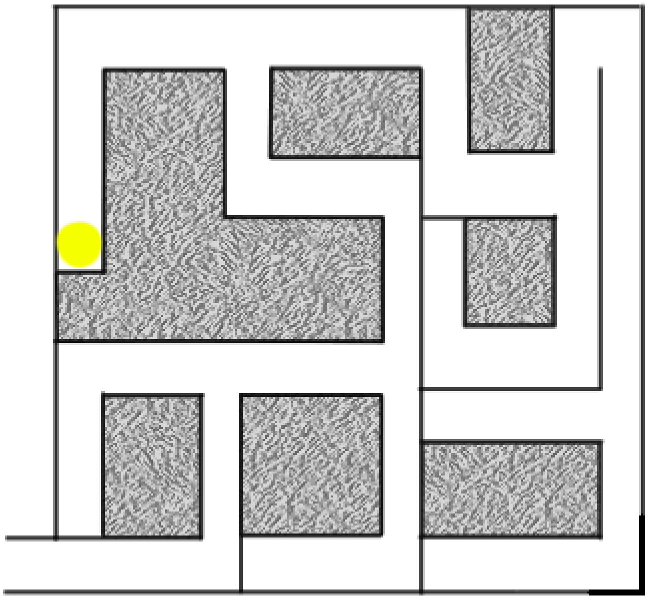

Fig. 6. Experimental maze – Experiment 3.

In this experiment, reaction of the mole-rats to light in a maze with peat was tested. We expected that the mole-rats would fill part of the maze exposed to light with soil. The opaque maze made of plastic material (110 x 100 x 10 cm, Fig. 6), simulating the burrow system, was used in this experiment. Before the experiment, the Plexiglass lid was covered by black color paper, where only one part of the tunnel was without paper. The animal was placed into the maze with horticultural peat and food. Then the maze was covered by the opaque lid. The translucent end of the tunnel was illuminated from a distance of 130 cm. The 40 W lamp was placed at the top of the tube (130 cm, diameter 12 cm) providing a centered cone of light (6 μmol photons/m^2 per s) reaching directly the bottom of the maze. A control temperature measurement on the bottom of the illuminated tunnel was done (a probe thermometer TESTO 425) before and after the experiment. The temperatures did not differ. Each animal (pair or threesome in case of the giant mole-rats) spent two hours in the maze.

4. Results

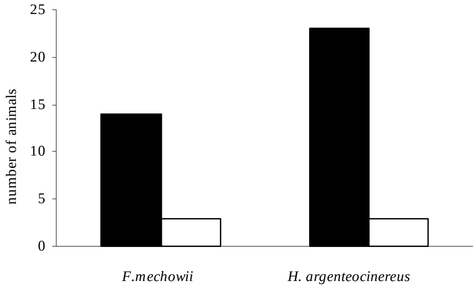

Fig. 7. Spontaneous preferences for building of nests between dark and illuminated box in two African mole-rats (black bar – dark box, white bar – illuminated box).

In Experiment 1 both bathyergids preferred the non-illuminated box for building of their nest; *F. mechowii* (χ^2 = 7.1, P = 0.007, *N* = 17; Fig. 7, Tab. 3); *H. argenteocinereus* (χ^2 = 15.38, P = 0.0008, *N* = 26; Fig. 7, Tab. 3).

In Experiment 2 (light color preference) no difference of spontaneous preference for building of nest between the dark box and the box illuminated by red light was found in both species; *F. mechowii* (χ^2 = 0.05, P = 0.80, *N* = 17; Fig. 8a, Tab. 4); *H. argenteocinereus* (χ^2 = 0.20, P = 0.65, *N* = 20; Fig. 8a, Tab. 4). On the contrary, both species preferred the non-illuminated box instead of the box illuminated by blue light for building of their nest; *F. mechowii* (χ^2 = 4.7, P = 0.029, *N* = 17; Fig. 8b, Tab. 5); *H. argenteocinereus* (χ^2 = 5.0, P = 0.025, *N* = 20; Fig. 8b, Tab. 5). Comparison of red light with blue light showed that both species preferred the box illuminated by red light instead of blue light for building of nests; *F. mechowii* (χ^2 = 4.0, P = 0.045, *N* = 16; Fig. 8c, Tab. 6); *H. argenteocinereus* (χ^2 = 11.63, P = 0.0006, *N* = 22; Fig. 8c, Tab. 6). No preference between blue and green light, was found in both species of mole-rats; *F. mechowii* (χ^2 = 0.28, P = 0.59, *N* = 14; Fig. 8d, Tab. 7); *H. argenteocinereus* (χ^2 = 0.25, P = 0.61, *N* = 16; Fig. 8d, Tab. 7). As in previous trial, no difference of spontaneus preference for building of nests between blue and green+yellow light, was found; *F. mechowii* (χ^2 = 0.69, P = 0.40, *N* = 13; Fig. 8e, Tab. 8); *H. argenteocinereus* (χ^2 = 0.25, P = 0.61, *N* = 16; Fig. 8e, Tab. 8).

