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Light or temperature;
That is the question.
The circadian rhythm of the silvery mole-rat (*Heliophobius argenteocinereus)*

Master thesis

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Annotation:

Subterranean rodents are interesting model group for studying of the circadian timing system due to their cryptic lifestyle and challenging living conditions. The filed data indicate that the locomotor activity of the silvery mole-rat (*Heliophobius argenteocinereus)* is influenced by temperature cycle, but the confirmation in laboratory study was to date missing.

Prohlašuji, že svoji diplomovou práci jsem vypracovala samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury. Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své diplomové práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

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Content

1. The rhythmicity of life

Living creatures are exposed to the cyclic changes on the Earth. These changes influence life of the most species including their physiology and behaviour. During the cycles animals show periodic pattern in activities called the biological rhythm (Gattermann et al., 2008), which is important for increasing of individual fitness (Urs & Eichele, 2003; Hastings, 1997).

The internal circadian system evolved to work together with these periodic changes (Reppert & Weaver, 2002). Proper functioning of circadian system ensures that activity of organism occurs in the most favourable part of the day (Bartness & Albers, 2000). The internal circadian system consists of the main, and numerous peripheral circadian clocks.

The main circadian clock is located in the brain in the suprachiasmatic nuclei (SCN) (Albrecht & Eichele, 2003; Saini et al., 2011). This clock, which uses photic information from the environment, can coordinate the peripheral circadian clocks. These are many individual oscillators located in all sorts of tissues in body (Balsalobre et al., 1998; Menaker et al., 2013). The peripheral clocks control many aspects of everyday life such as activity or physiological processes (Albrecht & Eichele, 2003; Brown & Azzi, 2013; Gatrermann et al., 2008).

To keep the circadian timing system, it is necessary to adjust endogenous period with the external cues of the environment. The ability of the clock to be reset by environmental stimuli is critical (Saini et al., 2011; Reppert & Weaver, 2002). This cooperation results in synchronization of one’s actions and cyclical changes of the environment (Brown & Azzi, 2013).

The clocks free-run in the conditions with absence of relevant environmental stimuli (such as continuous darkness), thus without clear signal when to activate or deactivate. In this situation the circadian clock maintain a genetically determined period *tau* (τ), which is close to 24 hours (Sharma, 2003). In this situation, the activity pattern is not adjusted by external cues, and its activity may differ from rhythms of the environment.

The external cues which are vital for proper function of the circadian clocks (Aschoff & Pohl, 1978) are called *zeitgebers*. These cues are able to adjust the length of period *tau* (τ). The process of synchronization is called entrainment (Albrecht & Eichele, 2003) during which the length of the period *tau* is modified to be equal to the period of the environment. If the light is *zeitgeber*, the activity oscillates with period 24 hours (Rosenwasser, 2010).

2. *Zeitgeber* – the key for synchronization

The circadian timing system is affected by various stimuli. Light is probably the most important *zeitgeber* for the most of the animals (Favreau et al., 2009). Nevertheless, there are no photoreceptors in the peripheral circadian clocks (Brown & Azzi, 2013), so these clocks have to be affected by non-photic stimuli – ambient temperature, food availability, social contact or interaction, and physical activity which may pay role as *zeitgebers* (Mendoza, 2006; Favreau et al., 2009; Refinetti, 2010; Van der Vinne et al., 2014; Weisgerber et al., 1997).

Food is essential for survival of the organism, so it is not surprising that the circadian timing system can react to the changes in feeding cycles (Mendoza, 2006). Experiments with mice bearing SCN lesions proved existence of food entrainable oscillator (FEO). These mice were arrhythmic when fed randomly but showed rhythmicity when food was available regularly (Pezuk et al., 2010). Signal generated by SCN can conflict with the one sent to the peripheral oscillators. If the food is available only for few hours per day, the mice will start to activate in this period. In case when food is provided during day light, even nocturnal species will be active during light phase of the day (Vujovic et al., 2008). Feeding during daytime inverses the phase of the peripheral oscillators, but it does not affect the central oscillator. These findings suggest that food could be important *zeitgeber* for peripheral clocks (Damiola et al., 2000).

