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**Ecology and behaviour of an enigmatic
fossorial rodent, the giant root-rat
(*Tachyoryctes macrocephalus*), endemic to the
Afroalpine habitat in the Bale Mountains,
Ethiopia**

Ph.D. Thesis

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Annotation

The research in this thesis concerns with the ecology and behaviour of an endangered fossorial rodent, the giant root-rat (*Tachyoryctes macrocephalus*), in the Afroalpine ecosystem of the Bale Mountains, Ethiopia, and the results are discussed in relation with available ecological data on other fossorial/subterranean rodents. Firstly, this thesis is focused on investigating the ecological role of the giant root-rat. The evaluation of root-rat's impact on various ecosystem features, in the first study, highly contributed to the knowledge not only about the species itself but also about the functioning of the ecosystem it inhabits. In fact, the results of the study indicated that the giant root-rat acts as an ecosystem engineer in the Afroalpine grasslands. Secondly, this thesis involves a pilot radio-telemetry study on the giant root-rat focusing on its temporal and spatial activity. Specifically, the results of the second study brought new light to giant root-rats' daily activity, its pattern, amount and seasonal change demonstrating the difference in activity patterns between strictly subterranean rodents and subterranean rodents with aboveground habits such as the giant root-rat. In the third study, we described the space-use patterns of the giant root-rat and revealed several trends in its spatial behaviour that can serve as a strategy to cope with the harsh and changeable environmental conditions in the Afroalpine ecosystem.

Declaration [in Czech]

Prohlašuji, že svoji disertační 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 disertační práce, a to v nezkrácené podobě 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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List of publications and author's contribution

This thesis is based on the following publications:

- I.** Šklíba, J., **Vlasatá, T.**, Lövy, M., Hrouzková, E., Meheretu, Y., Sillero-Zubiri, C. & Šumbera, R. (2017). Ecological role of the giant root-rat (*Tachyoryctes macrocephalus*) in the Afroalpine ecosystem. *Integrative Zoology*. 12(4), 333-344. (IF = 1.856)

Tereza Vlasatá participated in collecting and analysing data. She commented early stage of a draft.

- II.** **Vlasatá, T.**, Šklíba, J., Lövy, M., Meheretu, Y., Sillero-Zubiri, C. & Šumbera, R. (2017). Daily activity patterns in the giant root rat (*Tachyoryctes macrocephalus*), a fossorial rodent from the Afroalpine zone of the Bale Mountains, Ethiopia. *Journal of Zoology*. 302(3), 157-163. (IF = 1.955)

Tereza Vlasatá collected and analysed the data together with Jan Šklíba and Matěj Lövy. She wrote the manuscript with help of Jan Šklíba and Radim Šumbera.

- III.** Šklíba, J., **Vlasatá, T.**, Lövy, M., Hrouzková, E., Meheretu, Y., Sillero-Zubiri, C., & Šumbera, R. The giant that makes do with a little: small and easy-to-leave home ranges found in the giant root-rat, an endemic fossorial rodent of the Bale Mountains, Ethiopia (manuscript)

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Co-authors agreement

Radim Šumbera, the supervisor of this Ph.D. thesis and co-author of all the papers involved in this Ph.D. thesis and Jan Šklíba, the first author of the papers: „Ecological role of the giant root-rat (*Tachyoryctes macrocephalus*) in the Afroalpine ecosystem“, and „The giant that makes do with a little: small and easy-to-leave home ranges found in the giant root-rat, an endemic fossorial rodent of the Bale Mountains, Ethiopia” consent to the publication of the papers in the Ph.D. thesis of Tereza Vlasatá and support it by their signatures:

doc. Mgr. Radim Šumbera, Ph.D.

RNDr. Jan Šklíba, Ph.D.

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General Introduction

1. Introduction

1.1. Rodents with different degrees of underground lifestyle

The underground ecotope, utilised either as a temporary shelter (dens) or permanent habitat (tunnel networks), is ecologically important for a wide range of species, specifically for more than a half of the genera of extant terrestrial mammals (Kinlaw 1999). Of these, five groups are completely subterranean: subterranean rodents, insectivore moles, marsupial moles, golden moles, and certain armadillos. In this text, I will focus on subterranean rodents, since they represent the most numerous and most studied group of subterranean mammals. The underground environment provides them with protection from adverse weather conditions, climatic extremes, as well as from most of the predators (Nevo 1999). On the other hand, it has many limiting characteristics. The underground ecotope is permanently dark and animals are deprived of most of the external cues usually used for orientation and activity timing by their aboveground counterparts. While relatively stable, the microclimatic conditions underground are in many aspects stressful: low oxygen and high carbon dioxide concentrations, high humidity, and low gas ventilation (Begall et al. 2007). In addition, the energetic costs of digging are extremely high compared with any movement on the ground (Vleck 1979), and food resources are generally low and scattered (Begall et al. 2007, Burda 2003, Nevo 1999).

To cope with all these specificities of the subterranean ecotope, its inhabitants have evolved diverse structural, functional, and behavioural adaptations at all organizational levels to the life underground. The major evolutionary determinants of this adaptive convergence, both regressive and progressive, are specialization, competition, and isolation (Nevo 1999). Subterranean rodents share typical morphological similarities including small body size, a short or absent tail and external ears, teeth and/or forelimbs adapted for digging, and sight degeneration. Likewise, metabolism has been shaped by high energetic demands on digging and by the adverse microclimatic conditions thus adaptive metabolic response is

reflected in physiological syndromes such as a low basal metabolic rate, low body temperature and high thermal conductance (Nevo 1999).

On the other hand, the seemingly similar conditions imposed by the underground environment actually display a regional variation in climatic, soil and vegetation characteristics, which can be of great importance in generating adaptive differences among subterranean rodents. Thus, although the evolution of subterranean rodents' adaptations is, in many ways, convergent, there is also some diversity of adaptive ecological responses evident among taxa (Busch et al. 2000). For instance, the proportion of time spent underground differs among subterranean rodents, calling for a suitable categorization. In this text, I will use the term "strictly subterranean" for burrowing rodents living and foraging almost exclusively belowground. Those species which construct extensive burrow systems but forage primarily aboveground will be referred to as "fossorial". Naturally, a certain continuum of adaptations to the underground way of life exists between these two groups (Begall et al. 2007). A comparison of species with different degrees of underground lifestyle can be very useful for studying the evolution of specific characteristics and adaptations.

For example, the regular surface activity of fossorial rodents prevents regression of some of their senses, which are thus more similar to those of surface-dwelling rodents, rather than being highly specialized in strictly subterranean species. Substantial interspecific differences of eye reduction have been reported in recent studies. While an almost complete eye reduction was found in the subfamily Spalacinae, the eye size of *coruros* (*Spalacopus cyanus*) is normal for rodents of similar size; their retina is well-structured and cone proportion is high (Peichl et al. 2005, Withers et al. 2016). A moderate eye reduction has also been reported in the families Ctenomyidae and Geomyidae. This modest regression of the eye in above-mentioned species is supposedly related to their relatively frequent aboveground foraging (Borghini et al. 2002). Regarding hearing, the subterranean milieu is characterised by amplifying sounds of lower frequencies, the so-called stethoscope phenomenon, which requires special hearing adaptations. Whereas strictly subterranean rodents possess ear

adaptations such as a lack of auricles, hearing tuned to low frequencies, and hearing sensitivity reduced to avoid over-stimulation (Begall et al. 2007), fossorial rodents' hearing is adapted in accordance with the special need for subterranean as well as aboveground mode of communication (Heffner et al. 1994). For example, while the Chinese bamboo rat (*Rhizomys sinensis*) possesses ear adaptations for low frequency hearing typical for strictly subterranean species, the presence of relatively large auricles suggests that this species, although living underground, likely displays regular surface activity (Pleštilová et al. 2016).

In accordance with the degree of their commitment to the underground habitat, subterranean rodents also display different foraging strategies (see Table 1). Strictly subterranean rodents forage mostly underground on geophytes, i.e. plants with belowground storage organs (Busch et al. 2000, Huntly & Reichman 1994). Some examples are the bathyergids and blind mole-rats, whose diet contains only a relatively small proportion of aerial plant parts (Heth et al. 1989, Šklíba et al. 2011). In contrast, the species that spend some time foraging on the surface, such as *Tachyoryctes splendens*, consume also surface-growing vegetation apart from the subterranean plant parts (Jarvis 1973). Even more generalized is foraging in geomyids and ctenomyids, for which aerial plant parts comprise the most important part of their diets (Albanese et al. 2010, Vaughan 1967). Apart from foraging, interspecific comparisons suggest that there is also variation in other aspects of subterranean rodents' ecology such as activity and space-use patterns (Busch et al. 2000). This variability and how it is influenced by the combined effects of underground- and surface-related selective pressures is one of the main interests of this thesis and is discussed further.

Table 1. Foraging ecology and the amount of aboveground activity (three main degrees of aboveground activity are designated: rarely, occasionally, frequently) of selected species representing several families and subfamilies of subterranean rodents with a different degree of underground lifestyle.

Species (family)	Social system	Diet	Searching/ foraging	Aboveground activity
<i>Thomomys talpoides</i> (Geomyidae)	solitary	74% aerial, mainly forbs, rest are shrubs and grasses ^j	underground and aboveground, pulling down entire plants into the burrow ^j	occasionally ^l
<i>Bathyergus suillus</i> (Bathyergidae)	solitary	over 60% aerial veg. rest are roots and small geophytes ^a	underground and pulling aerial fraction into the burrow ^a	rarely ^a
<i>Heliophobius argenteocinereus</i> (Bathyergidae)	solitary	entirely geophytes and roots	underground	rarely ^{d, h}
<i>Ctenomys talarum</i> (Ctenomyidae)	solitary	97% aerial fraction, mainly grasses ^c	aboveground and underground ^c	frequently ^b
<i>Spalacopus cyanus</i> (Octodontidae)	social	aerial and succulent subterranean stems and tubers of herbs ^k	underground and aboveground ^k	occasionally ^g
<i>Spalax ehrenbergi</i> (Spalacidae, subfamily Spalacinae)	solitary	more than 50% geophytes, rest herbs and shrubs ^e	underground and pulling entire plants into the burrow ^e	rarely ^f
<i>Tachyoryctes macrocephalus</i> (Spalacidae, subfamily Rhizomyinae)	solitary	wide range of grasses and herbs including roots ^{i, m}	aboveground and underground pulling the vegetation down into the burrow ^{i, m}	frequently ^m

Sources: (a) Bennett et al. 2009, (b) Busch et al. 2000, (c) Comparatore et al. 1995, (d) Jarvis 1973, (e) Lövy et al. 2015 (f) Rado et al. 1992, (g) Rezende et al. 2003, (h) Šklíba et al. 2007, (i) Šklíba et al. 2017, this thesis, (j) Stuebe & Andersen 1985, (k) Torres-Mura & Contreras 1998, (l) Verts & Carraway 1999, (m) Vlasatá et al. 2017, this thesis.

1.2. Ecological role of subterranean rodents

Ecosystems are formed by complex interactions among species, thus the feedback between organisms and their environment is of great relevance to the understanding of ecosystem functioning (Davidson et al. 2010). Although all organisms influence the environment in some aspects, simply by their presence, only a few of them actively alter the physical properties of the environment and substantially affect other organisms living in the same environment. If their impact is large enough to modify, maintain and create habitats, they can be classified as ecosystem engineers and/or keystone species (Jones et al. 1994, Root-Bernstein & Ebersperger 2013). Both keystone species and ecosystem engineers are considered to have a strong positive effect on the ecosystem through their disturbance activities. They promote plant and animal diversity, and maintain the disturbance-dependent components of plant communities (Reichman & Seabloom 2002, Root-Bernstein & Ebersperger 2013).

Typically, subterranean rodents create disturbances through burrowing, strict herbivory and a combination of these activities (Huntly & Inouye 1988, Lara et al. 2007, Reichman 2007). Some of them have indeed been identified as ecosystem engineers: prairie dogs (Davidson & Lighfoot 2008); pocket gophers (Huntly & Inouye 1988, Reichman & Seabloom 2002); plateau zokors (Zhang et al. 2003); and African mole rats (Hagenah & Bennett 2013). Generally, subterranean rodents profoundly alter the structure and function of the ecosystems they inhabit in several ways (Reichman 2007). Primarily, they consume large amounts of vegetation, and thus directly affect individual plants and plant communities. Because the consumption of even a small fraction of the plant subterranean storage organ can considerably influence plant survival, growth, and reproduction, the effect of subterranean herbivory on vegetation is really extensive

(Huntly & Reichman 1994, Reichman 2007). As a consequence, subterranean rodents can cause damage to individual plants and a reduction of plant biomass. From a long-term perspective, however, the presence of subterranean rodents can have a positive effect on plant biomass (Davis 1990, Reichman & Seabloom 2002, see below).

The excavation and transportation of the soil by burrowing rodents cause numerous changes in the structure and nutrient content of the soil, which has an indirect impact on plant communities (Galiano et al. 2014, Reichman & Seabloom 2002). As the extensive burrow systems are excavated and refilled again (e.g. Šklíba et al. 2009), large spaces within the soil matrix are created (burrows, chambers), the soil from different horizons is mixed, mounds are built, and some plants are buried (Andersen 1987). All these effects originate from the dynamic process of burrowing activities over a given area and time, resulting in a continuous impact on the environment. Apart from the construction of the underground tunnels, fossorial rodents store various food plants, faeces, and other organic matter, which affects the soil nutrient content. As a consequence, the mounds formed by burrowing rodents have a different nutrient content and water-holding capacity than the inter-mound areas, generating thus a dynamic mosaic heterogeneity that increases plant biomass and the diversity of the plant community (Davidson & Lightfoot 2008, Huntly & Reichman 1994, Reichman 2007, Reichman & Seabloom 2002). Apart from their direct and indirect effects on plant communities, subterranean rodents also indirectly affect other animals. Through their burrowing activities, new living space and resource opportunities are formed for many animal species such as burrow-nesting birds, small rodents, reptiles, frogs and multiple groups of arthropods (Davidson & Lightfoot 2007, Davidson et al. 2008, Šklíba et al. 2016a, Šumbera et al. 2004).

To date, research on the ecological importance of subterranean rodents has been focused mainly on species from North and South America, and Asia (e.g. Albanese et al. 2010, Contreras et al. 1993, Galiano et al. 2014, Lara et al. 2007, Reichman & Seabloom 2002, Zhang et al. 2003, Zhang 2007). The most widely studied taxa in this respect are pocket

gophers. However, many other species of subterranean rodents remain insufficiently studied and their ecological role may thus be underestimated. The paucity of research on their ecological impact/importance is likely related to two main general limitations. First, as subterranean rodents cannot be observed readily due to their hidden way of life, other methods need to be used. In this respect, radio-tracking has become an essential tool to collect data. Second, any survey of the ecological importance of subterranean rodents requires long-term observation and experimental manipulation (Andersen 1987).

Long-term occupancy of fossorial rodents in a given area can have a striking effect on the landscape in the form of special elements called “mima mounds”. Mima mounds are specific hummocks characterized by a soil profile and plant composition different from the surroundings, reaching a diameter from 3 up to 50 m and a height from 30 cm up to 2 m (Cox & Roig 1986, Mielke 1977). Although their origin has been explained by numerous hypotheses, the primary driver of their formation is most commonly assumed to be the burrowing activity of subterranean rodents and the accumulation of soil deposits from burrows over many generations (Gabet et al. 2014). However, scientists have recently proposed that mima mounds might be formed by vegetation spatial patterning. As plants spread their roots and drain surrounding areas of water and nutrients, they can affect waterborne and windborne soil deposition and erosion, which can then lead to mound formation (Cramer & Barger 2014).

In addition, coexistence of species with large ecological roles can have strong complementary and additive effects on the ecosystem they inhabit. For example, megaherbivores and small burrowing rodents commonly coexist in grassland ecosystems on which they have not only separate, but also interactive impact (Davidson et al. 2010). Understanding their interactive roles in grassland ecosystems is very important in the context of conservation ecology, as the natural environment is greatly altered in terms of replacing the free-ranging herds of megaherbivores by domestic livestock, sometimes resulting in overgrazing (Suttie et al. 2005). An example of such coexistence of mammalian herbivores is found in

Afroalpine grasslands in Bale Mountains, Ethiopia, where the ecosystem is greatly influenced by the activity of an endangered fossorial rodent, the giant root-rat, along with the grazing of livestock (Vial 2010). The ecosystem role of the giant root-rat is discussed in Chapter I.



Figure 1. Afroalpine habitat in the Bale Mountains with signs of root-rat's activity along the swamp shore.

1.3. Daily activity patterns in subterranean rodents

Most animals are exposed to a complex of variables fluctuating within a distinct 24-hr periodicity in their natural environment. The daily routine in the behaviour of an individual animal can be viewed as a strategy to cope with this periodicity (Daan 1981). Proper timing of activity and rest, as well as the allocation of time budget to different activities, belong to the principal aspects increasing fitness and securing animals' survival (Bartness & Albers 2000). Animals use their endogenously regulated internal clocks to generate circadian rhythms which are simultaneously synchronized with various environmental cues called 'zeitgebers' (Aschoff 1979) resulting in specific activity patterns. Although the most important zeitgeber is light, many non-photic factors of animals' natural environment (both biotic and abiotic) can serve as one and/or cause changes in activity patterns (Bartness & Albers 2000). Thus, studying the daily activity patterns can help us better understand how the animal interacts with its environment.