In Experiment 3 both tested species localized the illuminated place and blocked it with soil; *F. mechowii* (χ^2 = 17.85, P = 0.000024, *N* = 15; Fig. 9, Tab. 9); *H. argenteocinereus* (χ^2= 20.44, P = 0.000006, *N* = 20; Fig. 9, Tab. 9).

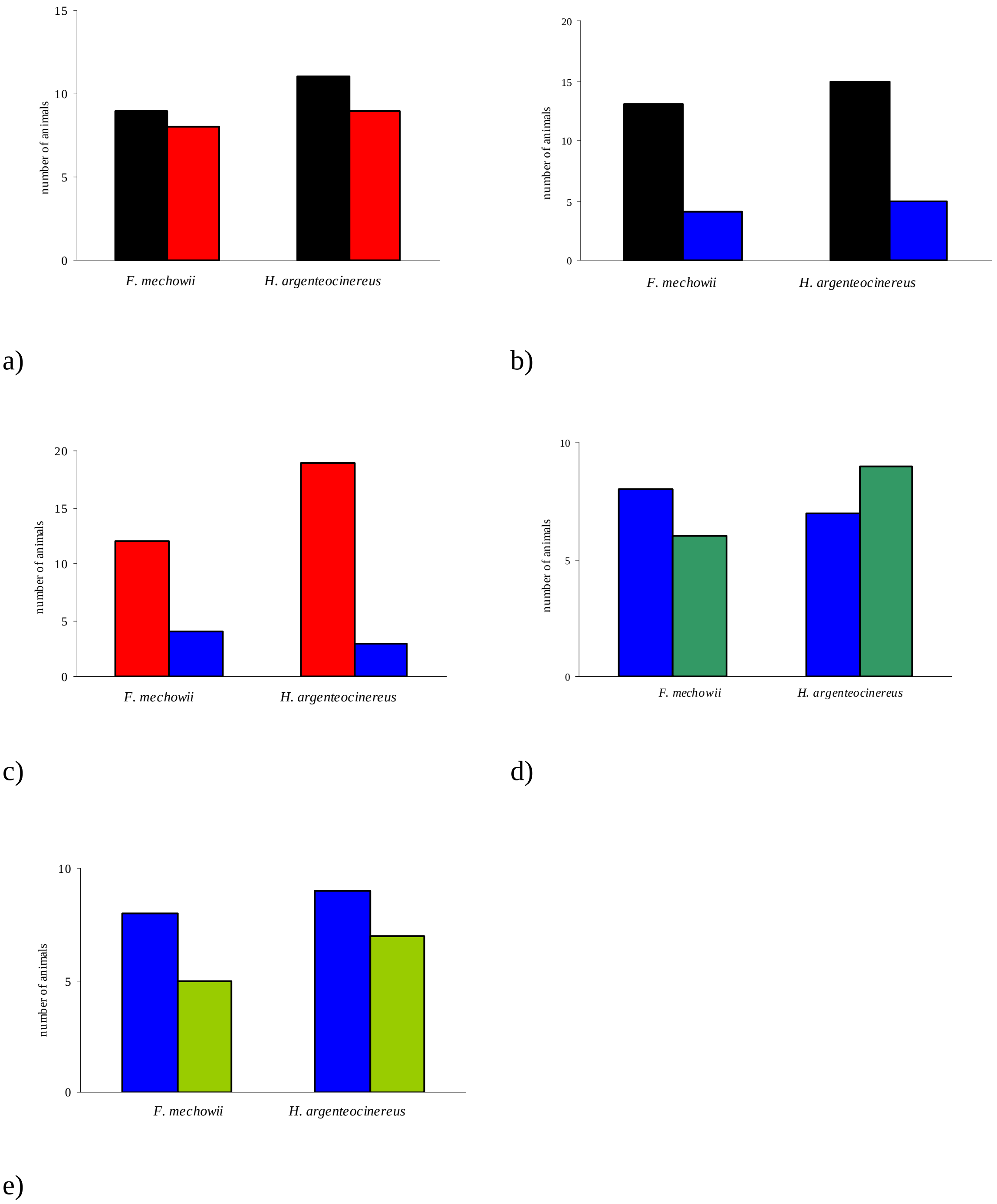

Fig. 8. Results of color preference test: a) dark vs. red (red bar – box illuminated by red light, black bar – dark box), b) dark vs. blue (blue bar – box illuminated by blue light, black bar – dark box), c) red light vs. blue (red bar – box illuminated by red light, blue bar – box illuminated by blue light), d) blue light vs. green (blue bar – box illuminated by blue light, green bar – box illuminated by green light), e) blue vs. green and yellow (blue bar – box illuminated by blue light, green-yellow bar – box illuminated by green and yellow light).

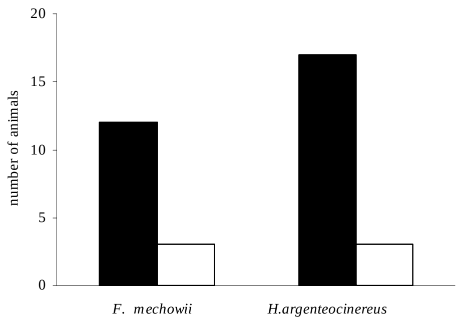

Fig. 9. Light localization in a dark maze (black bar – plug done, white bar – no plug).

5. Discussion

Tested African mole-rats species preferred the non-illuminated box for building their nests. This result suggests that both species, the silvery mole-rat (*Heliophobius argenteocinereus*) and the giant mole-rat (*Fukomys mechowii*), are able to perceive light similarly to bathyergids, as in the study carried out by Wegner *et al*. (2006). In addition, further experiments from my study indicate that these mole-rats perceive light at short and middle-wavelengths and they are probably not able to perceive long-wavelengths. Analysed results confirm expected visual abilities based on recent studies on the bathyergid eye morphology (see Introduction).

The African mole-rats possess (S-)cones dominance in their retinas which indicates perception of light mainly at short-wavelengths (Peichl *et al*. 2004). Our results showed that both mole-rats avoid blue light in experimental settings and prefer either red or dark, indicating perception of blue light. Since there is no preference for red light, when red light and dark were provided, suggests that the mole-rats probably do not discriminate red light from dark. This is highly probable, since there are only few (L-)cones in African mole-rat retina (Peichl *et al*. 