Social interaction can also strongly influence the rhythms mostly in social species. According to several studies, the activity rhythms of individuals can be influenced by social partners (Favreau et al., 2009). This kind of synchronization is important for example for bats flying out of the cave every day at the same time, although the cave probably lacks other regular environmental cues. Few bats fly close to the entrance to the cave and "test" the amount of the light outside. This information spreads as social cue to the rest of the colony. The bat held alone started to free-run (Marimuthu et al., 1981).

Amount and opportunity to perform physical activity, more exactly wheel running in laboratory setting, can influence the circadian activity. The amount of wheel running influences the length of tau. Hamsters (*Mesocricetus auratus*) with access to wheel have shorter period tau than animals without access to wheel-running (Weisgerber et al., 1997).

Among non-photic stimuli, the influence of ambient temperature belongs to the least known factors. The circadian timing system can be influenced by ambient temperature directly by manipulating processes in the main circadian clock, or indirectly by affecting reaction of the peripheral clock (Ruoff & Rensing, 2004). Changes of ambient temperature can slow down or accelerate the processes in the circadian timing system (Liu et al., 1998). Mostly for ectothermic animals, e.g. reptiles (Foa & Berolucci, 2001; Tosini et al., 2001), the temperature changes are strong *zeitgeber,* while homeothermic organisms are affected by temperature changes only to some extent and only if the change of temperature is significant (Buhr et al., 2010; Rensing & Ruoff, 2002). It is not clear if the change in activity is caused directly by temperature or indirectly thought effect on locomotor activity (Ruoff & Rensing, 2004). The Arabian camel (*Camelus dromedarius*) is exposed to the extreme temperature conditions during 24 hours. The melatonin secretion and the body temperature were used as output of the circadian clock, and both were entrained with the ambient temperature cycle in total darkness. In the light-dark cycle the body temperature shifted with the shift of the ambient temperature but the melatonin cycle was modified with temperature only in two of seven animals (Allali et al., 2013). Similarly, Australian desert dwelling marsupial mouse (*Sminthopsis macroura*) were entrained to the temperature cycle under constant darkness, and individuals were active during cool part of the day (Francis et al., 1990 in Rajaratnam & Redman, 1998).

3. Vertebrates living in dark environment

The most common signal for the synchronization of the circadian timing system is light-dark cycle. However, there are many animals evolved in the environment with restricted access to the light or even in absence of light. It could be supposed that individuals of these species do not need functional circadian clock. However, in some species opposite was demonstrated.

The blind Mexican cavefish (*Astyanax mexicanus*) is suitable model organism for study of the circadian activity, because there are isolated cave populations together with surface dwelling populations. In the laboratory studies, the cave fish show very weak circadian oscillations with reaction to the light, and the epigeic fish show clear synchronization with light-dark cycle (Beale, 2013; Erckens & Martin, 1982).

In spite the light is expected to be the most important *zeitgeber* for maintaining circadian activity in mammals (Albrecht & Eichele, 2003; Meijer et al., 2007), there are some mammalian species that have only limited, or none access to the light. For example, Schneider's leaf-nosed bats (*Hipposideros speoris*) live in caves which seem to lack any environmental cues for circadian synchronization. Nonetheless, they show functional timing system, as mentioned above (Marimuthu et al., 1981).

Special case of mammals living almost continuously in dark environment is subterranean rodents. The subterranean ecotope is characteristic for its stability, constant condition and predictability (Nevo 1999). In subterranean burrows there is absolute darkness, low hypoxic and hypercapnic atmosphere and diurnal temperature fluctuation is only within a few degrees, which contrast with condition aboveground. Despite of the animals are relatively save from predators and influence of weather, living in the underground is very energetically demanding because of energetic cost of burrowing (Du Toit et al., 1985; Zelová et al., 2010). Absence of light and constant conditions is the reason why these animals are suitable model organisms for study of the circadian timing system.