In this regard, subterranean rodents are interesting models for activity studies because the environment they inhabit is permanently dark, thus deprived of light as the most common zeitgeber used for the activity timing aboveground (Nevo 1999). This fact could lead to an assumption that the absence of circadian activity rhythms might be a common phenomenon in subterranean rodents (cf. Nevo et al. 1982). Most of the species, however, have been reported to display a predictable daily activity pattern. Despite a regressed visual system, even strictly subterranean rodents are able to perceive light and use it as a circadian pacemaker under laboratory conditions, reported for example in *Spalax ehrenbergi*, *Cryptomys hottentotus*, and *Fukomys anselli* (DeVries et al. 2008, Schöttner et al. 2006, Tobler et al. 1998). Whether the light serves as the main zeitgeber also under natural conditions remains a question, especially if we consider that strictly subterranean rodents are exposed to light only during very short periods of time while pushing the soil out of the burrows plus the rate of mound building can be very low during several months of a dry season (Šklíba et al. 2016b). According to Rado et al. (1993), even a

brief exposure to light can entrain the activity in free-living blind mole rats. However, several recent field studies have reported that the underground temperature cycle might entrain circadian activity rhythms and/or can serve as a secondary cue modulating the activity pattern in strictly subterranean rodents (Lövy et al. 2013, Rado et al. 1993, Šklíba et al. 2007, Šklíba et al. 2014). Although temperature fluctuation is minimal underground compared to the aboveground ecotope, daily temperature fluctuations in burrows depend on the depth of the burrows as well as on the season (Bennett et al. 1988, Busch et al. 2000). Specifically, at greater soil depths daily temperature fluctuations are substantially buffered and probably constant year-round, while at shallower depths both daily and seasonal variation of temperature can be prominent (e.g. Lövy et al. 2013, Šklíba et al. 2007, Šumbera et al. 2004). Consequently, daily and seasonal changes of thermal conditions in underground tunnels may shape activity timing of strictly subterranean rodents. Indeed, many species respond to an even slight underground temperature fluctuation by either preference or avoidance of high or low temperatures, depending on the species, latitude, or season (see Figure 2). For instance, blind mole-rats have been shown to adjust their activity by shifting the peak of their activity from late morning in summer to late afternoon in winter (Rado et al. 1993, Šklíba et al. 2016b, Zuri & Terkel 1996). While in summer the peak of the activity coincided with the lowest burrow temperature (in 20 cm belowground), in winter the activity culminated when the burrow temperature was the highest (Rado et al. 1993). Similarly, silvery mole-rats (*Heliophobius argenteocinereus*) increased their activity with soil temperature during cold season, while shifting the periods of enhanced activity to earlier hours characterised by colder temperatures during hot and dry season (Šklíba et al. 2007). Further, even a highly social species, Ansell's mole rat (*Fukomys anselli*), seems to adjust its activity pattern according to burrow temperature changes. In the study Šklíba et al. (2014), Ansell's mole rats positively correlated their activity with the highest burrow temperatures in colder parts of the year.

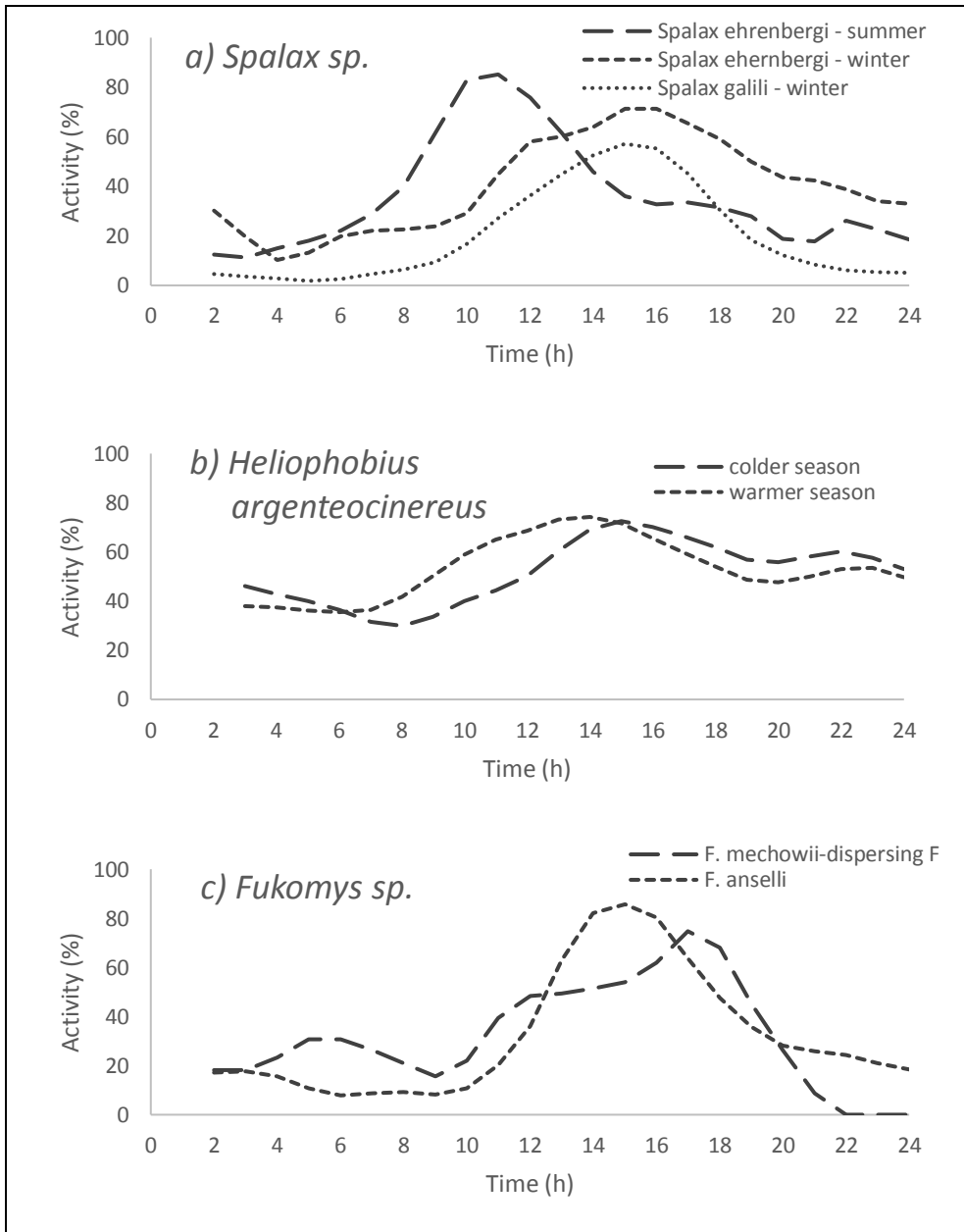


Figure 2. Examples of activity patterns in selected strictly subterranean rodents. a), b) seasonal shift in activity pattern according to changes in underground temperature, c) unimodal activity pattern synchronized with temperature in 10 cm belowground; Sources: (a) Rado et al. 1993, Šklíba et al. 2016b (b) Šklíba et al. 2007, (c) Lövy et al. 2013, Šklíba et al. 2014.

This trend of seasonal changes in activity patterns can serve as a useful way how to save energy on thermoregulation, and reduce the risk of overheating in strictly subterranean rodents.

In contrast to strictly subterranean species, fossorial ones such as tuco-tucos (Ctenomyidae), cururos (Octodontidae) or root-rats (Spalacidae) are regularly exposed to light and other environmental cues during regular periods of time they spend on the surface. Therefore, we can expect that circadian rhythmicity is driven primarily by the natural light/dark cycle in these species. On the other hand, they spend the overwhelming part of the day underground, which makes the question about their activity timing more complicated and we can assume that both underground and aboveground conditions may affect their overall activity pattern. The importance of aboveground determinants in their activity timing can be well illustrated on the fact that activity patterns differed considerably when the individuals of the same species were tested both under laboratory and free-ranging conditions. For instance, tuco-tucos (*Ctenomys knighti*), root-rats (*Tachyoryctes splendens*), and cururos (*Spalacopus cyanus*) display nocturnal activity pattern in laboratory (Begall et al. 2002, Katandukila et al. 2013, Valentuzzi et al. 2009) but a diurnal one in the field (Jarvis 1973, Tomotani et al. 2012, Urrejola et al. 2005). Obviously, it is unfeasible to simulate natural conditions in the lab and the way animals behave in natural and laboratory conditions differs, among other things, in that in the lab they do not perform emerging on the surface in order to forage and remove the soil. The absence of this behaviour and regular exposure to aboveground factors in laboratory facilities most likely makes the difference between the results of activity timing obtained in laboratory and natural conditions.

One of the potential determinants of fossorial rodents' activity timing is aboveground temperature (Kenagy et al. 2002, Rezende et al. 2003), when assuming it poses much greater thermoregulatory demands on the animals than temperature conditions underground. On the other hand, fossorial rodents emerge on the surface regularly but sparsely, thus the effect of aboveground temperature may apply only to aboveground activity,

whereas overall activity can have a tendency to be synchronized with the temperature in burrows, similarly to strictly subterranean rodents (see Figure 3 and 4). In Benedix (1994), free-living plain pocket gophers (*Geomys bursarius*) indeed synchronized their activity with temperature fluctuations in burrows with reducing the activity in both the highest and the lowest burrow temperatures, resulting in a bimodal activity pattern. Contrarily, the coruro (*Spalacopus cyanus*) has been reported to respond to changes in ambient temperature in their natural habitat (Rezende et al. 2003). Authors of the study suggested that low night air temperatures limited coruros' activity with aboveground habits, resulting in a diurnal activity pattern. Furthermore, coruros responded to changes in ambient temperature by altering their aboveground activity from a unimodal pattern during the winter to a bimodal one during the summer. Reduced aboveground activity during the course of the 24-h day was coincident with a particularly high surface temperature in the summer, increasing over 32°C, suggesting that high temperatures might be the factor limiting their aboveground activity. A similar trend of limitation by air temperature has been reported in a less fossorial *Clyomys laticeps*, displaying a nocturnal pattern of aboveground activity in response to high daytime temperatures (Ferrando & Leiner 2018). Adjusting the activity to ambient temperature fluctuation in terms of changing the overall pattern and/or re-allocating specific activities on a daily and/or seasonal basis is well-known from less fossorial species such as ground squirrels and marmots (Drabek 1973, Hayes 1976, Kenagy et al. 2002, Long et al. 2005, Melcher et al. 1990). Typically, they avoid exposure to heat during midday by decreasing aboveground activity, which results in shifts from a unimodal to bimodal activity pattern in the warmer season.

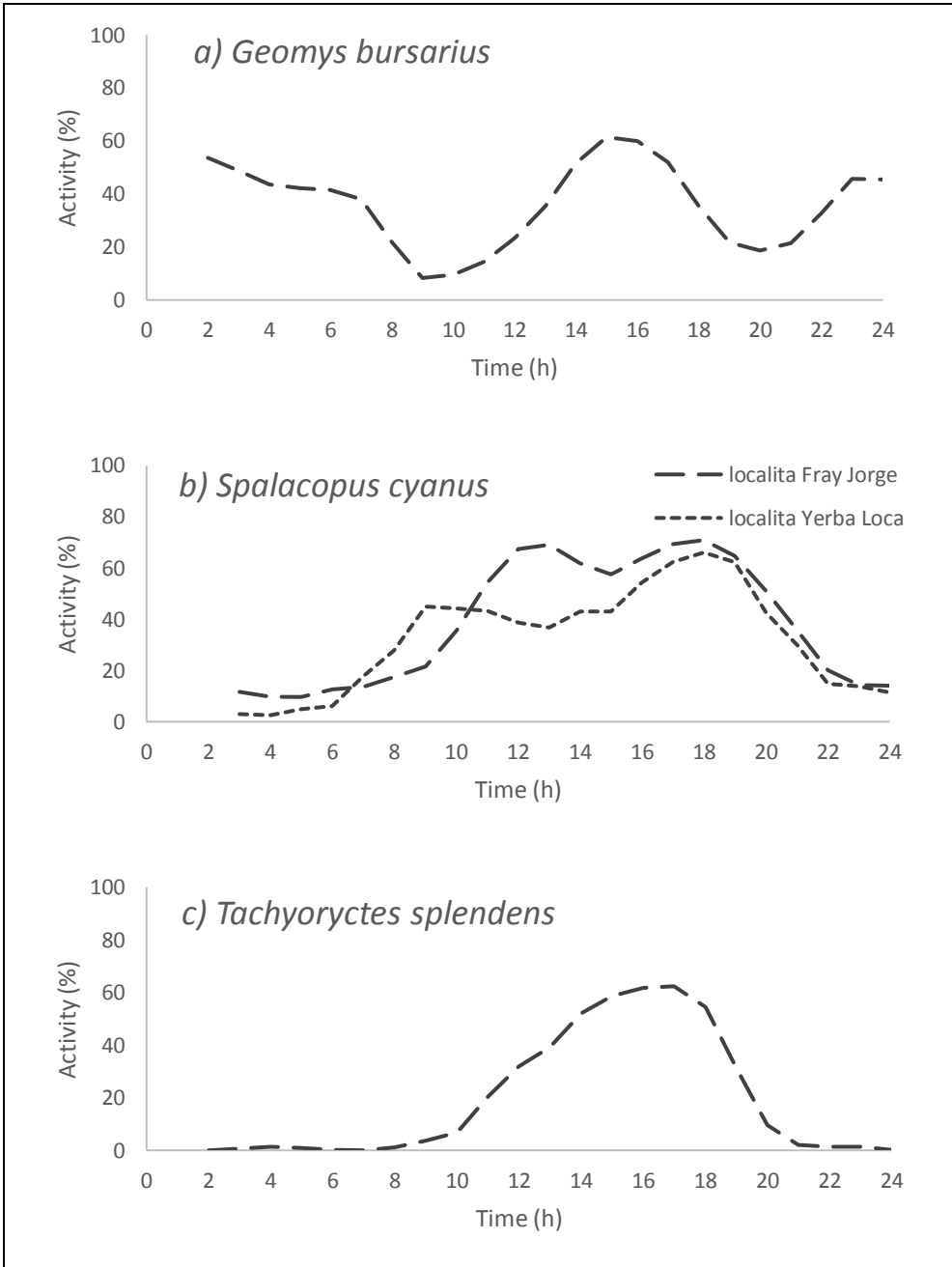


Figure 3. Examples of activity patterns in selected fossorial rodents. a) bimodal activity pattern avoiding both daily temperature extremes in burrows, b) diurnal activity with signs of bimodal pattern, c) diurnal activity with unimodal pattern; Sources: (a) Benedix 1994, (b) Urrejola et al. 2005, (c) Jarvis 1973.

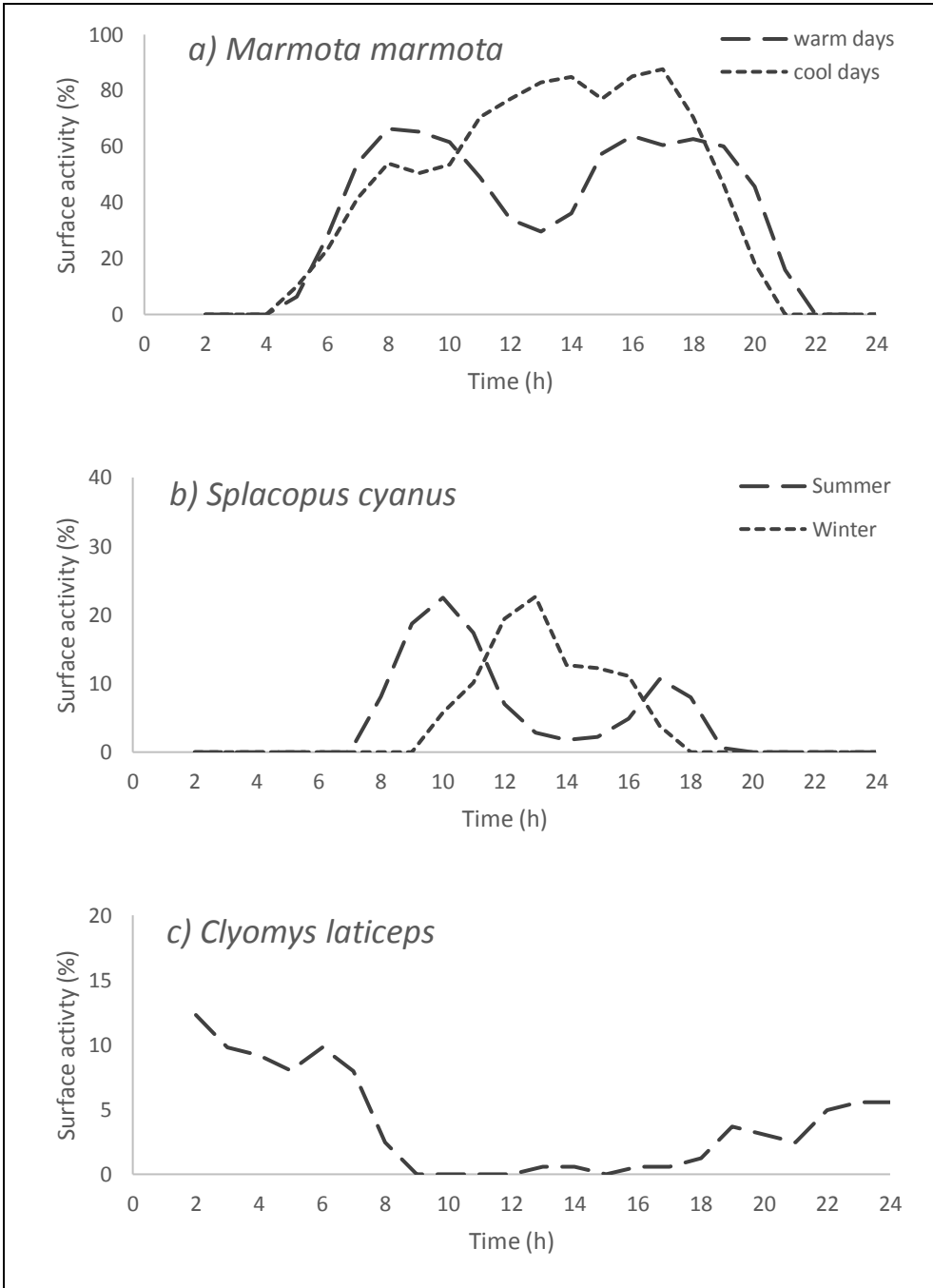


Figure 4. Examples of surface activity patterns. Diurnal pattern adjusted according to changes in aboveground temperature in a) less fossorial *Marmota marmota*, and b) fossorial *Spalacopus cyanus*. c) nocturnal pattern in less fossorial *Clyomys laticeps*. Sources: (a) Türk & Arnold (1988), (b) Rezende et al. 2003, (c) Ferrando & Leiner (2018).