2004). No differences could be observed in trials where the mole-rats could choose between short-wavelengths (blue light) and middle-wavelengths (green light, green and yellow light), suggesting the involvement of (S-)cones and rods, which probably have an absorbing maximum in middle-wavelengths (green light). A rod maximum peak sensitivity, about 500 nm, is known in other subterranean rodents, the cururo (*Spalacopus cyanus*) (Peichl *et al*. 2005) or the pocket gopher (*Thomomys bottae*) (Wiliams *et al*. 2005). In these trials, the mole-rats probably perceived light in both boxes, hence, no particular light was preferred. Interestingly, spectral sensitivity shift of (S-)cones to the UV segment of the light spectrum was described in several species of burrowing rodents (Chavéz *et al*. 2003, Peichl *et al*. 2005). I did not test UV perception in this study, so sensitivity to UV cannot be excluded. However, with regard to strictly underground life of these bathyergids, the similar ecological value cannot be expected (see Introduction).

There is still the unanswered question; why do the African mole-rats retain basic visual capabilities even after their long underground existence? The mole-rats spend most of their lives underground and they are hardly ever exposed to light (Burda *et al*. 1990, Nevo 1999). Some subterranean rodents, including several African mole-rats, use light as a zeitgeber (a circadian clock) of a circadian activity under laboratory conditions (Lovegrove *et al*. 1993, Lovegrove & Papenfus 1995, Riccio & Goldman 2000, Oosthuzien *et al*. 2003, Vasicek *et al*. 2005). Nevertheless, light entrainment of activity in free living, strictly subterranean rodents, is still an open question, especially in species which rarely emerges aboveground and with low rate of mound production (c. f. Šklíba *et al.* 2007). Some other factors such as burrow temperature can work as zeitgeber of circadian activity (Šklíba *et al.* 2007).