4. Control of the circadian clock in subterranean rodents

Due to the stability of the subterranean environment, burrow inhabitants, especially those which do not emerge aboveground regularly, seem to have not many chances to entrain with cyclic changes of the environment. Living in constant darkness, it was even considered that these animals do not exhibit circadian rhythms (Nevo, 1982; Davis-Walton & Sherman, 1994 in Riccio & Goldman, 2000). However, the opposite is true, and some of subterranean mammals (if not all) exhibit regular circadian rhythms.

It seems there are several factors influencing circadian activity in subterranean rodents. Similarly to other animals, most studies indicate crucial influence of light as a main factor. In many laboratory studies light was proven as strong *zeitgeber* for mole-rats, and even mole rats of genus *Spalax* which have eyes covered with skin (Bhagwandin et al., 2011; De Vries et al., 2008; Hart et al., 2004; Lovegrove et al., 1993; Oster et al., 2002; Riccio & Goldman, 2000; Schöttner et al., 2006; Tobler et al., 1998; Vasicek et al., 2005). Individuals exhibit monophasic, biphasic and polyphasic activity patterns, and both diurnal and nocturnal activity preference. The presence of the circadian rhythm was confirmed also in field studies (Jarvis 1973; Rado et al., 1993; Šklíba et al., 2007).

As mentioned, light is not the only factor which may play role in synchronization of activity the subterranean rodents. There are some indications that social interaction (Lovegrove et al., 1993; Lövy et al., 2013), and temperature (Benedix, 1994; Rado et al., 1993; Šklíba et al., 2007; Šklíba et al., 2014) synchronizes circadian clocks of subterranean rodents.

4.1 Light as a *zeitgeber* of activity of subterranean mammals

Although the strictly subterranean rodents are probably not regularly exposed to the light, authors of many laboratory studies suggested light as main or even only *zeitgeber* (Bhagwandin et al., 2011; De Vries et al., 2008; Schöttner et al., 2006; Vasicek et al., 2005). Surprisingly, blind mole-rat, *Spalax ehrenbergi* i.e. species with eyes covered with skin, was found to exhibit circadian locomotor activity after experimental manipulation with light (Nevo, et al. 1982; Tobler et al., 1998).

Nevertheless, among tested individuals of many species the individual variability in circadian rhythms was found. For example, Lesotho mole-rats (*Cryptomys hottentotus*) exhibited nocturnal, monophasic locomotor activity, and they *free-run* in constant conditions, but their activity pattern was variable toward light-dark cycle (Schöttner et al., 2006). Similarly, in other studies of circadian activity of mole-rats, the high variability in activity patterns was also found (Hart et al., 2004; Riccio & Goldman, 2000; Vasicek et al., 2005; Oosthuizen et al., 2003). This variation may indicate that light-dark cycle is not strong *zeitgeber* for subterranean rodents, at least not for all individuals (Schöttner et al., 2006). Alternatively, there are other non-photic cues that may influence circadian activity (Sharma & Chandrashekaran, 2005) but these were not taken into account in this studies.

For sure, effect of artificial condition in laboratory cannot be excluded due to fact that remarkable differences between results of several laboratory and field studies on the same species were found. For example, in fossorial coruro (*Spalacopus cyanus*) (Begall et al., 2002; Ocampo-garcés et al., 2006), it was found that this rodent exhibited nocturnal activity in laboratory. On the contrary, coruros exhibit diurnal activity in nature (Rezende et al., 2003; Urrejola et al., 2005). Similarly, in laboratory the Ansell´s mole-rats exhibited only very weak circadian pattern in activity (De Vries et al., 2008), but strict monophasic diurnal activity in the nature (Šklíba et al., 2014). Blind mole rats (*S. ehrenbergi)* exhibited monophasic diurnal activity in nature (Rado et al., 1993; Rado & Terkel, 1989; Hadid et al., 2013), but variable activity patterns occurred during laboratory testing (Nevo et al., 1982; Tobler et al., 1998). Rado & Terkel (1989) proposed that light is the main *zeitgeber* while soil and air temperature were the secondary cues for entrainment of circadian clock of mole rats. The possibility of more than one cue influencing circadian clock is supported also by results of the study of Oster et al., (2002). Authors propose that clock of blind mole rat can fluctuate in sensitivity to light as cue in order to prioritize the influence of other signals (i.e. temperature, humidity, social interaction).