Shifts in daily activity as a behavioural adaptive strategy are important especially for fossorial rodents inhabiting cold zones and/or high mountains where daily and seasonal temperature variation can be extreme (Hinze & Pillay 2006, Long et al. 2005, Melcher et al. 1990). Here, fossorial rodents are reported to cope with extreme thermal conditions by means of physiological and behavioural adaptations. On the one hand, they are usually physiologically adapted for coping with the cold, such that higher rather than lower temperatures are stressful for them (Armitage et al. 1990). Consequently, their activity is limited under heat stress during high midday temperatures and they switch from unimodal to bimodal activity patterns in a similar way as described above (Hinze & Pillay 2006). On the other hand, the extremely low night and winter temperatures too represent stressful conditions that these species need to cope with; and adjusting daily activity can serve as one of the behavioural energy-conserving strategies. For instance, the strictly subterranean plateau zokors, inhabiting a harsh alpine ecosystem, display reduced overall amount of activity (to only 10-15%) in response to low temperatures (Zhang et al. 2003). Another strategy relevant for fossorial species can be based on increasing aboveground activity to maximize the exposure to and absorption of solar radiation — the so-called basking (Hinze & Pillay 2006)

A lesser commitment to subterranean life associated with aboveground habits of fossorial rodents increases the risk of aboveground predation (Busch et al. 2000). Therefore, it is surprising that fossorial rodents' activity patterns have received little or no attention from a predation perspective. The effect of predation on activity was confirmed, for instance, by observation of less fossorial degus reducing their locomotor activity during the time predation risk is high (Ebensperger & Hurtado 2005). Furthermore, the allocating of time to different activities is usually influenced by conflicting demands, and foraging-related activities are typically traded off against those that decrease the risk of predation, thus it can be expected that predation risk would also affect the time budget of animals. For example, marmots adjust the time spent being alert and foraging in response to the risk of predation. Specifically, feeding time is

reduced in favour of looking around for predators when predation risk increases (Carey & Moore 1986).

In addition, limited food access is reported to be capable of entraining the circadian clock and serve as zeitgeber with similar effects on the internal clock as other entraining stimuli (Halle 2000). At the same time, we can expect that food availability can cause changes in overall activity pattern and affects daily activity in terms of changes of its amount and re-allocation of time to different activities in subterranean rodents. Generally, increased vegetation availability results in increased activity in subterranean rodents (Cox & Hunt 1992, Romañach et al. 2005b, Zuri & Terkel 1997). For example, strictly subterranean blind mole rats have been reported to increase their tunnelling activity in summer in order to gather food digging along the moisture gradient towards a moist soil (Zuri & Terkel 1997). However, we can observe reverse effect in the case of fossorial rodents' aboveground activity associated with the foraging since food-rich environments reduce the time necessary for food localization (Pigage & Pigage 2010).

The potential effect of above-mentioned factors such as aboveground temperature, predation, and food supply on activity timing could be well demonstrated in a fossorial species that inhabits an environment with extreme temperature fluctuations, seasonal changes in food supply and a high predation risk, such as the giant root-rat. Its daily activity patterns are depicted in Chapter II.

1.4. Space-use patterns and home-range dynamics in subterranean rodents

Animal spatial behaviour is usually described with the “home range” concept, which delimits the area of repeated utilization, where an animal displays routine behaviours associated with basic aspects of its life (Burt 1943). The home-range size is determined by both ecological requirements of the species and environmental factors, resulting in specific space-use patterns (Harestad & Bunnell 1979). The evaluation of home-range size, shape, structure, and degree of overlap plays a substantial role in understanding the species’ ecology.

Space-use patterns vary greatly among mammals, as they reflect the way of locomotion of the species associated with the environment in which that locomotion takes place. Subterranean mammals seem to be extremists in this respect because most of their activities take place underground, where their locomotion is confined to the self-constructed burrow systems (Nevo 1999). Importantly, these burrow systems represent both the home range and the exclusive and defended territory, therefore these two terms can be used as synonyms here (Nevo 1979). Since underground mobility is associated with the high energy expense of excavating the burrows (Vleck 1979), it has been supposed that underground burrow systems, once established, are relatively stable (Nevo 1999). Nevertheless, contrary to subterranean insectivores, subterranean rodents are vegetarians that need to continuously extend and alter their burrows to ensure access to food resources. Thus, we can assume that their burrow systems are dynamic structures where new tunnels are constantly built and the old ones abandoned and backfilled (Šklíba et al. 2009, Zuri & Terkel 1996). All the above-mentioned facts make subterranean rodents important models for studying home-range dynamics and for testing hypotheses about factors that delineate the space-use patterns.

Home-range size is primarily associated with cost-benefit considerations based on resource acquisition, which somewhat corresponds to the size of the animal (McNab 1963). In general, larger species occupy

larger home ranges to meet their higher requirements of resources (Tucker et al. 2014). This usual allometric relationship between home-range size and body mass is disproportioned in subterranean rodents due to the high energy expense of digging; they have smaller home-ranges compared to similarly sized aboveground rodents (Harestad & Bunnell 1979). Besides, space-use patterns of subterranean rodents vary due to various factors including resource availability (Cutrera et al. 2010, Reichman et al. 1982), soil conditions (Lövy et al. 2015, Zuri & Terkel 1997), population density (Ostfeld 1985), and predation risk (Lacey 2000).

Since subterranean rodents search for food by extremely energetically costly digging, they can be expected to economize their burrowing activity primarily in response to food supply, soil characteristics and their variation (usually associated with seasonal change in precipitation). Generally, species from areas where plant biomass is low are expected to have larger burrow systems than those from sites with a high plant productivity (Cutrera et al. 2010, Davies & Jarvis 1986, Kubiak et al. 2017, Reichman et al. 1982). Moreover, species that have a more generalized diet and/or forage occasionally/regularly aboveground are expected to occupy smaller home ranges than species depending mainly on a narrow range of food resources, i.e. strictly subterranean species foraging exclusively on underground plant storage organs. Indeed, a comparison of burrow lengths in two African solitary species close in their body sizes, but differing in their foraging ecology, *Tachyoryctes macrocephalus* and *Bathyergus suillus*, shows a significant difference. Contrary to *Bathyergus*, *Tachyoryctes* regularly emerges on the surface and forages on aboveground vegetation, which is proposed as one of the reasons why *Tachyoryctes* exploits a much smaller area (from discussion of the study Jarvis & Sale 1971).

The energetic demands of digging together with spatial behaviour are affected by soil conditions, particularly soil moisture and hardness, which are usually not consistent throughout the year. Consequently, different seasonal space-use patterns related to seasonal changes in soil conditions can be observed in subterranean rodents. Burrowing activity

usually increases during the rainy season, when the soil becomes wet and more easily workable, and digging is therefore energetically less demanding (Katandukila et al. 2014, Romañach et al. 2005a, Zuri & Terkel 1997). Some strictly subterranean species such as *Spalax ehrenbergi* and *Heliophobius argenteocinereus* are reported to seasonally modify their burrow system architecture. Whereas they usually excavate long linear tunnels during the rainy season, in the dry season they tend to excavate short side burrows and deposit soil in unused old tunnels mainly because of higher energetic costs related to pushing hard soil into the mounds (Lövy et al. 2015, Šumbera et al. 2003, Zuri & Terkel 1997). In addition, rainfall promotes plant growth, and the burrows may be extended for the primary purpose of food acquisition, especially in the cases where food resources occur below the ground (Davies & Jarvis 1986). On the other hand, animals are expected to utilise smaller areas when food abundance is high (Hubbs & Boonstra 1998). The latter might better fit to surface-foraging fossorial rodents because their food resources, contrary to geophytes, exhibit a relatively continuous local distribution and are easier (i.e. in a smaller area) to obtain when abundant. Indeed, pocket gophers were reported to decrease their home range size seasonally with an increasing food availability and vice versa (Pigage & Pigage 2010, Romañach et al. 2005b). An alternative scenario supposes that the decrease of the home range size is density-dependent, assuming that consumer density increases in response to food availability (Erlinge et al. 1990, Quirici et al. 2010). Nevertheless, increased population density can also lead to different spatial strategies, such as a spatial shift or relocation (Bowler & Benton 2005, Maher & Burger 2011).

Dispersing, as well as any other type of long-distance movement, represents a very risky strategy for any subterranean rodent, since it requires either energetically demanding digging of new tunnels or risky movements aboveground (Lacey 2000, Malizia et al. 1995, Németh et al. 2016). Therefore, we can expect it to occur infrequently and typically in young (or subadult) individuals that are forced to leave the maternal burrow systems and establish their own ones in order to avoid inbreeding and a

high level of competition with conspecifics (Rado et al. 1992, Williams & Cameron 1984). However, adults also make occasionally long movements far away from their original home range even in the case of strictly subterranean rodents. Naked mole rat adults of both sexes have been reported to travel average distances around 300 m (maximum 2 km) to establish their own new colonies (Braude 2000). In fossorial rodents, distances more than 500 metres, travelled mostly aboveground, were recorded in pocket gophers (Daly & Patton 1990, Vaughan 1963, Warren et al. 2017, Williams & Baker 1976). Dispersing individuals can either establish their territories in a new suitable unoccupied area (Vaughan 1963) or reutilize an existing but abandoned burrow system (Šumbera et al. 2012, Williams & Baker 1976). Leaving aside the above-mentioned avoidance of inbreeding and competition, the question then arises: what forces the adults to move from their original home range? Unfortunately, few studies have been conducted on this topic and from the little we know, dispersion of adult individuals can occur as a result of dramatic changes in habitat characteristics (Clobert et al. 2012, Barnard 2004). Specifically, intense flooding, drought, or a seasonal decrease in food availability can cause the abandoning of the original home range and a long distance relocation (Ingles 1949, Williams & Baker 1976)

Apart from the social and eusocial species, subterranean rodents occupy burrow systems individually (Nevo, 1979). Plural occupancy of burrows and home-range overlap are rather rare in solitary species, except during the breeding season (Hansen & Miller 1959). Sometimes, however, occasional excursions into a neighbouring burrow system have been reported, e.g. in *Spalax galili* (Šklíba et al. 2016b) and in solitary tuco-tucos, *Ctenomys rionegrensis* (Tassino et al. 2011). Spatial overlap recorded among adult tuco-tucos provides evidence of the existence of some social tolerance according to the authors. To date, no other cases of social tolerance in solitary subterranean rodents have been documented. It would be interesting to explore whether subterranean rodents relax the boundaries of their home ranges under certain circumstances, especially in species living in harsh environments and/or at high population densities,

where adjacent burrow systems are tightly packed. An example of such a species can be the giant root-rat, whose spatial behaviour is discussed in Chapter III.

1.5. A unique fossorial rodent, the giant root-rat (*Tachyoryctes macrocephalus*) as an example of a species adapted to harsh environmental conditions

The giant root-rat (*Tachyoryctes macrocephalus*, Rüppell 1842) belongs to myomorph fossorial rodents of the subfamily Rhizomyinae (family Spalacidae), consisting of four species of bamboo rats from southern Asia and two species of root-rats from eastern Africa (Wilson et al. 2017). Although the current diversity of the subfamily is modest, it enjoyed a greater diversification in the past, with 33 species known from the fossil record (López-Antoñanzas et al. 2013). The only African genus, *Tachyoryctes*, is discontinuously distributed over Ethiopia, Somalia, Kenya, Tanzania, Rwanda, Uganda, Burundi, and DR Congo at altitudes ranging from 1500 m to over 4000 m (Kingdon et al. 2013). The taxonomy of this genus is highly controversial. Many species and subspecies have been described but a strong dichotomy about the number of species and the systematics of this genus is found in literature. *Tachyoryctes macrocephalus* and *Tachyoryctes splendens* represent two major morphological forms within the genus and some authors accept them as two conventional species (Kingdon et al. 2013, Wilson et al. 2017). According to others, the genus can be divided into more than ten species (Monadjem et al. 2015). The latest study on the taxonomy of the genus *Tachyoryctes*, based on samples representing most of its geographic distribution, has established the existence of six separate genetic clades which should be treated as separate species (Šumbera et al. 2018).



Figure 5. The giant root-rat (*Tachyoryctes macrocephalus*) forages out of the burrow.

Tachyoryctes macrocephalus is morphologically well differentiated from any other member of the genus. It is distinguished by its large size, narrow width of the interorbital constriction, upper incisor width and geographic location. *T. macrocephalus* is endemic to highland grasslands and moorlands in the Afroalpine zone of the Bale Mountains National Park (BMNP), Ethiopia, occurring at very high altitudes (from 3200 to 4150 m a.s.l., Yalden 1985). It is considered to be endangered according to the IUCN Red List (Corti & Lavrenchenko 2009, Yalden 2013). Root-rats are diurnal, spending most of the time underground but regularly emerging on the surface in order to forage or remove the soil (Sillero-Zubiri et al. 1995). They forage on a wide range of grasses and herbs, which they typically collect around burrow openings with half of their body poking out of the burrow. Root-rats are solitary, individually occupying their self-constructed burrow systems. They prefer deep, well drained soils where they burrow tunnels about 12 to 15 cm in diameter with narrower entrances

which are regularly plugged to buffer against temperature extremes (Yalden 1985).

Among other *Tachyoryctes* species and fossorial rodents in general, it is one of the most peculiar due to the combination of several unusual features. First, the giant root-rat belongs to the largest fossorial/subterranean rodents with a weight of adults reaching up to one kilogram. Second, its dorsally placed eyes (the only analogy in mammals occurs in the aquatic hippopotamus) have likely evolved as an adaptation to detect predators during its relatively frequent aboveground activity. Third, despite the fact it lives in harsh climatic and environmental conditions of the Afroalpine ecosystem, the giant root-rat occurs in relatively high densities (17 – 40/ha, the highest population density was detected on swamp shores in Web Valley – 70/ha [see Chapter I]). Last but not least, this species is important from the conservation point of view because it is a staple food for the most endangered canid in the world, the Ethiopian wolf *Canis simensis*. Root-rats represent about 50 % of its diet in BMNP (Sillero-Zubiri et al. 1995, Yalden 1985). However, the giant-rat's ecosystem role is probably much greater and we elaborate it in Chapter I. It transforms the ecosystem through its burrowing activity and herbivory similarly to ecosystem engineers such as pocket gophers (Reichman & Seabloom 2002).

To conclude, as giant root-rats spend most of the time underground but forage regularly aboveground (Sillero-Zubiri et al. 1995) in challenging climatic and environmental conditions (high temperature fluctuation, limited food availability, and high predation risk), they represent an interesting model to study the combined effects of above- and underground selective pressures on various aspects of species biology, mainly daily activity timing and space-use patterns. Furthermore, the giant root-rat can be classified as an ecosystem engineer since its burrowing activity markedly disturbs the soil, enriches it with nutrients, and supports the growth of vegetation, all of which has a significant influence on plant composition, as well as other mammal species (see in Chapter I).



Figure 6. Ethiopian wolf (*Canis simensis*) – the most important predator of the giant root-rat.

2. Aims of the thesis

- completion of ecological and behavioural data on an exceptional fossorial rodent, the giant root-rat (*Tachyoryctes macrocephalus*) and contribution to interspecific comparisons of subterranean rodents with different levels of underground lifestyle helpful to understanding the evolution of specific characteristics and adaptations
- evaluation of the giant root-rat's impact on various ecosystem features and opening the new horizons for the management and conservation of the unique Afroalpine ecosystem
- determination of the daily amounts of outside-nest and aboveground activity of the giant root-rat in its natural habitat, and assessment of its daily activity pattern and how it is affected by environmental conditions, using the radio-tracking method
- quantification of home-range size of the individual root-rats and overlap of neighbouring individuals' home ranges and description of how root-rats change their space-use patterns in response to seasonal environmental changes

3. References

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Chapter I

*Ecological role of the giant root-rat (*Tachyoryctes macrocephalus*) in the Afroalpine ecosystem.*

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ORIGINAL ARTICLE

Ecological role of the giant root-rat (*Tachyoryctes macrocephalus*) in the Afroalpine ecosystem

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Abstract

Rodents with prevailing subterranean activity usually play an important role in the ecosystems of which they are a part due to the combined effect of herbivory and soil perturbation. This is the case for the giant root-rat *Tachyoryctes macrocephalus* endemic to the Afroalpine ecosystem of the Bale Mountains, Ethiopia. We studied the impact of root-rats on various ecosystem features within a 3.5-ha study locality dominated by *Alchemilla* pasture, which represents an optimal habitat for this species, in 2 periods of a year. The root-rats altered plant species composition, reducing the dominant forb, *Alchemilla abyssinica*, while enhancing *Salvia merjame* and a few other species, and reduced vegetation cover, but not the fresh plant biomass. Where burrows were abandoned by root-rats, other rodents took them over and *A. abyssinica* increased again. Root-rat burrowing created small-scale heterogeneity in soil compactness due to the backfilling of some unused burrow segments. Less compacted soil tended to be rich in nutrients, including carbon, nitrogen and phosphorus, which likely affected the plant growth on sites where the vegetation has been reduced as a result of root-rat foraging and burrowing.

Key words: Afroalpine, ecosystem engineer, fossorial rodent, soil disturbance, *Tachyoryctes macrocephalus*

INTRODUCTION

Fossorial rodents (i.e. those adapted to digging) have a high impact on ecosystems (Reichman & Seabloom 2002; Reichman 2007; Zhang 2007). Their selective consumption of plants, including subterranean parts, di-

rectly affects plant communities. However, the burrowing of these animals, consisting of the perturbation and transport of large amounts of soil, may have an even greater effect. The ecological impacts of burrowing include the aeration and irrigation of soil, alteration of nutrient availability, hindering or facilitation of soil erosion, increasing microhabitat heterogeneity, and the creation of an environment for a variety of other invertebrate and vertebrate commensals, including other rodents (Reichman & Seabloom 2002; Zhang *et al.* 2003).

Burrowing and the subsequent backfilling of unused

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tunnels by fossorial rodents reduces soil hardness and bulk density (Wang *et al.* 1993; Huntly & Reichman 1994; Galiano *et al.* 2014). Because it involves mixing soil from different horizons, it can also affect soil nutrient concentrations. Soil from the deeper horizons is usually nutrient-poor. However, deposition of the soil on the surface may promote nitrification and mineralization (Reichman 1988; Wang *et al.* 1993; Sherrod & Seastedt 2001; Reichman & Seabloom 2002; Zhang *et al.* 2003; Zhang 2007). Changes in nutrient concentrations as well as the physical properties of soil affect plant biomass and composition. For example, areas around mounds usually have a higher plant biomass than control sites, even though, on a larger scale, the biomass can decrease (Mielke 1977; Grant *et al.* 1980; Wang *et al.* 1993; Zhang *et al.* 2003). Mounds can also effectively suppress short vegetation underneath, while providing fresh ground for early plant succession (Wang *et al.* 1993; Huntly & Reichman 1994).

The activity of fossorial rodents creates dynamic microhabitat heterogeneity, which usually increases the number and/or diversity of plant species (Huntly & Reichman 1994; Reichman & Seabloom 2002; Reichman 2007). An exception to the rule seems to be the Plateau zokor *Eospalax fontanierii* living in the alpine meadows of the Tibetan Plateau, which has been reported to decrease the number of plant species while increasing the dominance of plants unpalatable to zokors (Zhang & Liu 2003; Zhang *et al.* 2003, 2004; Zhang 2007). The impact of zokors on the ecosystem was found to be further increased by livestock grazing (Zhang *et al.* 2003; Zhang 2007). This illustrates the complexity of ecological relationships between fossorial rodents and other ecosystem features.