Another explanation could be related to the mole-rat surface activity. Mole-rat remains found in owl pellets are an indicator of surface activity of these animals (De Graf 1981, Kawalika 2002). Diverse items, such as rests of plastic bags, nylon stockings, green leaves, etc. were found in the nests of the giant mole-rats (*Fukomys mechowii*) which could also indicate surface activity (Kawalika 2002). Aboveground activity seems to be more frequent than expected minimally in some species (see Scharff & Grüjten 1997, Kawalika 2002). Except for some one way activities such as natal dispersal or flooding of burrow systems, mole-rat surface activity could be more regular as suggested by the separation and isolation of burrow systems and paternity analysis in *Heliophobius* – at least during the breeding season (Šumbera *et al.* 2007, Patzenhauerová unpubl. data). However, based on neuroanatomical findings (see Introduction Němec *et al.* 2004, Crish *et al.* 2006) it seems to be unlikely that they could effectively entrain vision during surface activity.

Only recently Wegner *et al.* (2006) suggested that adaptive meaning of vision in mole-rats could be related to an antipredatory behavior. Vision could play a role of a detector of light when a tunnel is damaged (by predators or incidentally by the activity of large herbivores, rain, etc.). It could warn the animal not to approach the opening too closely (Wegner *et al.* 2006). Many subterranean rodents, including the African mole-rats, react to damage of their tunnels by blocking that part with soil. This behavior is also used for trapping of subterranean rodents (see Šklíba *et al.* in press). However, it is not clear what is the cue eliciting this behavior. Beside light, the influence of some other factors such as sound from outside of the system or increased ventilation could be relevant. The results of Experiment 3 showed that both species easily localized the illuminated place and blocked it with soil. It clearly showed that blocking is a behavioral reaction connected with the presence of light, which was the only one cue provided, since the whole maze was tightly covered with a lid. The illumination of tunnels eliciting a plugging behavior in pocket gophers (*Thomomys talpoides* and *T. mazama*) under laboratory conditions was also described (Werner *et al.* 2005).

An enigma still remains why the retinas of mole-rats possess (S-)cone dominance and why they are able to perceive light at short-wavelengths. It could be concluded that the (S-)opsin dominance in bathyergids is associated with their superficial eyes which are, contrary to *Spalax*, directly reached by spectrally unfiltered light (David-Gray *et al*. 1998). This is also supported by European mole (*Talpa europaea*) which also possess superficially positioned eyes. However, a mole has an abundant proportion of (L-)cones, while the bathyergids do not. It seems life underground is associated with different cone arrangements and opsin expression patterns. More detailed information about species-specific frequencies of light exposure and light related behavior patterns will be required to formulate useful hypotheses (c.f. Peichl *et al*. 2004). For example, twilight has a higher level of short-wave components than daylight or moonlight (McFarnald & Munz 1975). Here, specific light composition could serve as a stimulus for aboveground activity when needed.

New retino (photoreceptor properties, exact spectral tuning of cone opsins, etc.) and neurophysiological (brain capacity) studies in other species of bathyergids are needed. At the same time, more detailed research focused on biology of mole-rats (mainly dispersal and antipredatory behavior) in natural habitats, and related behavioral experiments (movement analysis, light and color discrimination, etc.) under controlled laboratory conditions could shed light on the adaptive value of sight in mole-rats and subterranean mammals in general.

6. Conclusions

Based on acquired results, I can conclude that both mole-rat species studied are able to perceive light and use it as a stimulus to make a decision. Our behavioral data confirm new morphological findings and confirm the perception of blue light in these animals.