4.2 Temperature as a possible *zeitgeber* of activity of subterranean rodents

As already mentioned, the circadian clocks of the subterranean mammals are not necessarily influenced by only single *zeitgeber* (Oster et al., 2002). In spite of fact that many those mammals react to the dark-light cycle, it could not be necessarily the main cue (c.f. Begall et al., 2002; c.f. De Vries et al., 2008; Lövy et al., 2013; c.f. Oosthuizen et al. 2003; Šklíba et al., 2014). Due to the stability of underground environment, everyday regular cycling of soil temperature could play role in synchronization of the circadian clocks of subterranean rodents.

Temperature of soil shows less fluctuation with increasing depth, and it stays constant in depths under 60 cm (Bennett et al., 1988). Moreover, due to the thermal capacity of soil (it takes longer to soil to get hotter/cooler in comparison with air) the soil is the coldest few hours after sunrise and the hottest few hours after sunset (Šumbera et al., 2004, Burda et al. 2007).

Unfortunately, not many laboratory studies deal with influence of temperature on the circadian activity of mole-rats. Recently, it was found that Damaraland mole-rats (*Fukomys damarensis*) were most active at 25°C, the least at 30°C, and there was intermediate amount of activity in 20°C. This is explained by need of animal to maintain their body temperature as the ambient temperatures are lower than mole-rat’s thermoneutral zone. The activity differs from reproductive and non-reproductive individuals while non-reproductive individuals were more active in lower temperatures (Oosthuizen & Bennett, 2015). Only in the study of Goldman et al. (1997) authors focused on activity patterns of blind mole rats (*S. ehrenbergi*), and it was found that some individuals entrained to the temperature cycle, while most of them reacted to the dark-light cycle.

There are field studies indicating that influence of temperature on the circadian activity of subterranean rodents is relevant. According to Benedix (1994), plain pocket gophers (*Geomys bursarius*) decrease its activity in the hottest and the coldest part of day displaying thus bimodal activity pattern. Among African mole-rats, Ansell's mole-rat exhibited monophasic diurnal activity with peak of activity during highest temperatures in depth of the foraging tunnels (Šklíba et al., 2014). In another species, the giant mole-rat (*Fukomys mechowii*), the activity of several members of one family did not show any correlation with burrow temperature (Lövy et al., 2013). Only single dispersing individual displayed peak of activity during the maximal temperature in the foraging tunnels. The most convincing study about influence of temperature on activity patterns indicates similar pattern. The silvery mole-rats (*Heliophobius argenteocinereus)* were radiotracked during two periods of dry season in Malawi (Šklíba et al., 2007). Mole-rats responded by activity shifts to temperature changes in burrow system, in spite that diurnal changes were small, about 3°C (Šklíba et al., 2007). Additional seven individuals radiotracked during hot dry season were most active during minimal burrow temperatures (Šklíba & Lövy – unpublished data).

From above it is possible to see that activity of subterranean rodents could be influenced by ambient temperatures. Nevertheless, based on hitherto knowledge we cannot say if these mammals simply avoided inconvenient temperatures, or they use temperature as *zeitgeber* of circadian activity in nature. Unfortunately, authors of laboratory studies which may provide convincing test of influence of temperature as *zeitgeber* did not pay attention to this factor. Only in the study of Goldman et al. (1997) was found that some individuals of blind mole rat entrained to the temperature cycle. Therefore we decide to test influence of temperature on activity of mole-rats during controlled laboratory study.

5. Goals of the study

The main goal of this study is to determine if the circadian activity of the silvery mole-rat (*Heliophobius argenteocinereus*) is influenced by ambient temperature or light, or alternatively both. In case of latter option, I will try to distinguish which factor is more relevant.

6. Materials and methods

Následující pasáž o rozsahu 14 stran obsahuje utajované skutečnosti a je obsažena pouze v archivovaném originále diplomové práce uloženém na Přírodovědecké fakultě JU

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8. Appendix

Následující pasáž o rozsahu 15 stran obsahuje utajované skutečnosti a je obsažena pouze v archivovaném originále diplomové práce uloženém na Přírodovědecké fakultě JU.