An example of a unique ecosystem inhabited by a fossorial rodent is the Afroalpine ecosystem of the Bale Mountains in south-eastern Ethiopia. The alpine ecosystem in Africa covers many isolated mountain blocks of which that of the Bale Mountains is the largest (Yalden 1983). The giant root-rat (giant molerat) *Tachyoryctes macrocephalus* Rüppell, 1842 (Rhizomyinae, Spalacidae), is a fossorial rodent endemic to this mountain range (Yalden & Lagen 1992) and is considered Endangered according to the IUCN Red List (Corti & Lavrenchenko 2008). The giant root-rat is known as the most important prey of the Ethiopian wolf *Canis simensis* in the Bale Mountains (Sillero-Zubiri & Gottelli 1995), but its ecological role is much broader. It constructs elaborate underground burrows and forages on plants usually in the immediate vicinity of the bur-

row openings (Yalden 1975, 1985; Sillero-Zubiri *et al.* 1995b; Yaba *et al.* 2011). Areas of high root-rat density are characterized by “spongy” soil and mounds covering a large proportion of the ground surface (Yalden 1985).

We studied the ecology of the giant root-rat in a representative study locality of the Afroalpine pasture, which has been recognized as its optimal habitat (Sillero-Zubiri *et al.* 1995b), in the early dry season (shortly after the last heavy rains) and in the late dry season (with very dry soil and vegetation). The aims of our study were: (i) to identify ecosystem features (including other vertebrates) affected by the activity of the giant root-rat; (ii) to describe vegetation and soil characteristics in the giant root-rat’s optimal habitat and their changes in the course of the dry season; (iii) to evaluate the impact of the activity of the giant root-rat on plant species composition, vegetation cover and fresh plant biomass; and (iv) to evaluate the impact of the activity of the giant root-rat on soil characteristics, such as hardness and nutrient contents.

MATERIALS AND METHODS

Study locality

The study was conducted in the Web Valley, Bale Mountains National Park, Ethiopia (N6°59.6′, E39°42.0′, 3500 m a.s.l.). The study locality of 3.5 ha is situated on a gently sloping Afroalpine meadow formed by *Alchemilla abyssinica* pasture, and grass pasture (vegetation classes established by Tallents & Macdonald [2011]), adjacent to a periodic wetland (Fig. 1). The locality is subjected to grazing by cattle, horses, sheep and goats. The annual rainfall in the area is around 1000 mm and climatic conditions are characterized by a warm April–October rainy season and a November–March dry season, with warm days and sub-zero night temperatures (Sillero-Zubiri 1994).

Field work

Data were collected in the early dry season (December 2013) shortly after the end of the last heavy rains, and in the late dry season (March 2014). Root-rats and other vertebrates emerging out of the root-rat burrows (or utilizing them in another way) were noted across the study locality during the parallel radio-tracking study which involved 28 radio-collared root-rats. The root-rats were monitored from 0600 to 2100 hours over 18 radio-tracking days during which an observer traversed the study locality once per hour. In addition, we con-



Figure 1 Study locality in the Web Valley, Bale Mountains. The dashed line marks a 10-m wide strip along the shore of the periodic wetland with a conspicuously high population density of the giant root-rat.

ducted five complete 24h radio tracking days (T. Vlasatá *et al.* 2007). The population density of root-rats across the study locality was established based on the observation of both marked and unmarked individuals.

Data on vegetation and soil characteristics were collected in each of the 2 periods of the dry season at 60 sampling points across the study locality located using a handheld GPS and randomly generated coordinates. At each of the points, we delimited a 4×4 m square where we estimated vegetation cover (%), and the cover of the 16 most dominant plant species of the study area, plus grasses treated as a single category, as they were impossible to identify to the species level (%). The size of square was chosen to be comparable to root-rat home range size (J. Šklíba, unpubl. data) but still easy to survey in estimating plant species covers. We did not record rare and diminutive plant species (with the cover less than 1% in all squares) because they are unlikely to be important food for root-rats. The amount and character of root-rat activity marks within the respective 4×4 m squares were quantified using the following 3 parameters: (1) number of fresh burrow openings, (2) number of old burrow openings (recognized by weathered soil plugs) and (3) area covered by mounds (%). These 3 parameters of root-rat activity were selected to reflect current utilization and past utilization, as well as the intensity of soil perturbation over a longer period. In addition to these parameters we calculated the number of

root-rat burrow openings used by other rodents within the respective 4×4 m squares. These burrow openings were recognized by an incidence of mice droppings and/or typical aboveground rodent highways connecting the burrow openings.

In the center of each 4×4 m square we delimited a 20×20 cm square where we collected all fresh vegetation, including fleshy rhizomes and bulbs up to the depth of 10 cm. The size of this square was selected to roughly fit the scale at which the soil and vegetation is directly affected by root-rats burrowing and foraging. The collected fresh plant biomass was weighed per species, again with the exception of grasses, which were pooled into a single category. Because the 20×20 cm square was too small to estimate vegetation cover, we calculated this parameter for a 1×1 m square with the same center. In the late dry season only (i.e. after prolonged experience with the observation of root-rat activity marks), we also classified the 20×20 cm squares into 4 groups according to the presence and estimated age of the root-rat activity marks: fresh, recent, old and none. Fresh (up to few weeks old) marks were defined as presently used burrows found beneath the 20×20 cm square and fresh (not weathered) mounds or burrow openings nearby (up to approximately 1 m). Recent marks (up to a few months old) were indicated by easy-to-track backfilled tunnels beneath the 20×20 cm square and weathered mounds and burrow openings

nearby. Old (several months to years) marks were indicated by barely traceable backfilled tunnels and levelled mounds, overgrown burrow openings and burrows used by other rodents nearby.

In the sides of the excavated 20 × 20 cm squares, at the depth of 15 cm, we measured soil hardness (cone resistance, N·cm⁻²) using a hand penetrometer (06.06, Eijkelkamp, Agriresearch Equipment, Giesbeek, Netherlands). Five measurements more than 10-cm apart were taken for each sampling point, for which the mean and variance coefficient (CV) was calculated. Additional soil analyses, measuring soil bulk density, were conducted in the early dry season only (in the late dry season the soil became too hard to take the samples in the same way). Next to each of the 20 × 20 cm squares, at a depth of between 12 and 18 cm, we collected 100 cm³ of soil using a soil sample ring pushed horizontally into the soil profile. The soil samples were weighed and then sun-dried in a paper bag to a constant weight. Ten grams of dry soil per sample was then collected for an analysis of soil nutrients.

Analysis of soil nutrients

The concentrations of nitrogen and carbon in the soil samples collected at the 60 randomly placed points in the early dry season were determined using a CHNS vario MICRO cube elemental analyzer (Elementar Analysensysteme GmbH, Germany). Soil samples were ground up in a ball mill (Mixer Mill MM 200, Retsch, Germany) and then completely oxidized using the dry combustion method (Nelson & Sommers 1996). Plant available phosphorus, potassium, sodium, calcium and magnesium concentrations were analyzed by means of Mehlich 3 extractant (Mehlich 1984). Concentrations of phosphorus were determined according to Murphy and Riley (1969), using a flow injection analyzer (Quick-Chem 8500, Lachat, USA). Concentrations of Ca, Mg, K and Na were measured using an atomic absorption spectrometer (Varian AA 240Z, Varian, Australia).

Statistical analyses

Throughout the text, means are presented ± SD and with range, where appropriate. Multivariate analyses (redundancy analyses [RDA] and detrended canonical correspondence analyses [DCCA]) were performed using the software package CANOCO for Windows, version 4.52 (ter Braak & Šmilauer 2002). Other statistical tests were performed with the R statistical package (R Core Team 2013).

To compare parameters of vegetation, soil and root-

rat and other rodent activity between the early and late dry season, we used beta regression (BR) and generalized linear models (GLM). The BR was used to test differences in vegetation cover and area covered by mounds (both expressed as a proportion) using the Betareg package (Cribari-Neto & Zeileis 2010). GLM was used to compare numbers of fresh burrow openings, old burrow openings and burrow openings used by other rodents (all approximated by the quasi-Poisson distribution), and soil hardness and fresh plant biomass (both approximated by the gamma distribution with the log link function). To treat overdispersion in our data we used the quasipoisson instead of Poisson family distributions in all models where dependent variables were counts.

In each period, parameters of vegetation, soil and root-rat and other rodent activity were also computed for the 10-m wide strip of land along the shore of the periodic wetland with a conspicuously high population density of root-rats. In this strip the parameters were computed based on 6 out of the 60 sampling points. These 6 points were compared with the remaining 54 sampling points located in the rest of the study locality using BR and GLM (for statistical details see the previous paragraph).

The effect of the 3 parameters of root-rat activity (number of fresh burrow openings, number of old burrow openings and area covered by mounds) on plant species composition (set of 17 variables representing cover by the respective plant species in the 4 × 4 m squares) was tested by redundancy analysis (RDA). The log-transformed distance of the sampling squares from the edge of the periodic wetland was used as a covariate. Forward selection and Monte Carlo permutation tests were used to select the optimal set of explanatory variables. Species values were centered and standardized (to have zero mean and unit variance). RDA is a method requiring a linear response of species (response variables) to environmental gradients. This assumption was tested using the detrended canonical correspondence analysis (DCCA) run with the same variables in CANOCO for Windows, version 4.52 (ter Braak & Šmilauer 2002). Using the DCCA we computed the lengths of gradients measuring the beta diversity in plant species composition along the individual independent gradients (ordination axes). The longest gradient was always smaller than 4, which generally justifies using linear methods (Lepš & Šmilauer 2003). The relationships of individual plant species cover to the respective parameters were subsequently tested by Spearman's correlations with Bonfer-

roni correction, where alpha was divided by the number of species tested (17).

To test the effect of the presence and estimated age of root-rat activity marks on fresh plant biomass, vegetation cover and soil hardness, and the CV of soil hardness we used GLM with gamma distribution and log link function, BR, GLM with Gaussian distribution and identity link function, and GLM with gamma distribution and log link function, respectively. For post-hoc comparisons we used Tukey's honest significant difference test for unequal *N*. The relationship between soil hardness and bulk density was tested by linear regression. The relationship between soil bulk density and nutrient concentrations was tested by Spearman's correlation with Bonferroni correction where alpha was divided by the number of nutrients tested (7).

Ethical statement

The protocol for the research project was approved by the Ethics Committee of the Faculty of Science, University of South Bohemia and by the Ethiopian Wildlife Conservation Authority. The study conforms to the provisions of the Declaration of Helsinki (as revised in Tokyo 2004), available at <http://www.wma.net/e/policy/b3.htm>.

RESULTS

The population density of the giant root-rat across the study locality, based on observations of individuals emerging above ground, was 22 individuals per hectare and was highest in the 10-m wide strip along the edge of the periodic wetland (approximately 70 ha⁻¹). Root-rats generally displayed 2 modes of foraging. They either simply plucked the aboveground parts of plants in close proximity of a burrow opening (eating them *in situ* or transporting them into the burrow) or they extended their burrow opening into a shallow ditch, up to a few decimeters long, which was the result of harvesting plant material, including roots and rhizomes. Root-rats constructed mounds of excavated soil and mounds of partially decomposed old nest bedding. Other rodents were regularly observed utilizing abandoned root-rat burrows (recognized by their large tunnel diameter) of various ages. The most frequently observed species were the black-clawed brush-furred rat *Lophuromys melanonyx* and Blick's grass rat *Arvicanthis blicki* during the day and the white tailed Ethiopian rat *Stenocephalemys albocaudata* at night. A zorilla *Ictonyx striatus* was also recorded entering into a root-rat burrow

Table 1 Parameters of vegetation, soil and root-rats' and other rodents' activity in the whole study locality of Web Valley, Bale Mountains based on 60 randomly placed sampling points and separately for the 10-m wide strip along the wetland shore based on 6 of these sampling points

Area	Season	Vegetation cover (%)	Fresh plant biomass (g·m ⁻²)	Soil hardness (N·cm ⁻²)	Soil bulk density (g·cm ⁻³)	Area covered by mounds (%)	Fresh burrow openings (ha ⁻¹)	Old burrow openings (ha ⁻¹)	Burrow openings used by other rodents (ha ⁻¹)
Whole study locality	Early dry	68.9 ± 13.7	384 ± 160	191 ± 71	1.05 ± 0.11	8.0 ± 12.5	1510 ± 2273	7396 ± 4904	1542 ± 1871
	Late dry	47.7 ± 18.1	208 ± 166	473 ± 107	n.a.	14.7 ± 20.7	634 ± 1136	7313 ± 3872	1917 ± 2146
	Test statistic	$\chi^2 = 43.3$	$F = 26.3$	$F = 254.9$		$\chi^2 = 0.81$	$F = 8.1$	$F = 0.0$	$F = 1.0$
	<i>P</i>	<0.0001	<0.0001	<0.0001		0.37	0.005	0.92	0.31
Strip along the wetland shore	Early dry	64.2 ± 19.9	384 ± 119	138 ± 81	1.05 ± 0.13	26.8 ± 24.0	6458 ± 1614	6875 ± 5123	0 ± 0
	Test statistic	$\chi^2 = 0.6$	$F = 0.3$	$F = 4.4$	$F = 0.0$	$\chi^2 = 10.8$	$F = 28.0$	$F = 0.1$	$F = 10.2$
	<i>P</i>	0.42	0.6	0.039	0.92	<0.0001	<0.0001	0.78	0.002
	Late dry	35.8 ± 22.5	426 ± 324	425 ± 107	n.a.	46.7 ± 22.1	2500 ± 1311	8958 ± 3104	104 ± 255
Test statistic	$\chi^2 = 3.8$	$F = 10.6$	$F = 1.4$		$\chi^2 = 15.1$	$F = 12.4$	$F = 1.1$	$F = 9.2$	
<i>P</i>	0.05	0.002	0.235		<0.0001	<0.001	0.294	0.004	

Means are presented ± SD. The statistical analyses test differences between seasons in the part concerning the whole study locality and differences between the strip and the rest of the study locality in each season in the part concerning the strip. n.a., not applicable.

once. The moorland chat *Cercomela sordida* was observed in close association with the giant root-rats regularly feeding on invertebrates from root-rat nest bedding deposited aboveground. Ethiopian wolves were routinely observed hunting root-rats and occasionally other diurnal rodents at the study locality and occasionally slept on the root-rats' old nest bedding mounds.

The parameters of vegetation, soil, and root-rats' and other rodents' activity in the study locality computed separately for the early and late dry season are presented in Table 1. There was a significant decrease in vegetation cover and fresh plant biomass and an increase in soil hardness between the early and late dry season. In addition, there was a decrease in the density of fresh burrow openings (see Table 1 for statistical details). In the shore of the periodic wetland, characterized by a

high root-rat population density, there was a larger proportion of the area covered by mounds, a higher density of fresh burrow openings, and a lower density of burrow openings used by other rodents. Vegetation cover tended to be lower in this strip in the late dry season, which was approaching significance, but this was not true for the fresh plant biomass, which was even higher in the strip than in the rest of the study locality in the late dry season. Soil hardness was lower in the strip than in the remaining part of the study locality, but it was significant only in the early dry season.

A list of the most abundant plants (out of roughly 50 species of vascular plants excluding grasses found in the study area), with their respective biomasses and covers, for both periods is presented in Table 2. By far the most abundant plant was *A. abyssinica*, followed by grass-

Table 2 List of dominant plant species of the study locality, their biomasses, covers and associations with parameters of giant root-rats' and other rodents' activity

Plant	Fresh biomass (g·m ⁻²)		Cover (%)		Related parameters of root-rats' and other rodents' activity
	Early dry season	Late dry season	Early dry season	Late dry season	
<i>Alchemilla abyssinica</i>	205.4	112.4	39.3	30.9	ORB ^{†,‡} (positive), FB ^{†,‡} (negative)
Grasses	38.0	33.3	6.3	6.5	M, [‡] OB, [‡] ORB [†] (all negative)
<i>Salvia merjame</i>	25.2	7.7	4.0	1.4	OB, ^{†,‡} M ^{†,‡} (positive)
<i>Alchemilla pedata</i>	18.6	23.8	3.6	0.7	FB [†] (positive)
<i>Plantago afra</i>	14.9	<0.1	4.9	1.0	M [‡] (negative)
<i>Polygonum afromontanum</i>	12.4	12.0	0.7	0.9	OB ^{†,‡} (positive)
<i>Dicrocephala alpina</i>	8.3	0.2	<0.1	<0.1	
<i>Swertia lugardae</i>	8.2	<0.1	1.4	<0.1	
<i>Geranium arabicum</i>	7.7	3.6	<0.1	<0.1	
<i>Cotula cryptocephala</i>	7.7	2.8	0.4	<0.1	M, [†] FB [†] (positive)
<i>Oxalis</i> sp.	6.1	0.4	<0.1	<0.1	
<i>Urtica simensis</i>	5.5	1.0	0.5	0.2	M, ^{†,‡} FB, [‡] OB [†] (positive)
<i>Artemisia afra</i>	5.3	1.6	1.9	2.5	
<i>Carex</i> sp.	3.7	3.2	0.2	0.7	M ^{†,‡} (negative)
<i>Trifolium cryptopodium</i>	3.7	1.0	<0.1	<0.1	FB [†] (positive)
<i>Cineraria abyssinica</i>	2.2	0.6	<0.1	<0.1	
<i>Carduus camaecephalus</i>	2.0	0.8	<0.1	<0.1	
All plants	390.4	219.9	68.9	48.6	

Only the parameters whose relationship to the particular plant species cover (based on the randomly placed 4 × 4 m sampling squares) are significant (Spearman's correlation with Bonferroni correction applied; alpha = 0.05/17) in the [†]early dry or [‡]late dry season are included. The parameters are: number of fresh burrow openings (FB), number of old burrow openings (OB), area covered by mounds (M) and number of root-rat burrow openings used by other rodents (ORB).

es, *Salvia merjame*, and *Alchemilla pedata*. The amount of root-rat activity marks quantified using the 3 parameters (number of fresh burrow openings, number of old burrow openings and area covered by mounds) significantly affected plant species composition in both periods (RDA: all canonical axes explained 12.2% and 12.0% of the data variability; $F = 3.1, 2.7; P = 0.0003, 0.0005$, respectively). In both periods, the amount of explained variability significantly increased in each step in which an explanatory variable was added until all of the 3 variables were included (Monte Carlo permutation test, $P < 0.05$). Relationships between plant species covers and the parameters of root-rat and other rodent activity which were significant in either period (Spearman's correlations with Bonferroni correction, $P < 0.0029$) are presented in Table 2. The following relationships were significant in both periods. In squares with a higher density of fresh burrows there was a lower cover of *A. abyssinica*. In squares with a higher density of old burrows there was a larger cover of *S. merjame* and *Polygonum afromontanum*. In squares with a large cover of mounds (i.e. with high soil disturbance), species such as *Urtica simensis* and *S. merjame* had larger covers, whereas *A. abyssinica* and *Carex* sp. had smaller covers. Squares with a higher density of burrows inhabited by other rodents had a higher cover of *A. abyssinica*.