7. Appendix

Table 3. The binary choice experiment results (LIGHT/DARK);
HA = *Heliophobius argenteocinereus*, FM = *Fukomys mechowii*, 1 = nest built,
0 = no nest, NO = no nest built at all

MOLE - RAT	SEX	LIGHT	DARK
HA 9585	F	1	0
HA 1805	F	0	1
HA 0142	F	0	1
HA 5649	F	0	1
HA 1520	F	0	1
HA 7818	F	0	1
HA 8495	F	0	1
HA 8255	F	0	1
HA 9678	F	0	1
HA 5515	F	0	1
HA 5514	F	0	1
HA 1335	F	0	1
HA 7699	F	0	1
HA 1496	F	0	1
HA 1436	M	0	1
HA 1460	M	0	1
HA 6406	M	1	0
HA 1361	M	0	1
HA 0816	M	0	1
HA 1361	M	0	1
HA 6506	M	0	1
HA 6045	M	0	1
HA 1503	M	0	1
HA 0953	M	0	1
HA 2791	M	NO	NO
HA 0154	M	1	0
HA 0312	M	0	1
TOTAL 27	**14F/13 M**	**3**	**23**
FM F85D/A959	F/M	0	1
FM F31C8/7E14	F/M	0	1
FM FD2A/DDDC	F/M	1	0
FM 3322/05BD	F/M	0	1
FM B25E/25EO	F/M	0	1
FM 0D85/E28E	F/M	0	1
FM ABX1/F284/EF50	F	0	1
FM 5882/08B5	F/M	0	1
FM FC11/DC2A	F/M	0	1
FM B2XC/13D2	F	0	1
FM 0394/FC57	F/M	0	1
FM D7EB/3164	F/M	0	1
FM 0949/1634	F/M	0	1
FM 6048/4329	F/M	0	1
FM 339F/3094	F	0	1
FM 603F/2351	F	1	0
FM 33D6/9012	F	1	0
TOTAL 35	**23F/12M**	**3**	**14**

Table 4. The binary choice experiment results (DARK/RED);
HA = *Heliophobius argenteocinereus,* FM = *Fukomys mechowii*, 1 = nest built,
0 = no nest, TBOX1= temperature in the box 1., TBOX2 = temperature in the box 2.

MOLE - RAT	**SEX**	**DARK**	**RED 665-735 nm**	**TBOX1 °C**	**TBOX2 °C**
HA 9585	F	0	1	26.4	26.7
HA 1805	F	1	0	26.0	25.6
HA 0142	F	0	1	26.9	26.8
HA 5649	F	1	0	26.4	26.9
HA 7818	F	1	0	25.8	26.3
HA 8495	F	1	0	26.3	26.5
HA 9678	F	0	1	26.5	26.7
HA 5514	F	0	1	26.8	26.5
HA 1335	F	0	1	26.7	26.1
HA 7699	F	0	1	25.9	26.4
HA 1436	M	0	1	26.6	26.3
HA 1460	M	1	0	26.7	26.2
HA 6406	M	1	0	26.6	26.1
HA 1361	M	0	1	26.2	26.3
HA 8221	M	1	0	26.5	26.2
HA 6045	M	1	0	26.1	26.3
HA 1503	M	1	0	26.8	26.5
HA 0953	M	1	0	26.2	26.8
HA 0154	M	1	0	25.9	26.5
HA 0312	M	0	1	26.0	26.4
TOTAL 20	**10F/10M**	**11**	**9**	**----**	**----**
FM F85D/A959	F/M	0	1	26.2	26.6
FM 2522/2BX6	M	1	0	25.9	26.3
FM 31C8/7E14	F/M	0	1	25.7	26.0
FM FD2A/DDDC	F/M	1	0	26.4	26.2
FM 3322/05BD	F/M	0	1	26.7	26.3
FM B25E/25EO	F/M	1	0	25.7	25.9
FM 0D85/E28E	M	1	0	26.5	29.7
FM F4C1/F284	F/M	0	1	26.3	26.1
FM 5882/08B5	F/M	1	0	26.7	26.8
FM FC11/DC2A	F/M	0	1	26.3	25.8
FM B2XC/13D2	F	1	0	26.0	25.9
FM 0394/33D6	F	1	0	26.7	26.5
FM 6048/4329	F/M	0	1	26.2	26.1
FM 339F/2351	F	0	1	26.8	26.4
FM 603F/9012	F	0	1	26.3	26.7
FM D7EB/3164	F/M	1	0	25.9	26.5
FM 0949/1634	F/M	1	0	26.2	26.7
TOTAL 34	**19F/15M**	**9**	**8**	**----**	**----**

Table 5. The binary choice experiment results (DARK/BLUE);
HA = *Heliophobius argenteocinereus*, FM = *Fukomys mechowii*, 1 = nets built, 0 = no nest, NO = no nest built at all, TBOX1= temperature in the box 1., TBOX2 = temperature in the box 2.

MOLE - RAT	**SEX**	**DARK**	**BLUE 420-490 nm**	**TBOX1 °C**	**TBOX2 °C**
HA 9585	F	1	0	25.9	25.8
HA 1805	F	1	0	26.2	26.5
HA 0142	F	1	0	26.6	26.7
HA 5649	F	1	0	26.4	26.9
HA 7818	F	0	1	26.4	26.3
HA 9678	F	1	0	26.7	26.5
HA 5514	F	0	1	25.8	26.0
HA 8495	F	1	0	26.2	26.5
HA 1335	F	0	1	26.5	26.8
HA 7699	F	1	0	26.5	26.2
HA 1436	M	1	0	26.1	26.1
HA 1460	M	1	0	26.8	26.5
HA 6406	M	1	0	26.2	26.8
HA 1361	M	1	0	26.4	26.5
HA 8221	M	1	0	25.8	26.3
HA 6045	M	0	1	26.1	26.0
HA 1503	M	1	0	26.8	26.6
HA 0953	M	1	0	26.4	26.9
HA 0154	M	1	0	26.0	25.7
HA 0312	M	0	1	26.8	26.3
TOTAL 20	**10F/10M**	**15**	**5**	**----**	**----**
FM F85D/A959	F/M	0	1	26.4	26.1
FM 2522/2BX6	M	1	0	26.7	26.5
FM 31C8/7E14	F/M	1	0	25.9	26.2
FM FD2A/DDDC	F/M	1	0	26.6	26.6
FM 3322/05BD	F/M	0	1	26.4	26.8
FM B25E/25EO	F/M	1	0	26.6	26.7
FM 0D85/E28E	M	1	0	26.5	26.1
FM F4C1/F284	F/M	1	0	26.5	26.7
FM 5882/08B5	F/M	0	1	26.8	26.5
FM FC11/DC2A	F/M	1	0	26.7	26.9
FM B2XC/13D2	F	1	0	26.4	26.8
FM 0394/33D6	F	1	0	26.9	26.5
FM 6048/4329	F/M	1	0	26.2	26.5
FM 339F/2351	F	1	0	26.0	25.8
FM 603F/9012	F	0	1	26.1	26.3
FM D7EB/3164	F/M	1	0	26.8	26.5
FM 0949/1634	F/M	1	0	25.9	26.4
TOTAL 34	**19F/15M**	**13**	**4**	**----**	**----**

Table 6. The binary choice experiment results (BLUE/RED);
HA = *Heliophobius argenteocinereus*, FM = *Fukomys mechowii*, 1 = nets built, 0 = no nest, NO = no nest built at all, TBOX1 = temperature in the box 1., TBOX2 = temperature in the box 2.