The presence and estimated age of root-rat activity marks assessed during the late dry season significantly affected vegetation cover (BR: $\chi^2 = 41.8, P < 0.0001$; see Fig. 2a for post-hoc comparisons) but not plant biomass (GLM: $F = 0.6, P = 0.6$). Furthermore, it significantly affected the composition of plant species biomasses, even though it explained only 6.5% of data variability (RDA: $F = 1.4; P = 0.03$). The presence and estimated age of root-rat activity marks also affected soil hardness (GLM: $F = 19.5, P < 0.0001$) and the CV of soil hardness (GLM: $F = 4.3, P = 0.008$, see Fig. 2b,c for post-hoc comparisons). Soil hardness was positively correlated with soil bulk density (linear regression: $F_{1,58} = 5.7, R^2 = 0.89; P = 0.02$). Concentration of nutrients in the soil samples is presented in Table 3. Concen-

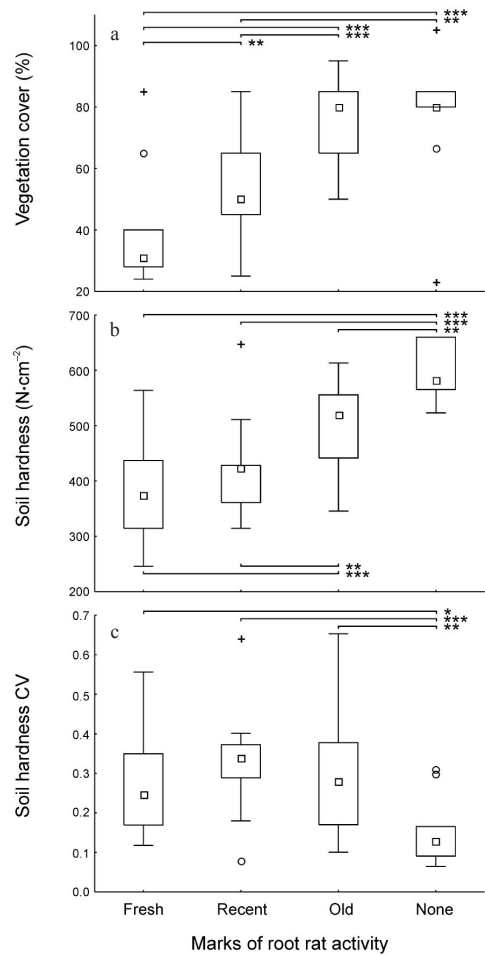


Figure 2 Vegetation cover (a), soil hardness (b) and variance coefficient (CV) of soil hardness (c) on sites differing in presence and age of root-rat activity marks in the late dry season. Medians, quartiles, non-outlier ranges and extremes are plotted. Horizontal lines link statistically different groups (Tukey's honest significant difference test for unequal N ; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Table 3 Concentration of nutrients in the soil samples (%)

Nutrient	C	N	P	K	Na	Ca	Mg
Mean	2.6	0.25	0.025	0.42	0.39	1.96	0.29
SD	0.9	0.07	0.032	0.14	0.02	0.37	0.04
Range	1.5–7.8	0.16–0.72	0.004–0.227	0.20–0.84	0.35–0.45	0.83–2.68	0.19–0.36

trations of all 7 nutrients analyzed (Table 3) were negatively correlated with the soil bulk density. In C, N, P and Mg it was significant even after Bonferroni correction was applied (Spearman's correlations, $P < 0.007$).

DISCUSSION

Giant root-rats were shown to affect many ecosystem features in the Web Valley of Bale Mountains under the existing livestock grazing pressure. They reduced vegetation cover (but not biomass) and altered plant species composition. They created a small-scale heterogeneity in soil hardness, likely as a result of backfilling unused tunnels with less compact soil, which also affected nutrient concentrations. They also created a mosaic of sites differing in the age of their activity marks, which had different vegetation and soil characteristics. Several other rodents apparently benefitted from the root-rats' presence, occupying their abandoned burrows.

Tropical-alpine zones in general are characterized by relatively small seasonal and large daily climatic variation. This represents a major factor determining the characteristics of vegetation, which typically contains a limited number of life forms, often with stunted growth (Headberg & Headberg 1979; Körner 2003). The effect of such climatic conditions on height and other attributes of vegetation may resemble the effect of herbivores. It is, therefore, interesting to study ecosystems where the 2 effects are combined. Besides the root-rat, the study locality is heavily grazed by domestic livestock. We were unable to control the effect of livestock grazing but it seemed to be even across the area, as we did not observe any patches preferred or avoided by the livestock during the period of our study. However, the root-rat activity marks were conspicuously concentrated at some sites, especially along the shore of the periodic wetland.

Except for their preference for swamp shores, giant root-rats are known to concentrate in mima mounds, slightly elevated patches with different vegetation and soil properties supposedly created as a consequence of their own long-term activity (Sillero-Zubiri *et al.* 1995b). In our study locality mima mounds could not be clearly delimited and root-rats reached the highest population density (70 ha^{-1}) mainly along the shore of the periodic wetland. Maximum population densities estimated by Sillero-Zubiri *et al.* (1995b) in the same locality was even higher, reaching 90 ha^{-1} . Tallents (2007) estimated the maximum population density on the swamp edges to be 60 ha^{-1} and the maximum population density per Landsat pixel ($28.5 \times 28.5 \text{ m}$) to be 17.5 ha^{-1} ,

which is very similar to our results. The shore of the periodic wetland was characterized by reduced vegetation cover, especially in the late dry season, a large area covered by mounds and a very low incidence of abandoned root-rat burrows with marks of utilization by other rodents (Table 1). In the course of the dry season some root-rats extended their home ranges from the shore to the wetland but others remained resident even on sites where plant cover was severely reduced (T. Vlasatá, unpubl. radio-telemetry data). This might signify that the physical properties of soil, such as hardness and bulk density, which are, in turn, affected by the root-rats' own long-term activity, may play an important role in their habitat selection. In other words, at least in some sites, a high population density resulting in conspicuous habitat disturbance does not seem to lower the attractiveness of these sites for the root-rats over time. This may also explain the formation of mima mounds elsewhere in the Bale Mountains.

Giant root-rats usually feed at a very close distance (approximately a body length) from burrow openings either by digging out whole plants or by biting aboveground parts only. Both foraging modes severely affect vegetation cover and other characteristics but at a small range only. Another way root-rats affect vegetation is by pushing soil aboveground, which buries existing vegetation while creating sites for early plant succession. In our study, root-rat activity reduced vegetation cover (Fig. 2a) but not plant biomass, which may be considered surprising. A possible reason for this is either that changes of nutrient contents stimulate the growth of individual plants (Mielke 1977; Grant *et al.* 1980; Wang *et al.* 1993) or that the plants species more adapted to the perturbed sites are generally larger. The long-term effect of pocket gophers (*Thomomys talpoides*) was identified to even increase overall plant biomass (Grant *et al.* 1980). The decomposition of biomass buried under mounds can also increase the availability of nutrients and balance the negative effect of mound building on the plant biomass in this way (Sherrod & Seastedt 2001).

The creation of mounds can locally favor larger plants which are less vulnerable to burying. This can be the case with *U. simensis* and *S. merjame*. The former species, together with *Carduus camaecephalus*, whose association with fresh molehills was also positive but not statistically significant, is also characterized by mechanical defense against herbivores. This is similar to a high abundance of unpalatable plants observed in the Tibetan plateau as a consequence of the activity of the

plateau zokors (Zhang & Liu 2003). The roots of *C. ca-maecephalus* contain succulent tissue that is readily consumed by root-rats (J. Šklíba, unpublished observation), but protected by a thick layer of woody tissue. *S. mer-jame* together with *P. afroontanum* were also abundant at sites with older root-rat burrows. These species likely represent early succession plants growing on leveled molehills or at sites where vegetation has been depleted.

The species with the highest biomass of all plants across the study area was *A. abyssinica*. This short hemicryptophyte is also one of the main food plants of the giant root-rat (Yaba *et al.* 2011). Its abundance was severely reduced in areas with a high density of fresh burrow openings and mounds, likely as a consequence of both consumption and overlying by mounds. In contrast, the plant was more abundant at sites where abandoned root-rat burrows were occupied by other rodents. This species is likely a dominant late successional plant in the study area under the current livestock grazing pressure (see below).

The effect of root-rat activity on soil properties was best illustrated by reduction of soil hardness while increasing its small-scale spatial heterogeneity, which is indicated by the higher CV of soil hardness (Fig. 2b,c). Fossorial rodents usually backfill some unused tunnels with soil (Andersen 1987), which reduces soil hardness and bulk density (Huntly & Reichman 1994; Galiano *et al.* 2014). Interestingly, less compacted soil contained higher concentrations of nutrients. This is surprising, because soil from deeper horizons is usually nutrient-poor (Reichman 1988). The higher nutrient concentrations might be a consequence of a specific behavior of the giant root-rat. This species gathers large amounts of plant material as food and nest bedding. Old nest bedding, mixed in various proportion with soil and feces, is then disposed of both aboveground and in abandoned tunnels (J. Šklíba, unpubl. observation), which likely causes an increase in nutrient concentrations. A similar increase in soil phosphorus and potassium at a depth of 10–20 cm was detected by Galiano *et al.* (2014) at sites inhabited by *Ctenomys minutus*. The loosening of soil can also enhance nitrification and mineralization simply by increasing the surface area of soil aggregates (Litaor *et al.* 1996; Sherrod & Seastedt 2001). As a whole, soil in the study locality is characterized by a relatively low concentration of C and a relatively high concentration of N (Table 3). Whereas the former might be a consequence of low primary production as well as a fast decomposition of organic material, the latter may be partly a consequence of livestock grazing (see below).

For an evaluation of the role of the giant root-rat in the Afroalpine ecosystem of Bale Mountains one has to take into account its likely interaction with the grazing of domestic livestock. The numbers of cattle, horses, sheep and goats in the Bale Mountains National Park has grown continually in recent decades (Vial *et al.* 2011c), under some scenarios even approaching the ecosystem collapse threshold (Vial *et al.* 2011a). The effect of the livestock grazing on Afroalpine rodent fauna, including the giant root-rat in the Bale Mountains, is not yet well understood. The only published study on this phenomenon using livestock-proof enclosures was short-term only and revealed no clear trend in rodent densities following the removal of livestock (Vial *et al.* 2011b). Vial (2010) also related rodent abundances to livestock grazing impact estimated using a dung census in randomly placed 40 × 40 m plots. The relationship was generally negative, but with some variation according to species, season and year. For example, the livestock impact on *L. melanonyx* was significantly negative during the wet season of the first year of the study but significantly positive during the wet season of the second year. The negative relationship is surprising, because most common rodents of the Afroalpine ecosystem of the Bale Mountains, including the giant root-rat, are apparently adapted to open habitat and on a large scale they remain very abundant even in heavily grazed areas: Tallents (2007) surveyed rodent biomass across the whole Afroalpine zone of the Bale Mountains and found the highest value (9–12 kg·ha⁻¹) in short pastures in the Web Valley (where our study locality is situated), which is also the area with the highest livestock density (Vial 2010). In the Afroalpine ecosystem of the Guassa area in the central highlands (3200–3700 m a.s.l.) the population of *Arvicanthis abyssinicus* was found to respond positively to grazing and grass cutting (Ashenafi *et al.* 2012).

Considering the absence of unambiguous data, some studies on other ecosystems can help us to assess the relationships between the rodent fauna and livestock grazing in the Bale Mountains Afroalpine ecosystem. As parallels we can consider especially ecosystems characterized by high altitude, low primary production and/or low concentrations of nutrients. In ecosystems with low primary production, ungulate grazing can seriously affect nutrient cycles, especially increasing the availability of N for rapid regrowth of the grazed plants (Hobbs 1996). This can improve the quality of food for other herbivores, such as rodents, due to the increased biomass of young, highly palatable plant tissues. The

compensatory growth of plants can increase primary production above the level that would be reached in the absence of grazing. Nevertheless, this is unlikely to occur if the livestock grazing is heavy (Hobbs 1996). Ungulate grazing can also either increase or decrease plant species richness and the spatial heterogeneity of vegetation. In nutrient-poor ecosystems or ecosystems with slow regrowth these effects are usually negative (Proulx & Mazumder 1998; Hobbs 1996) but could possibly be altered or even reversed by the presence of burrowing herbivores, which usually increase both habitat heterogeneity and plant species richness (but see Zhang and Liu [2003] and Zhang *et al.* [2003] for the opposite), although they act on a much smaller scale (Huntley & Reichman 1994; Davidson *et al.* 2012). Ungulate grazing often suppresses grasses in favor of forbs (e.g. Medin & Clary 1989; Saetnan & Skarpe 2006), which might contribute to the dominance of the apparently grazing-tolerant *Alchemilla* in our study locality.

Ungulates change structural attributes of grassland habitats, which can severely influence rodent communities. Species most affected by changes in vegetation cover are litter-dwelling herbivores. Surface-dwelling species (usually granivores and omnivores) are much less affected by ungulates and can even profit from them (e.g. if the grazing increases the abundance of forbs and annual grasses with a higher seed production; Grant *et al.* 1982). In the alpine grasslands of the Tibetan plateau, even heavy livestock grazing increases the abundance of rodents, including the subterranean plateau zokor (Zhang *et al.* 2003, 2004). Ungulate grazing can also affect the ecosystem in interaction with a burrowing rodent. On the Mongolian steppe, each of 4 combinations of livestock grazing (presence/absence) and marmots (presence/absence) formed a unique habitat (Yoshihara *et al.* 2010). Ungulate trampling also compacts soil, which is antagonistic to the loosening of soil by burrowing root-rats, and the collapse of shallow root-rat burrows, resulting in more hiding opportunities for other rodents. We found signs of utilization by other rodents in a large proportion (over 20 %) of old root-rat burrow openings. These were almost all burrow openings outside active root-rat territories unless they were blocked by soil. The root-rats even responded to the alarm calls of *L. melanonyx* (E. Hrouzková, unpubl. data; Gemechu 2010). This indicates the existence of another interesting ecological relationship between root-rats and the other rodents.

The giant root-rat is the most important prey of the Ethiopian wolf in the Bale Mountains (Sillero-Zubiri &

Gottelli 1995). Conservation plans for the wolf would, therefore, need to consider mainly the habitat requirements of this rodent. Besides swamp edges and mima mounds, which are habitats largely modified or even created by the root-rats themselves, habitat classes with the highest mean root-rat densities, as identified by Tallents (2007) using satellite imagery and land survey, were *Alchemilla* pasture, *Kniphofia* swamp/mesa edge and grass pasture. All these habitats are currently very much affected by livestock grazing, which is one, if not the only, factor that could be effectively controlled by the national park management to secure the conservation of these habitats. To anticipate the response of root-rat and other rodent populations to a potential decrease of livestock grazing pressure we would need either data from long-term experiments based on exclosures (large enough to establish root-rat population density within them) or a reliable dataset on the rodent populations prior to the rapid increase of human settlements in Bale in the 1970s. Unfortunately, such data are not available. Because there is a possibility that some levels of grazing may affect the rodent population positively (see above), lowering livestock numbers seems to be a better option than its complete exclusion from certain areas.

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Chapter II

*Daily activity patterns in the giant root rat
(Tachyoryctes macrocephalus), a fossorial rodent from
the Afro-alpine zone of the Bale Mountains, Ethiopia.*

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Daily activity patterns in the giant root rat (*Tachyoryctes macrocephalus*), a fossorial rodent from the Afro-alpine zone of the Bale Mountains, Ethiopia

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Keywords

activity patterns; Afro-alpine; fossorial rodent; giant root rat; radio-tracking; behavioural thermoregulation; *Tachyoryctes macrocephalus*.

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Introduction

Choosing the right times to be active or to rest, as well as performing specific activities at the most appropriate time of the day, results in better survival and/or increased reproductive success (Halle, 2000). In most mammals, it leads to a distinct daily pattern of activity. Many rodents and other small mammals spend a certain part of the day in underground nests where they are protected from predation as well as adverse climatic conditions. They preferentially leave them during periods when the environmental and ecological conditions make their aboveground activity the least risky and/or most energetically profitable. Some rodents substantially reduce the time spent aboveground (fossorial species) or even remain permanently within their microclimatically stable burrow systems (strictly subterranean species). As a consequence, arrhythmic activity would be expected in these species (Nevo, 1999). Surprisingly, even some strictly subterranean rodents were found to exhibit clear daily activity patterns under natural conditions (Gettinger, 1984; Rado *et al.*, 1993; Benedix, 1994; Šklíba *et al.*, 2007, 2014, 2015). These activity patterns can be explained by daily temperature fluctuations in the shallow soil layers where the animals construct their foraging tunnels. The studied animals generally tended to be more active in the warm part of the

Abstract

Rodents adjust their activity to environmental conditions. The adjustment can be especially pronounced in climatically challenging environments. We studied activity patterns in the free-living giant root rat (*Tachyoryctes macrocephalus*), a large fossorial rodent endemic to the Afro-alpine ecosystem of the Bale Mountains, Ethiopia, by means of radio telemetry. We radio-tracked 17 adults during two periods of a dry season differing in temperature and food supply. In both periods, root rats spent a large part of the day (around 79%) in their underground nests. The proportion of time the animals were active aboveground decreased from 6.9 to 3.8% between the early and late dry season, which contradicts our prediction that aboveground activity would increase under lower food supply. We propose that there are thermoregulation advantages of prolonged aboveground activity during warm hours in the colder early dry season. In both periods, the root rats displayed diurnal activity with a unimodal pattern positively related to the temperature at the soil surface. Unlike in some other burrowing rodents, there was no tendency to decrease activity in the warmest part of the day even in the relatively warm late dry season.

day, although this trend could be reversed during the hottest part of the year (e.g. Rado *et al.*, 1993). In less fossorial diurnal rodents, such as ground squirrels and marmots (Sciuridae), the aboveground temperature cycle seems to be an important factor affecting their activity pattern, as these animals typically switch from a unimodal activity pattern during cold days to a bimodal pattern during warm days (Hayes, 1976; Chappell & Bartholomew, 1981; Türk & Arnold, 1988; Sharpe & Van Horne, 1999; Bacigalupe *et al.*, 2003). There are few data for rodents whose aboveground activity is sparse, but regular, such as root rats (Spalacidae), tuco-tucos (Ctenomyidae) and coruros (Octodontidae). However, it is possible that aboveground conditions would still be more important for determining the timing of their activity than the daily temperature cycle at the depth of their burrows (Rezende *et al.*, 2003).

Studying rodents inhabiting climatically challenging environments, such as cold geographical areas and high mountains, can be very useful for understanding how environmental factors affect activity. In these rodents, the increased costs of thermoregulation during the night result in a predominantly diurnal activity (Roll, Dayan & Kronfeld-Schor, 2006), sometimes with a bimodal pattern (decrease of activity around midday) during warm days (Hinze & Pillay, 2006). Extreme conditions in these regions create a trade-off between the need

for energy gained by foraging and the increased cost of thermoregulation during foraging (Melcher, Armitage & Porter, 1990). Rodents can meet this energetic challenge by either conserving or acquiring energy (Schultz, Collier & Johnson, 1999). Some species reduce the overall amount of activity (Busch *et al.*, 2000), sometimes even becoming torpid (Kenagy, 1973). Other energy-conserving strategies are basking (e.g. Hinze & Pillay, 2006) and food hoarding (e.g. Conner, 1983).

The giant root rat, *Tachyoryctes macrocephalus* Rüppell, 1842, is a solitary fossorial rodent living in the climatically challenging Afro-alpine ecosystem of the Bale Mountains, south-eastern Ethiopia. This ecosystem is characterized by a large amplitude of daily temperatures and seasonal variation in precipitation. The giant root rat is unique in many ways. First of all, it is endemic to <1000 km² area at altitudes from 3000 to 4150 m a.s.l. (Yalden, 1985, 2013) where it is the main prey of the endangered Ethiopian wolf (*Canis simensis*) (Sillero-Zubiri & Gottelli, 1995). Furthermore, it is one of the largest fossorial rodents (reaching 1000 g, Yalden, 1985). Finally, it is known to locally reach extremely high population densities of up to 90 individuals/ha (Sillero-Zubiri, Tattersall & Macdonald, 1995). Although giant root rats spend most of the time underground, they emerge briefly but regularly on the surface to feed on grass and forbs collected near their burrow openings (Yalden, 1985, 2013; Sillero-Zubiri *et al.*, 1995). Sillero-Zubiri *et al.* (1995) considered the giant root rat to be a diurnal species since it emerges aboveground most often between 10:00 and 15:00 h, but neither the daily amount of outside-nest activity nor its daily pattern have so far been studied in detail.

In this study, we analysed the outside-nest and aboveground activity of radio-tracked giant root rats in two periods corresponding to the colder early dry season with a relatively high food supply and the warmer late dry season with a lower food supply (Šklíba *et al.*, 2017). The aims of the study were to: (1) determine the daily amounts of outside-nest and aboveground activity, and their seasonal changes. We predicted that the amount of outside-nest activity would be relatively low, especially in the colder period, in order to save energy. We also predicted that, in the period with a lower food supply, the animals would spend more time aboveground in order to collect enough food. (2) Reveal the daily pattern of outside-nest activity and to determine its relationship to the daily temperature cycle aboveground and at various depths of soil. We predicted that activity is related to the aboveground temperature cycle because its amplitude is higher than that of the temperature cycles at any soil depth at which root rats normally occur. We also predicted the animals would have a unimodal activity pattern in the colder period and bimodal activity pattern in the warmer period.

Materials and methods

Study locality

The study was carried out in the Web Valley, Bale Mountains National Park, southeastern Ethiopia (N6°59.6' E39°42.0',

3500 m a. s. l.). The 3.5 ha study locality was situated on gently sloping Afro-alpine grassland dominated by *Alchemilla abyssinica* surrounded by a periodic wetland on one side and steeper rocky slopes covered by *Artemisia afra* bushes on the opposite side (for more details on the study locality and the root rat population see Šklíba *et al.*, 2017). In the late dry season, the study locality was enlarged to approximately 7 ha to encompass root rats which moved out of the initial area, mostly into the periodic wetland. Annual rainfall in the area is 1157 mm and climatic conditions are characterized by a colder April–October rainy season (897 mm) and a November–March dry season (260 mm), with relatively warm days and sub-zero night temperatures. March, April and May are the warmest months of the year (www.worldclim.org, accessed April 2014).

Field work

The giant root rats were captured between 20 and 29 October, 2013 by snare traps placed around fresh burrow openings. The traps were checked approximately every 10 min to prevent any injury to the animals. The captured animals were weighed and sexed, fitted with radio collars (Brass collar, Pip transmitter with a position-based activity indicator; Biotrack Ltd, Dorset, UK) under light anaesthesia by ketamine and xylazine, and released back into their burrow systems within 12 h of their capture. The weight of the collars was <5% of the body mass of the smallest individual. Altogether, 28 root rats were radio collared, of which 17 individuals: five males [637 ± 101 (507–753) g] and 12 females [714 ± 187 (465–1040) g], provided full radio-tracking data. The remaining individuals were lost due to predation (6), mortality by unknown cause (2), migration far from the study locality (2) and loss of collar (1).

We radio-tracked the animals in two periods corresponding to the early (12 Nov–6 Dec 2013) and late (23 Feb–30 Mar 2014) dry season. Both periods consisted of eight radio-tracking days. Since pilot radio-tracking trials showed that root rat activity is negligible during the night, we restricted the time of radio-tracking to 6:00–21:00 in all radio-tracking days except for 2 days in the first period and 1 day in the second period when the complete 24 h were covered. In each radio-tracking day, we fixed the position of each individual hourly using an IC-R20 receiver (Icom America Inc.) and a 3-element handheld Yagi antenna. Radio-tracking started with an observer listening to the signal of the transmitter for about 1 min from a distance >20 m to determine whether the animal was in motion or resting. If the signal rate was continually changing, the animal was considered to be in motion. A predominantly stable, slow signal rate indicated that the animal was most likely curled up and therefore was considered to be resting. A fast but stable signal rate was interpreted as motion if the animal was outside the nest (a single location where the animal spent most of the time) and as resting if inside the nest (Šklíba *et al.*, 2007). When approaching the animal, binoculars were used to detect any aboveground activity. If the animal was seen aboveground, we recorded whether it was collecting food or not. If the animal was not seen aboveground, its location was fixed by triangulation from a distance of 1–4 m after careful approach. We estimated the accuracy of our radio-fixes at 0.5 m based on

results from our previous telemetry studies on subterranean rodents (Šklíba *et al.*, 2009; Lövy, Šklíba & Šumbera, 2013). All fixes within a 0.5 m radius of the nest were therefore treated as being inside the nest. To precisely record root rat locations, we established a geo-referenced 4 m-cell grid of numbered landmarks over the burrow systems which were used by the radio-collared animals before the radio-tracking began. After the end of the radio-tracking, the root rats were recaptured and their collars removed before they were released back to their burrow systems.

During the course of both periods, the temperature on the surface and at depths of 10, 20, 30 and 40 cm was recorded every 30 min by a set of six temperature loggers (Comet System s.r.o., Rožnov pod Radhoštěm, Czech Republic). Food supply, expressed as fresh plant biomass per m², was determined for each radio-tracked root rat at the end of each radio-tracking period. We evenly placed five sampling points within each individual's home-range approximated as a minimum convex polygon encompassing all fixes of the particular individual. At each of the points, we placed a 20 × 20 cm square where we collected and weighed all fresh vegetation including bulbs and fleshy rhizomes. To estimate the food supply of the whole 3.5 ha study locality, we carried out the same procedure at 60 sampling points located using randomly generated GPS coordinates in both the early and late dry season.

Ethic statement

All procedures were approved by the Institutional Animal Care and Use Committee of the University of South Bohemia and the Ministry of Education, Youth and Sports, Czech Republic (n. 7942/2010-30) and the Ethiopian Wildlife Conservation Authority (EWCA). The study conforms to the provisions of the Declaration of Helsinki (as revised in Tokyo 2004), available at <http://www.wma.net/e/policy/b3.htm>.

Statistical analysis

All statistical analyses were performed with R (R Core Team, 2015). Seasonal differences in the mean, minimum and maximum daily surface temperature (approximated by a Gaussian distribution) and fresh plant biomass across the study locality (approximated by a Gamma distribution, with log link function) were tested by generalised linear models (GLM). Seasonal differences in fresh plant biomass within the root rat home-ranges (approximated by a Gamma distribution, with log link function) were tested by the marginal generalised estimating equation (GEE) with the independent correlation structure in the model with the geepack package (Halekoh, Højsgaard & Yan, 2006). We used GEE because the data from a particular individual represented repeated observations.

Each hourly fix of an animal was characterized by four variables indicating the presence (1) or absence (0) of the following features: (1) motion; (2) activity outside the nest; (3) aboveground activity; and (4) collecting food. To reduce bias, which would be caused by incomplete radio-tracking data from the night hours, missing values were filled in with the mean

value of the particular variable computed for the corresponding hour and period out of all non-missing values of all individuals (there were only zeros in both seasons for the last two variables). These data were used to quantify four parameters of activity, all expressed as a proportion of a 24-h day, for each individual and season: (1) proportion of time with motion; (2) proportion of time spent outside the nest; (3) proportion of time spent aboveground; and (4) proportion of time collecting food. Seasonal differences in these four activity parameters were tested by marginal generalised least squares models (GLS) with the nlme package (Pinheiro *et al.*, 2015). In addition to the four parameters, we also tested for seasonal difference in the proportion of time spent aboveground but not collecting food. All five parameters were arcsine transformed prior to the analyses.

The effects of sex, body mass and food supply (fresh plant biomass within home-ranges, log transformed) on the five activity parameters were tested by linear models for each season separately. We applied a Bonferroni correction ($\alpha = 0.05/3$) since we repeatedly tested the same dependent variable. The relationship between the seasonal change of the five activity parameters in individual root rats and seasonal change of their food supply (both expressed as the difference between the second and first period values) was tested using Spearman's rank correlation.

The relationship of the mean hourly proportions of outside-nest fixes (arcsine transformed) to the temperature on the surface and at various soil depths (10, 20, 30, and 40 cm) was tested for each period separately by linear models. We applied a Bonferroni correction ($\alpha = 0.05/5$) since we performed the test repeatedly for the same dependent variable.

Results

Environmental conditions in the study area changed considerably between the two periods (see Table 1 for details and statistical comparisons). While minimum daily temperature decreased, the mean and maximum daily temperatures increased in the late dry season. The progress of the dry season also led to a significantly lower fresh plant biomass across the study locality. However, the mean fresh plant biomass within the root rat home-ranges increased (although not significantly). This was because of a dramatic increase in the food supply within the home-ranges of six individuals which came about as a consequence of their relocation (complete or partial) into the periodic wetland. The mean fresh plant biomass within the home-ranges of these six individuals was six times higher than within the home-ranges of the remaining 11 individuals in the late dry season (1085 ± 631 and 175 ± 91 g m⁻², respectively).

The giant root rats were in motion 30.5 ± 5.3 (21.0–39.0) % of the day, spent 21.4 ± 3.2 (14.9–29.2) % of the day outside the nest, were active above ground 5.4 ± 1.9 (2.3–8.9) % of the day and were collecting food 1.9 ± 1.2 (0.3–4.2) % of the day (based on pooled data from the two seasons). Whereas there were no significant differences in the amounts of outside-nest activity and food collecting between the two periods, the proportion of time root rats were in motion, active

Table 1 Selected environmental and ecological characteristics of the study locality in the early and late dry season. The differences between the two seasons were tested by generalised estimating equation (for fresh plant biomass across the study locality) and generalised linear models (for all remaining variables). Means \pm SD and ranges are presented

Variable	Early dry season	Late dry season	Test statistics, <i>P</i>
Mean daily temperature on the surface (°C)	9.6 \pm 1.4 (7.3–12.1)	11.0 \pm 1.2 (8.9–14.1)	$F_{1,61} = 19.5, P < 0.0001$
Minimum daily temperature on the surface (°C)	2.8 \pm 3.3 (-2.1–8.2)	-0.3 \pm 3.0 (-5.9–5.4)	$F_{1,61} = 15.3, P < 0.001$
Maximum daily temperature on the surface (°C)	17.9 \pm 2.1 (13.8–21.9)	26.6 \pm 5.0 (16.6–37.5)	$F_{1,61} = 68.5, P < 0.0001$
Fresh plant biomass within <i>T. m.</i> home ranges (g m ⁻²)	371 \pm 146 (140–785)	497 \pm 575 (76–2151)	$\chi^2 = 0.97, P = 0.32$
Fresh plant biomass across the study locality (g m ⁻²)	384 \pm 160 (124–770)	208 \pm 166 (0–908)	$F_{1,118} = 27.4, P < 0.0001$

Table 2 Activity parameters of radio-tracked root rats in the early and late dry season. The differences between the two seasons were tested by the generalised least squares models. Means \pm SD and ranges are presented

Parameter	Early dry season	Late dry season	Test statistics <i>P</i> (d.f. = 1,32)
% of time with motion	33.3 \pm 5.9 (23.4–41.6)	27.8 \pm 6.5 (16.6–42.1)	$F = 12.7, P = 0.0012$
% of time spent outside nest	21.4 \pm 3.6 (15.6–28.7)	21.4 \pm 5.9 (14.2–40.2)	$F = 0.0, P = 0.94$
% of time spent aboveground	6.9 \pm 2.7 (2.6–13.0)	3.8 \pm 2.6 (1.6–12.0)	$F = 17.3, P < 0.0001$
% of time collecting food	2.1 \pm 1.3 (0–4.2)	1.7 \pm 1.5 (0–5.2)	$F = 1.3, P = 0.27$
% of time spent aboveground, but not collecting food	4.8 \pm 2.0 (2.1–9.4)	2.1 \pm 1.5 (0.5–6.8)	$F = 25.0, P < 0.0001$

aboveground and active aboveground but not collecting food, decreased significantly in the late dry season (see Table 2 for statistical details).

There were no significant effects of sex, body mass or food supply on the activity parameters in either season after the Bonferroni correction was applied ($\alpha = 0.05/3$) except for two positive relationships: (1) between the proportion of time with motion and food supply in the late dry season ($F = 7.5, P = 0.015$) and (2) between the proportion of time spent aboveground but not collecting food and body mass ($F = 9.2, P = 0.008$) in the early dry season. A seasonal change in the proportion of time spent outside the nest was positively related with the seasonal change in food supply ($r_s = 0.54, P = 0.03$). The relationships between the seasonal change in food supply and seasonal changes in other activity parameters were not significant.

In both periods, root rats exhibited a unimodal pattern of outside-nest activity with more than 90% of the outside-nest activity taking place between 9:00 and 18:00 h with the maximum between 13:00 and 16:00 h (Fig. 1). In both periods, the hourly proportion of outside-nest fixes was related most tightly with surface temperature. Significant, but negative, relationships were detected with temperatures at depths of 20 and 30 cm; for a complete statistical analysis, see Table 3. There was no sign of a bimodal pattern of outside-nest activity and only a weak tendency to reduce aboveground activity between 12:00 and 14:00 h in the late dry season (Fig. 1).

Discussion

The radio-tracked giant root rats spent only 21.4% of the time outside their nests and they emerged aboveground for only

5.4% of the time. They decreased their aboveground activity in the late dry season compared to the early dry season, but the frequency of observations where the animals were collecting food remained unchanged. In both seasons, the root rats exhibited a unimodal pattern of outside-nest activity tightly related to the aboveground temperature cycle.

The detected small amount of outside-nest (21.4%) and aboveground (5.4%) activities likely represents a means of coping with adverse climatic (cold temperature and its large daily amplitude) and ecological (high risk of predation in a habitat lacking cover) conditions of the Afro-alpine ecosystem. This would require reaching and collecting sufficient food resources within a relatively short time. Even lower outside-nest activity (10–15% of the day) has been reported for the strictly subterranean *Eospalax fontanierii* in the climatically challenging Tibetan Plateau (Zhang, 2007). Such low activity might be enabled by preference for habitats with soft soils (and therefore also low digging costs) and high primary productivity. The short time budget devoted to foraging could also be related to the generally high nutrient contents of plant tissues which is typical for high-altitude herbaceous vegetation (Körner, 1989). Outside-nest activity almost as low as that revealed in the present study was detected in other spalacids, *Spalax ehrenbergi* (24%; Zuri & Terkel, 1996) and *S. galili* (17%; Šklíba *et al.*, 2015), but only under the conditions of the rainy Mediterranean winter with low temperatures, easily workable soil and accessible food. Interestingly, the outside-nest activity in *S. ehrenbergii* was reported to increase to 45% during the hot summer (Zuri & Terkel, 1996). The relatively brief aboveground activity of root rats is well understandable considering the high predation risk from Ethiopian wolves and other diurnal predators (Yalden, 1985).

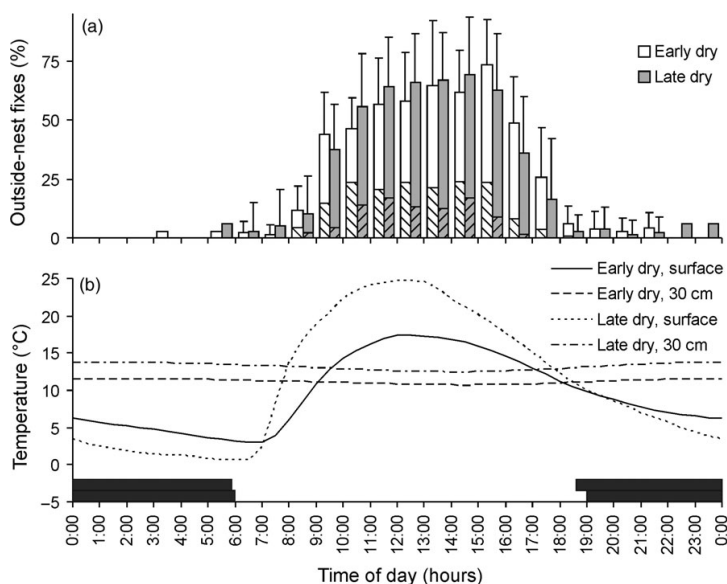


Figure 1 Mean \pm SD hourly proportions of outside-nest fixes of the radio-tracked root rats (a) and mean temperatures on the surface and at a depth of 30 cm during a 24-h day (b) in the early and late dry season. Striped parts of the columns represent proportions of radio fixes with aboveground activity. Dark horizontal bars represent a dark phase of the day in the early (top) and late dry (bottom) season.