MOLE - RAT	**SEX**	**BLUE 420 - 490 nm**	**RED 665 -735 nm**	**TBOX1 °C**	**TBOX2 °C**
HA 9585	F	0	1	28.9	29.3
HA 1805	F	NO	NO	-----	-----
HA 0142	F	NO	NO	-----	-----
HA 5649	F	0	1	29.1	28.9
HA 7818	F	0	1	29.3	29.3
HA 8495	F	0	1	28.7	28.9
HA 8255	F	0	1	28.6	28.4
HA 9678	F	0	1	29.0	29.3
HA 5515	F	0	1	28.2	28.2
HA 5514	F	0	1	29.0	28.7
HA 1335	F	1	0	28.3	28.6
HA 7699	F	0	1	28.8	28.9
HA 1496	F	0	1	29.1	29.0
HA 1436	M	0	1	29.2	29.5
HA 1460	M	0	1	29.1	29.2
HA 6406	M	0	1	29.3	29.1
HA 1361	M	0	1	29.2	29.6
HA 8221	M	0	1	28.8	29.0
HA 6045	M	0	1	29.0	29.1
HA 1503	M	0	1	28.9	28.6
HA 0953	M	1	0	28.1	28.4
HA 2791	M	0	1	28.1	28.7
HA 0154	M	1	0	28.4	28.5
HA 0312	M	0	1	29.3	29.0
TOTAL 24	**13F/11M**	**3**	**19**	**----**	**-----**
FM F85D/A959	F/M	1	0	26.6	26.2
FM 31C8/7E14	F/M	0	1	26.2	26.3
FM FD2A/DDDC	F/M	0	1	26.7	26.5
FM 3322/05BD	F/M	0	1	26.2	26.4
FM 325E/25EO	F/M	1	0	26.2	26.0
FM OD85/E28E	F/M	0	1	26.2	26.3
FM AB1X,F284,EF50	F/M	0	1	26.5	26.3
FM 5882/08B5	F	NO	NO	-----	-----
FM FC11/DC2A	F/M	0	1	26.8	26.5
FM B2XC/13D2	F/M	0	1	26.0	26.3
FM 0394/FC57	F	1	0	26.9	26.5
FM 07EB/3164	F	0	1	27.1	26.7
FM 0949/1634	F/M	0	1	26.5	26.8
FM 6084/4329	F	1	0	26.1	26.3
FM 339F/3094	F	0	1	26.4	26.2
FM 603F, 2351	F	0	1	26.6	26.7
FM 33D6,9012	F	0	1	27.0	26.8
TOTAL 35	**25F/10M**	**4**	**12**	**-----**	**-----**

Table 7. The binary choice experiment results (BLUE/GREEN);
HA = *Heliophobius argenteocinereus*, FM = *Fukomys mechowii*, 1 = nets built, 0 = no nest, NO = no nest built at all, TBOX1 = temperature in the box 1., TBOX2 = temperature in the box 2.

MOLE - RAT	**SEX**	**BLUE 420-490 nm**	**GREEN 470-550 nm**	**TBOX1 °C**	**TBOX2 °C**
HA 9585	F	NO	NO	----	----
HA 1805	F	0	1	26.6	26.9
HA 0142	F	0	1	25.7	25.6
HA 5649	F	NO	NO	----	----
HA 7818	F	NO	NO	----	----
HA 8495	F	1	0	26.7	26.5
HA 8255	F	0	1	26.2	26.3
HA 9678	F	1	0	26.5	26.7
HA 5515	F	1	0	26.1	26.0
HA 5514	F	NO	NO	----	----
HA 1335	F	0	1	26.4	26.7
HA 7699	F	1	0	26.4	26.1
HA 1436	M	NO	NO	----	----
HA 1460	M	1	0	26.5	26.5
HA 6406	M	NO	NO	----	----
HA 1361	M	0	1	26.8	29.9
HA 8221	M	0	1	26.5	26.7
HA 6045	M	0	1	26.3	26.4
HA 1503	M	NO	NO	----	----
HA 0953	M	1	0	26.3	26.5
HA 2791	M	0	1	26.6	26.3
HA 0154	M	1	0	26.5	26.5
HA 0312	M	0	1	26.6	26.4
TOTAL 23	**12F/11 M**	**7**	**9**	**----**	**----**
FM F85D/A959	F/M	1	0	25.8	25.9
FM 31C8/7E14	F/M	NO	NO	----	----
FM FD2A/DDDC	F/M	0	1	26.3	26.4
FM 3322/05BD	F/M	1	0	26.8	26.4
FM 325E/25EO	F/M	0	1	26.2	26.6
FM OD85/E28E	F/M	1	0	26.4	26.1
FM EF50, F284	F/M	0	1	26.7	26.5
FM 5882/08B5	F	1	0	25.9	26.3
FM FC11/DC2A	F/M	NO	NO	----	----
FM B2XC/13D2	F/M	NO	NO	----	----
FM 0394/FC57	F	0	1	26.7	27.0
FM 07EB/3164	F	1	0	26.5	26.5
FM 0949/1634	F/M	0	1	26.4	26.7
FM 6084/4329	F	1	0	25.8	26.4
FM 339F/3094	F	0	1	26.4	26.2
FM 603F, 2351	F	1	0	26.8	27.0
FM 33D6,9012	F	1	0	26.2	26.0
TOTAL 34	**24F/10M**	**8**	**6**	**-----**	**-----**

Table 8. The binary choice experiment results (BLUE/GREEN+YELLOW);
HA = *Heliophobius agrgenteocinereus*, FM = *Fukomys mechowii*, 1 = nest built, 0 = no nest, NO = no nest built at all, TBOX1= temperature in the box 1., TBOX2 = temperature in the box 2.

MOLE - RAT	**SEX**	**BLUE 420 - 490 nm**	**GREEN+YELLOW 495-590 nm**	**TBOX1 °C**	**TBOX2 °C**
HA 9585	F	1	0	26.2	26.3
HA 1805	F	0	1	26.4	26.2
HA 0142	F	0	1	26.4	26.7
HA 5649	F	NO	NO	----	-----
HA 7818	F	1	0	26.6	26.2
HA 8495	F	1	0	26.4	26.0
HA 8255	F	1	0	26.4	26.4
HA 9678	F	0	1	26.5	26.3
HA 5515	F	0	1	26.7	26.8
HA 5514	F	NO	NO	-----	-----
HA 1335	F	1	0	26.7	26.5
HA 7699	F	1	0	26.3	26.5
HA 1436	M	0	1	26.5	26.7
HA 1460	M	1	0	26.3	26.5
HA 6406	M	NO	NO	-----	-----
HA 1361	M	0	1	26.2	26.0
HA 8221	M	NO	NO	-----	-----
HA 6045	M	NO	NO	-----	-----
HA 1503	M	NO	NO	-----	-----
HA 0953	M	0	1	26.4	26.8
HA 2791	M	NO	NO	-----	-----
HA 0154	M	1	0	26.1	26.5
HA 0312	M	1	0	26.3	26.1
TOTAL 23	**12F/11 M**	**9**	**7**	**----**	**-----**
FM F85D/A959	F/M	1	0	26.2	26.4
FM 31C8/7E14	F/M	1	0	25.8	25.6
FM FD2A/DDDC	F/M	0	1	26.3	26.4
FM 3322/05BD	F/M	1	0	26.6	26.2
FM 325E/25EO	F/M	0	1	26.8	26.4
FM OD85/E28E	F/M	1	0	26.5	26.3
FM AB1X, F284	F/M	0	1	26.4	26.9
FM 5882/08B5	F	0	1	26.7	26.6
FM FC11/DC2A	F/M	1	0	26.0	26.5
FM B2XC/13D2	F/M	NO	NO	----	----
FM 0394/FC57	F	1	0	26.8	27.0
FM 07EB/3164	F	1	0	27.1	26.6
FM 0949/1634	F/M	NO	NO	----	----
FM 6084/4329	F	NO	NO	----	----
FM 339F/3094	F	NO	NO	----	----
FM 603F, 2351	F	1	0	26.8	26.5
FM 33D6,9012	F	0	1	26.3	26.4
TOTAL 34	**24F/10M**	**8**	**5**	**-----**	**-----**

Table 9. Light localization experiment

MOLE - RAT	SEX	PLUG	NO PLUG
HA 9585	F	0	1
HA 1805	F	1	0
HA 0142	F	1	0
HA 5649	F	1	0
HA 7818	F	1	0
HA 9678	F	1	0
HA 5514	F	1	0
HA 8495	F	1	0
HA 1335	F	1	0
HA 7699	F	1	0
HA 1436	M	1	0
HA 1460	M	1	0
HA 6406	M	1	0
HA 1361	M	0	1
HA 8221	M	1	0
HA 6045	M	1	0
HA 1503	M	1	0
HA 0953	M	0	1
HA 0154	M	1	0
HA 0312	M	1	0
TOTAL 20	**10F/10M**	**17**	**3**
FM F85D/A959	F/M	1	0
FM 2522/2511	M	0	1
FM 31C8/7E14	F/M	1	0
FM FD2A/DDDC	F/M	1	0
FM 3322/05BD	F/M	1	0
FM B25E/25EO	F/M	1	0
FM 0D85/E28E	M	0	1
FM F4C1/F284	F/M	0	1
FM FC11/DC2A	F/M	1	0
FM B2XC/13D2	F	1	0
FM 6048/2351	F/M	1	1
FM 339F/33D6/D6E8	F	1	0
FM 603F/9012	F	1	0
FM D7EB/3164	F/M	1	0
FM 0949/1634	F/M	1	0
TOTAL 33	**18F/15M**	**12**	**3**

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