Table 3 The relationship of soil temperatures at different depths to the hourly proportion of outside-nest fixes of the radio-tracked giant root rats revealed by linear models separately for the early and late dry season. [Statistically significant results after Bonferroni correction ($\alpha = 0.05/5$) are marked with asterisks]

Explanatory variable	Early dry season			Late dry season		
	Variability explained (%)	<i>F</i>	<i>P</i>	Variability explained (%)	<i>F</i>	<i>P</i>
Surface temperature	84.6	121.2	<0.0001*	86.8	144.7	<0.0001*
Temperature at a depth of 10 cm	5.3	1.2	0.281	9.2	2.2	0.149
Temperature at a depth of 20 cm	65.6	41.9	<0.0001*	65.5	41.9	<0.0001*
Temperature at a depth of 30 cm	83.1	108.2	<0.0001*	76.8	72.8	<0.0001*
Temperature at a depth of 40 cm	0.0	0.0	0.968	0.0	0.0	0.973

The increased temperatures in the late dry season were accompanied by decreased fresh plant biomass across the study locality. We would expect that a lower food supply needs to be compensated for by a higher proportion of time devoted to foraging. Surprisingly, root rats decreased their aboveground activity in the late dry season, which could imply that they foraged even less. Nevertheless, closer analysis of the data revealed that the proportion of time root rats was observed collecting food was comparable in both periods (around 2% of the day). The longer amount of time spent aboveground not devoted to foraging in the colder early dry season would imply that thermoregulation may also be involved in the aboveground activity of this species.

Since some individuals moved their home-ranges into the food-rich wetland, while others remained sedentary, an

interesting question arose: how the change in food supply within an individual's home-range could influence the amount of its outside-nest and aboveground activities. The relationship was positive in the former, but negative although not significant in the latter. While the latter tendency is in accord with our prediction that more abundant food would reduce the time needed to collect enough food aboveground, the former relationship is not as easy to explain. We would expect that animals whose food supply increased in the late dry season would reduce outside-nest activity because of the lower need to burrow to reach areas with new food resources (cf. Zuri & Terkel, 1996; Pigage & Pigage, 2010). Nevertheless, we found exactly the opposite. A possible reason could be related to the fact that the individuals which entered the periodic wetland needed to excavate new burrows in their newly built burrow

systems. Another explanation could be that, when the food supply is high, root rats no longer need to conserve metabolic energy by minimizing their locomotion (Cox & Hunt, 1992). On the other hand, root rats, when sedentary, can drastically reduce vegetation in their home-ranges. In the late dry season, <100 g of fresh plant biomass per m² was found in several of the examined home-ranges (Table 1), which equals to about 5 kg of food per home-range (T. Vlasatá, unpublished data). It seems that the root rats economize their energetic expenses to the point where they can live on relatively low food biomass.

The hourly proportion of outside-nest activity of root rats during the 24 h day was closely related to the temperature on the soil surface. This might be surprising, since aboveground activity makes up a relatively small part of their outside-nest activity. Since most root rat burrows occur at a depth of 30 cm (J. Šklíba, unpublished data), we would expect activity to be positively correlated mainly with the temperature at this depth. In fact, the correlation with this temperature was significant, but negative (Table 3, Fig. 1). Nevertheless, temperature amplitude at this depth is already negligible (around 1°C). We can assume that conditions aboveground place much higher thermoregulatory demands on the animals, and thus they would adjust their overall activity pattern to that. In this respect, the giant root rats seem more similar to rodents with more pronounced aboveground activity (e.g. Melcher *et al.*, 1990; Long, Martin & Barnes, 2005) than to strictly subterranean rodents (Gettinger, 1984; Rado *et al.*, 1993; Benedix, 1994; Šklíba *et al.*, 2007, 2014, 2015). This is also the case with *Spalacopus cyanus* (Rezende *et al.*, 2003; Urrejola *et al.*, 2005).

Mean temperature as well as its daily amplitude increased between the two periods of the study (Fig. 1). If root rats adjust their activity to temperature, we would expect that the higher surface temperatures in the late dry season may limit root rat aboveground activity during the middle of the day in a manner similar to marmots whose physiological adaptations for coping with cold cause high sensitivity to heat stress (Melcher *et al.*, 1990). This was not confirmed in our study, as the outside-nest activity of root rats followed the same pattern in both periods. There was only a slight shift of the period of maximum activity to earlier hours in the second period corresponding with the earlier warming of the surface in the morning (Fig. 1). In contrast to marmots, root rats spend most of the time in their underground burrows where convective cooling is ineffective. Thus, their thermal optimum should be set to higher temperatures to prevent overheating during digging. As a result, a limitation on their activity would likely be connected with low rather than high ambient temperatures. In fact, we found a significant decrease of aboveground activity in the second period indicating that behavioural thermoregulation may serve as a mechanism for coping with cold. We propose that the prolonged time spent aboveground during warm hours in the colder early dry season could be attributed to basking (cf. Sillero-Zubiri *et al.*, 1995). Basking is well documented for example in the ice rat *Otomys sloggetti* living at high altitudes (Hinze & Pillay, 2006).

Reducing locomotory activity, adjusting its pattern to the surface temperature and occasional basking can all be

considered as energy saving behavioural adaptations in the giant root rat to cope with the local harsh climatic conditions. Other potential strategies could include torpors during the night or during periods of bad weather, and food hoarding. However, during radio telemetry, we were able to 'wake up' a resting root rat at any time of the day, simply by approaching close to its nest, which would indicate that the existence of deep torpors is unlikely in this species. Also, the amount of food kept in or close to the nests was relatively small (51 ± 47 [7–145] g; J. Šklíba, unpublished data). Therefore, deep torpors and food hoarding are unlikely to be of much importance. To evaluate the significance of the behavioural strategies in a broader context, knowledge about root rat physiology, especially concerning body temperature and the thermoneutral zone, would be extremely helpful.

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Chapter III

The giant that makes do with little: small and easy-to-leave home ranges found in the giant root-rat, an endemic fossorial rodent of the Bale Mountains, Ethiopia

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The giant that makes do with little: small and easy-to-leave home ranges found in the giant root-rat, an endemic fossorial rodent of the Bale Mountains, Ethiopia

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Short title: Space-use in *Tachyoryctes macrocephalus*

Abstract

Mammalian space-use patterns are largely determined by the resources utilized as well as by given habitat/ecotope characteristics, as can be illustrated by rodents displaying predominantly subterranean activity. These rodents are largely limited in their use of space by their burrow systems. This results in smaller home ranges than is usual for rodents of a similar size. However, there is little information regarding how stable these home ranges are over time. We studied space use in the giant root-rat *Tachyoryctes macrocephalus*, a large fossorial rodent endemic to the Bale Mountains of southern Ethiopia where it is the principal prey of the Ethiopian wolf *Canis simensis*. We radio-tracked 22 root-rats during a period of 36 days in the early dry season and 17 of them once again during a period of 37 days in the late dry season. The root-rats occupied very small (around 100m²) home ranges which were often tightly packed, especially on a wetland shore that was a part of the study locality, but displayed little overlap. Almost 30 % of the radio-collared root-rats of either sex dispersed (80 – 428 m from their original home range) during the five months of the study, mostly in a period between the early and late dry season characterized by a decreasing food supply and the soil becoming dry and hard. Individuals who did not disperse during this time usually shifted their home range in some direction. Root-rats living on the wetland shore, which were the largest and therefore likely competitively strongest individuals, shifted their home ranges into the wetland, likely for the purpose of increasing their food supply.

Keywords: dispersal, radio tracking, space use, home range, fossorial rodent, *Tachyoryctes*, Afroalpine

Introduction

Mammals exhibit a variety of space-use patterns, but during prolonged periods of time they usually remain within an area which can be approximated as a home range (Burt, 1943). Such home ranges differ in size and can be abandoned on a regular or irregular basis preceding dispersal or other type of movement (Barnard, 2004). Home-range size depends primarily on the species' ecology (resources utilized and the way they are utilized) and body size (Harestad & Bunnell, 1979), but it largely depends also on habitat parameters (e.g. availability of food, shelter, mates, etc.) as well as on the intensity of competition. Habitat parameters and intensity of competition may vary in time; individuals may respond either by adjusting their home-range size, or by dispersing. In fact, variation in these factors, along with inbreeding avoidance, is a principal evolutionary cause of dispersal (Barnard, 2004; Clobert *et al.*, 2008).

Some mammals confine most of their movements to burrow systems. Except in cases of colonial and social species (e.g. Begall & Gallardo, 2000; Šklíba *et al.*, 2012), they individually occupy burrow systems, which are most of the time isolated from those of their neighbours (Hickman, 1990; Nevo, 1999). The size of the burrow system needs to be large enough to provide access to sufficient food resources and possibly also potential mates. Thus, the burrow system size largely determines the individual's home-range (and territory) size. In rodents with prevailing subterranean activity, home ranges are smaller than in other rodents of a similar size (Harestad & Bunnell, 1979), but can be very dynamic, as their owners constantly excavate new burrows and backfill parts of older ones with soil (Šklíba *et al.*, 2009). Dispersal is probably very risky in these animals, because of their low ability for avoiding aboveground predation (cf. Németh *et al.*, 2016). Therefore, we can expect that it occurs infrequently, typically as natal dispersal, and then mainly as a response to dramatic changes in habitat characteristics.

Dispersing individuals of subterranean rodents can take advantage of existing networks of tunnels excavated by other individuals in the past (Lövy, Šklíba & Šumbera, 2013) and can even settle down in abandoned parts of existing burrow systems (Šumbera *et al.*, 2012), however, aboveground dispersal is unlikely to be avoided completely in these animals (cf. Hazell *et al.*, 2000).

The giant root-rat (also known as the giant mole rat or big-headed mole rat) *Tachyoryctes macrocephalus*, Rüppell, 1842 (Rhizomyinae, Spalacidae), is a solitary fossorial rodent endemic to the Bale Mountains in Ethiopia where it occurs in Afroalpine grasslands and moorlands (Sillero-Zubiri *et al.*, 1995). It is an important prey of the Ethiopian wolf (Sillero-Zubiri & Gottelli, 1995), and has an important ecosystem role affecting vegetation as well as the populations of other rodents (Šklíba *et al.*, 2017). It feeds on grasses and forbs usually collected close to burrow openings, but spends the majority of its time underground (Vlasatá *et al.*, 2017), in burrow systems excavated using its chisel-like incisors. In suitable habitat patches, such as on wetland shores, it reaches population densities of 60 – 90 ha⁻¹ (Sillero-Zubiri *et al.*, 1995; Šklíba *et al.*, 2017), which is very high for a species with a body mass approaching 1 kg. This would lead one to assume that these root-rats defend small, tightly packed territories in these habitats. Such a preference for the wetland shores could be derived from the access to the higher quality food resources when the wetland is drying out gradually during the dry season. Since fresh plant biomass in the study locality decreases during the dry season (Šklíba *et al.*, 2017), we can expect that giant root-rats enlarge their home ranges during this period to provide access to a sufficient amount of food, and disperse out of the home ranges if the food supply becomes insufficient.

We studied the space use of 22 radio-tagged giant root-rats in the Web Valley, Bale Mountains, in a locality representing an optimal habitat

of the species (see Sillero-Zubiri *et al.*, 1995, Šklíba *et al.*, 2017, and Wilson *et al.* 2017 for further details) during two periods of a single dry season. The aims of the study were: 1) to quantify the home-range (HR) size of the individual root-rats and overlap with neighbouring individuals' HRs, and 2) to describe how root-rats change their space-use patterns in response to environmental changes as the dry season progresses. We expected root-rats would mostly increase their HR sizes as a response to a decreasing food supply and only rarely disperse out of the HR, given the high risk involved with such behaviour.

Materials and Methods

Ethic statement

All procedures were approved by the Institutional Animal Care and Use Committee at University of South Bohemia, Ministry of Education, Youth and Sports, Czech Republic (n. 7942/2010-30), and Ethiopian Wildlife Conservation Authority (EWCA).

Study locality

The study was carried out in the Web Valley, Bale Mountains National Park, Ethiopia (N6°59.6' E39°42.0', 3,500 m a. s. l.). The study locality of approximately 3.5 ha was situated on a gently sloping Afroalpine pasture dominated by *Alchemilla abyssinica* adjacent to a periodic wetland. In the late dry season, the study locality was enlarged to approximately 7 ha to encompass the HRs of those root-rats which moved outside of its initial boundaries. Climatic conditions in the area are characterized by a colder April-October rainy season (897 mm) and a November-March dry season (260 mm), with relatively warm days and sub-zero night temperatures (www.worldclim.org, accessed April 2014). Environmental change in the

study locality in the course of the dry season included a decrease in fresh plant biomass (from 385 to 208 g m⁻²) and an increase in soil hardness (Šklíba *et al.*, 2017).

Fieldwork

The giant root-rats were captured 20–29 October 2013 by snare traps placed around fresh burrow openings. The traps were checked approximately every 10 minutes to prevent any injury to the animals. The captured animals were shortly immobilized with ketamine and xylazine, and then weighed, sexed, and fitted with radio-collars (Brass collar, Pip transmitter with a position-based activity indicator; Biotrack Ltd, Dorset, UK). They were released back into their burrow systems within 12 hours of their capture. The weight of the collars was less than 5 % of the body mass of the smallest individual handled. Altogether 27 adults and 1 likely subadult root-rat were radio-collared (see Supplementary material). The number of animals successfully radio-tracked was 22 in the early dry season and 17 in the late dry season (all adults). The fates of all radio-collared animals are described in the Supplementary material.

Radio-tracking started four days after releasing the last animal. We radio-tracked the animals in two periods marked as the early (2 Nov – 7 Dec 2013) and late (23 Feb – 31 Mar 2014) dry season. The periods contained ten and eight radio-tracking days, respectively. Since pilot radio-tracking trials showed that the activity of root-rats is negligible during the night (see Vlasatá *et al.*, 2017 for details), we reduced the time of radio-tracking to 6:00 – 21:00 in all radio-tracking days except for two days in the first period and one day in the second period where 24 hours were covered. In each radio-tracking day, we fixed the position of each individual hourly using the IC-R20 receiver (Icom America Inc.) and a 3-element handheld Yagi antenna. When approaching the animal,

binoculars were used to detect any aboveground activity. If the animal was not seen above ground, its location was fixed by triangulation from a distance of 1 – 4 m after carefully approaching. We estimated the accuracy of our radio-fixes at 0.5 m from our previous telemetry studies on subterranean rodents. All fixes within a 0.5m radius of the nest (a single location where the animal spent most of the time) were therefore treated as inside the nest. To precisely record root-rat locations, we established a geo-referenced 4m-cell grid of numbered landmarks in the locality before the radio-tracking began. After the end of radio-tracking, the root-rats were recaptured and their collars were removed before they were released back into their burrow systems.

Data processing

Radio-tracking data were digitized and processed in QUANTUM GIS (Quantum GIS Development Team 2016). For each radio-tracked root-rat and radio-tracking period, the home-range (HR) size was estimated based on 192 fixes from the early dry season and 136 fixes from the late dry season as the area of grid cells (GCs) of a 2-m cell grid covering a minimum spanning tree that interconnected all radio-fixes of the particular individual in the shortest way. For comparative purposes, the HR size was also calculated as an area of 95% and 100% minimum convex polygon (MCP) based on outside-nest fixes only. Overlap between HRs from the early and late dry season was calculated as percentage of the late dry season HR that was also utilised in the early dry season. Any relocation of the radio-tracked animals which resulted in no overlap between their old and newly established HR was considered as dispersal.

Statistical analyses

Generalised linear models (GLM) with a Gaussian distribution were used to compare body masses between male and female root-rats and between root-rats living along the shore of the periodic wetland and in the remaining part of the study locality in the early dry season. GLM with a Gamma distribution were used for testing the effect of sex and body mass on the root-rats' HR size in the early dry season. The root-rats under study were then divided into three groups according to their capture site and space use between early and late dry season: dispersers (individuals who completely abandoned their initial HR), wetland shore dwellers (individuals who occupied periodic wetland shore), and Afroalpine pasture dwellers (all remaining individuals). Linear mixed effect models (LME) were used for testing whether there was a significant seasonal change in HR size (log transformed) in wetland shore dwellers and in Afroalpine pasture dwellers. The animal ID was introduced to these tests as a random factor in order to avoid pseudoreplications. All the above tests were performed with the R statistical software (R Core Team 2016). Means are reported with SD and range.

Results

There was no difference in body mass between radio-collared males and females (M: 647 ± 198 [311 – 1045] g, F: 700 ± 176 [460 – 1040] g; GLM: $F_{1,26} = 0.5$, $p = 0.48$). However, root-rats captured on the shore of the periodic wetland (two males, six females) were significantly heavier than those from the rest of the study locality (850 ± 240 [715-1045] g and 616 ± 96 [311-980] g, respectively, GLM: $F_{1,26} = 14.2$, $p < 0.001$).

Table 1: Home-range sizes of the radio-tracked root-rats in two periods of the dry season. Minimum convex polygons (MCP) are based on outside-nest fixes only.

Method	Sex	Home-range size (m ²)	
		Early dry season (n=22)	Late dry season (n=17)
GC	Females	89 ± 23 (56-132)	93 ± 20 (64-120)
	Males	97 ± 23 (64-124)	63 ± 21 (48-100)
	Total	92 ± 23 (56-132)	84 ± 24 (48-120)
95% MCP	Females	74 ± 45 (30-202)	72 ± 28 (31-126)
	Males	111 ± 69 (29-200)	39 ± 22 (23-77)
	Total	86 ± 55 (29-202)	62 ± 30 (23-126)
100% MCP	Females	92 ± 52 (38-232)	92 ± 34 (37-142)
	Males	129 ± 65 (39-209)	48 ± 32 (24-104)
	Total	104 ± 57 (38-232)	79 ± 38 (24-142)

The mean HR size of the root-rats in the early dry season (first radio-tracking period) was $92 \pm 23 \text{ m}^2$ (n=22, Table 1). Males and females had similar HR sizes (Table 1; GLM: $F = 0.6$, $p = 0.45$). There was no significant effect of body mass on the HR size (GLMs: $F_{1, 20} = 0.0$, $p = 0.83$). The HRs of some individuals were tightly packed, especially on the shore of the periodic wetland (Fig. 3). However, we recorded only two cases of considerable overlap between the HRs of neighbouring

individuals. First, the HR of male M334 overlapped the HRs of three females (F271, F633, F574) on the shore of the periodic wetland (Fig 3). In two occasions, the male was observed to emerge out of the same burrow opening as females F574 and F271. Second, the male M532 was observed emerging from a burrow opening previously used by female F966. Except for these two cases, the overlap of neighbouring HRs was either zero or negligible.

Root-rats usually utilized a single nest at a time, however, nine out of the 22 individuals radio-tracked during the first radio-tracking period started to use another nest (M602 even twice in a sequence) during this period. M532 started to use the nest of another radio-collared male (M083) no more than six days after the latter was predated. One case of successful dispersal was detected during the early dry season (F143; see Fig. 1 for all detected dispersal attempts and Supplementary material for the distances travelled). One day, F143 was detected 57 m from her nest and by the following morning had travelled a further 217 m before she established her new HR. She probably travelled aboveground as can be supposed from the fact that she relocated quickly and crossed an area with damp soil.

In the time between the first and second radio-tracking periods, six individuals (M022, M175, M803, M203, F233, F362) dispersed out of their original HRs. Only three of them (all males) were successfully radio-tracked in the late dry season (along with other 14 individuals). The remaining individuals dispersed too far to be radio-tracked on a regular basis, i.e. each hour (M203) or died before the radio-tracking was finished (F233, F362). Two males (M175 and M803) and one female (F233) moved to the food-rich wetland, one male and one female (M022, F362) travelled in the opposite direction. M203 travelled along the wetland and settled down on its shore 428 m from his original HR (Fig. 1).

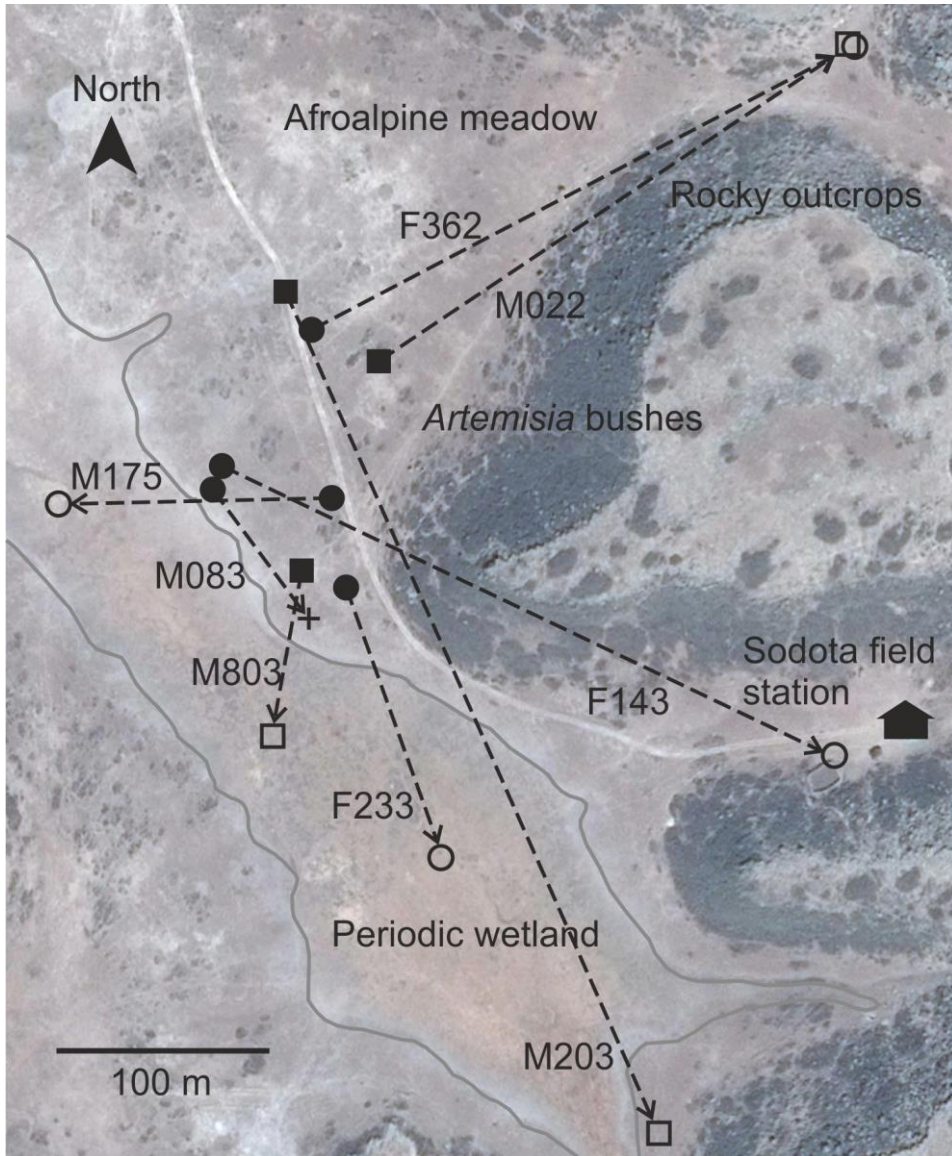


Figure 1. Dispersal events of the radio-collared giant root-rats. Squares and circles represent males and females, respectively. Solid symbols mark positions of the first detected nests of a particular individual; open symbols show positions of nests newly established by these individuals following their dispersal. Map source: “Sodota research station and surrounding”. GOOGLE EARTH. March 28, 2016).

In the late dry season, the wetland shore dwellers (six individuals that had occupied the shore of the periodic wetland in the early dry season – all of them large females) shifted their HR deeper into the wetland, which was accompanied by a significant increase in HR size (Fig. 2, LME: $F = 14.2$, $p = 0.01$). As much as 61 ± 19 (42-93) % of their new HRs were outside their original (early dry season) HRs. The Afroalpine pasture dwellers (M532, M603, F045, F302, F392, F424, F451, and F774) also shifted their HRs to some direction; 43 ± 24 (11 – 86) % of their new HRs were outside their original ones. Their new HRs were smaller than the original ones ($102 \pm 17 \text{ m}^2$ in the early dry season, $77 \pm 24 \text{ m}^2$ in the late dry season, LME: $F = 6.3$, $p = 0.04$). No changes of nests were detected in the late dry season in any radio-tracked individual except for male M175 who established his HR in “peaty” soil in the middle of the wetland.

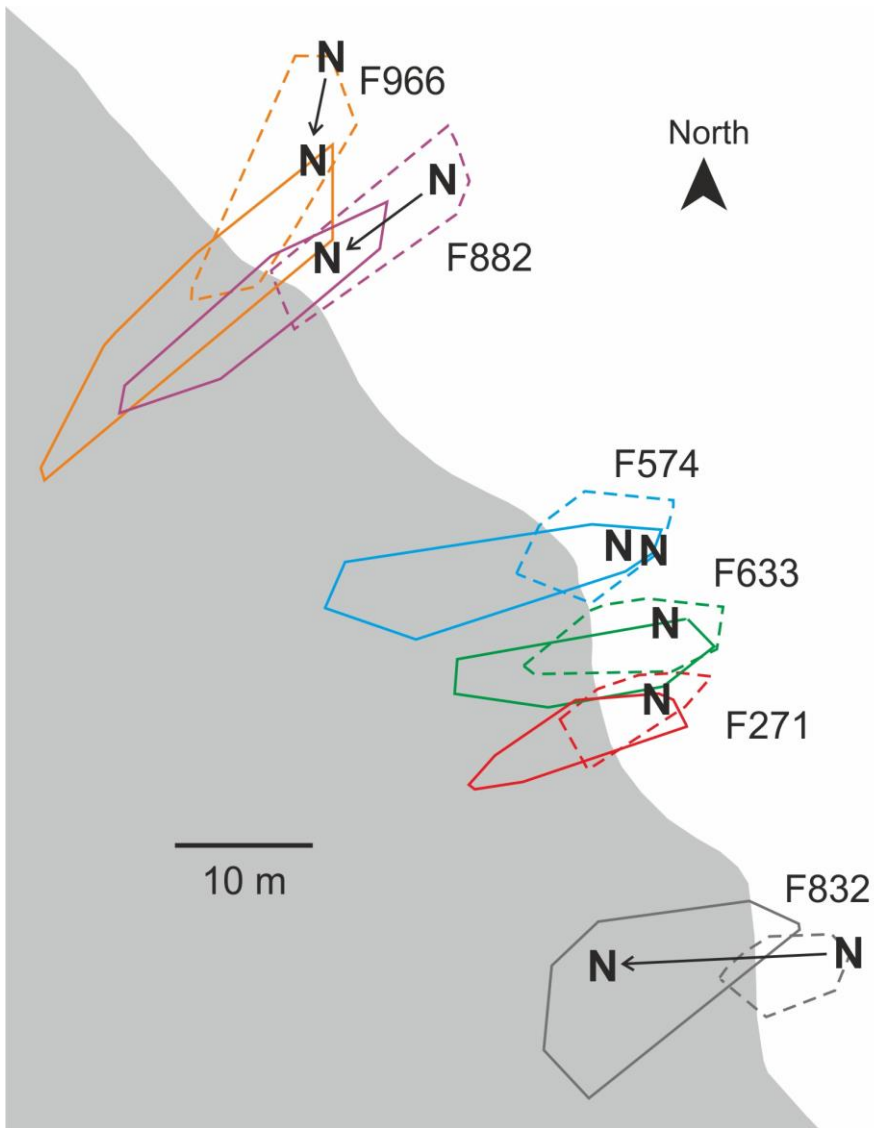


Figure 2. Shifts of home ranges of six radio-tracked female giant root-rats (wetland shore dwellers) towards a periodic wetland (marked in grey) between the early and late dry season. Dotted and solid lines encompass minimum convex polygons (MPC) covering all radio-fixes of the respective individual in the early dry and late dry season, respectively. N marks positions of nests, small arrows point to the nests used only in the late dry season.

Discussion

We found that the giant root-rats occupy very small HRs (about 100 m²), which can be tightly packed with little overlapping at sites with a high population density, such as on wetland shores. Environmental changes taking place during the dry season did not lead to an increase of HR sizes, except for individuals occupying the wetland shore who invariably shifted HRs into the wetland. On the other hand, a large proportion of individuals (almost 30 %) dispersed out of their HR up to few hundred meters before the late dry season.

The mean HR size of an adult giant root-rat of around 100 m² is approximately 200 times smaller than expected for a mammalian herbivore of the same body mass (Tucker *et al.*, 2014). This is very small even for a fossorial rodent (Harestad & Bunnell, 1979). The most probable explanation for such small HR sizes involves nutrition. The giant root rat feeds on grasses and forbs. In alpine zones such vegetation is usually dwarfed and therefore it often forms a dense cover close to the soil surface (Headberg & Headberg, 1979). Moreover, plants of high altitude are rich in nutrients (Körner, 2003). Finally, the strong livestock grazing pressure currently affecting the Bale Mountains Afroalpine zone (Vial *et al.*, 2011) promotes the growth of young plant tissues which usually have a higher palatability (Hobbs, 1996).

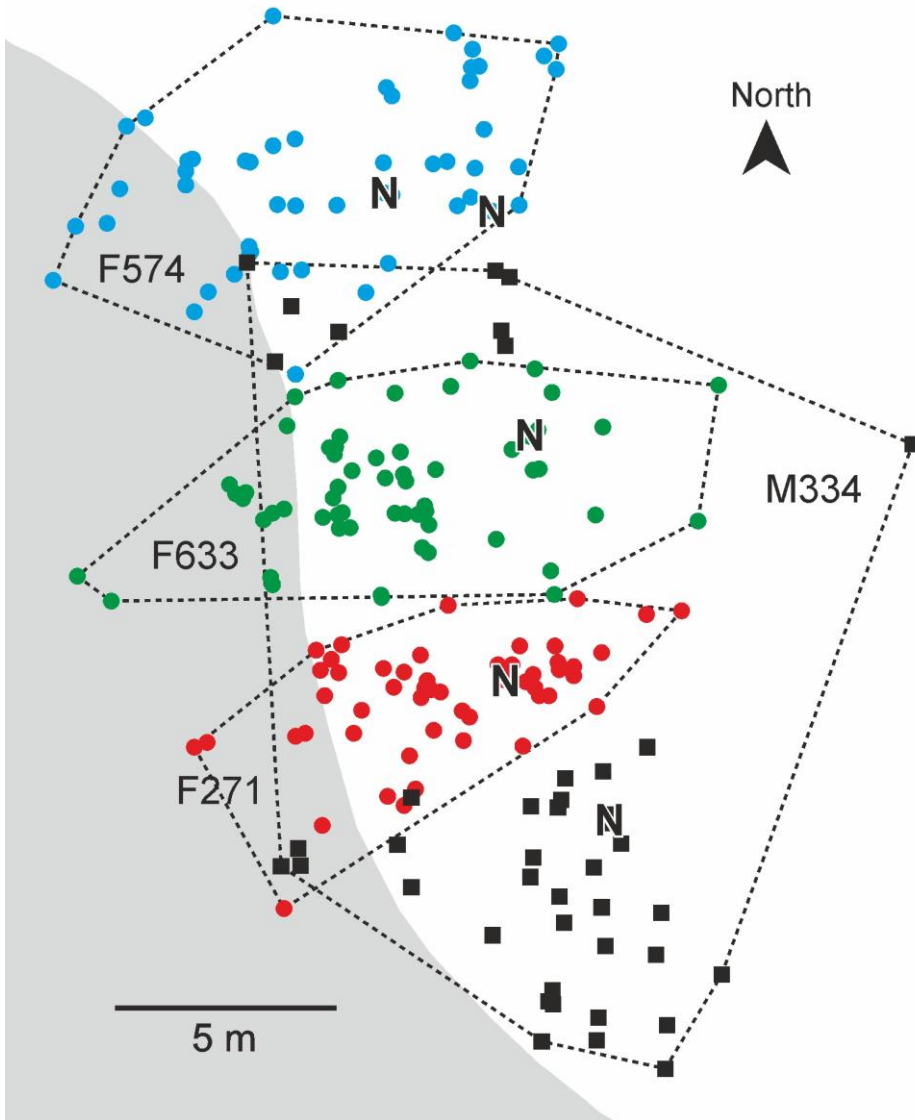


Figure 3. Overlap between home range of a male (M334) and three female (F271, F633 and F574) giant root-rats in the early dry season as revealed by radio-tracking. Small symbols represent radio fixes of the respective individuals; dotted lines encompass minimum convex polygons (MPCs) covering all radio fixes of the respective individual. N marks position of a nest; grey area is a periodic wetland. It seems that the male accessed the territory of the female F574 via a tunnel leading around the territories of the other two females rather than by travelling across them.

There were only small overlaps detected between the HRs of neighbouring individuals. The most conspicuous of the HR overlaps were detected between a male and one or more females in the early dry season. There were a few cases when a male and a female were successively observed emerging from the same burrow opening. A similar observation was recorded by Yalden (1975). This indicates that these neighbouring burrow systems must have been temporarily or even permanently interconnected. Nevertheless, the males probably moved mostly along the females' HR boundaries rather than freely wandered across them, as can be seen in Fig. 3. The detected HR overlaps might possibly indicate courtship or mating, as similar behaviour was observed in related blind mole rats during the reproductive season (Šklíba *et al.*, 2016). Neighbouring individuals were sometimes observed aboveground very close to each other (tens of cm) without any sign of agonistic or territorial behaviour. This contrasts with the frequent use of head drumming as a territorial signal produced underground (Hrouzková *et al.* 2018). Aboveground tolerance between neighbouring individuals might help them to defend against predators. In spite of that, the low level of detected HR overlapping indicates a solitary and territorial habit in both sexes of this species, similarly to that of most other subterranean rodents (Nevo, 1999).

Root-rat HRs remained small even in the late dry season. Even the (non-dispersing) Afroalpine pasture dwellers did not enlarge their HRs in the late dry season despite the general decrease of food biomass (Šklíba *et al.*, 2017). This contradicts the expected negative relationship between food supply and HR size as has been proved experimentally for example in the Arctic ground squirrel (*Spermophilus parryii*), a burrowing rodent of a similar size (Hubbs & Boonstra, 1998). Simple enlargement of the HR might not be an energetically profitable response to decreasing food

supply in more fossorial *Tachyoryctes* because of the energetically costly burrowing in hard dry soil it would involve and the increased cost of maintaining and defending a larger burrow system. Such HR enlargement might only pay off if it involves entering an area with a substantially higher food biomass, such as the periodic wetland in the study area, when the soil is still relatively easy to burrow. It may be advantageous for these root-rats to retain part of their original territory on the wetland shore as an area where they can return during the following rainy season.

Besides their small size, HRs of the radio-tracked root-rats were not stable in time. Most non-dispersing individuals shifted HR position markedly between the early and late dry season, which was most conspicuous in animals occupying the wetland shore. An easy access to a high food supply following a decrease of water level in the late dry season makes the shore the highest quality habitat available, which can be inferred from the high population density (see also Šklíba *et al.*, 2017) and from the fact that the largest (and therefore likely the competitively strongest) animals were captured here. HR shifts in general can be viewed as a strategy preventing depletion of food resources within the HR while reducing the cost of maintaining and defending a large territory.

About 40 % of the individuals changed the position of their nest at least once during the 36 days of the first radio-tracking period in the early dry season, whereas only one individual out of 17 (6 %) did so in the late dry season (M175 who settled down at a site with soft peaty soil had no stable nest there). The nest is a complicated structure consisting of a large chamber filled with a large amount of plant material as bedding (own unpublished data) and a surrounding labyrinth of tunnels. It can be assumed that it is energetically costly to build one, especially in the dry season, therefore these nests represents a valuable resource. Colonization of the freshly abandoned nest of other individual, as detected in M532, supports this.

There were altogether eight dispersal attempts detected during the five months of the study. The attempts were not cases of natal dispersal since the body mass of the dispersing individuals was not significantly lower than in sedentary individuals, they previously moved within a HR not shared with another individual and they were not conspicuously sex biased (although there were more males than females dispersing). Since most of these attempts took place in a period between early and late dry season, it can be supposed that the dispersal might have been triggered by decreasing food supply and at the same time it may have been limited by the increasing hardness of the soil, which might have made it hard to establish a new burrow system later in the dry season.

Some other factors such as presence of competitors or the absence of unrelated mates can also play a role in the decision to disperse in the root-rats. An anecdotal observation of two dispersers, male M022 and female F362, who established their new HRs very close to each other (nests 2.7 m apart, Fig. 1) supports the latter possibility. Relatively frequent dispersal attempts may therefore increase the rate of sexual encounters and thus compensate for the small HR size in this species. Frequent dispersal can also have a substantial effect on the genetic structure of root-rat populations. It should be noted that populations of fossorial rodents are thought to be genetically viscous as a result of supposed low dispersal ability (e.g. Nevo, 1999). In future, it would be interesting to find out how the high dispersal frequency affects genetic relatedness of various root-rat populations isolated by geomorphology and habitat-based barriers within the heterogeneous landscape of the Bale Mountains.

Acknowledgments

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Conclusion and future perspectives

The aim of my dissertation thesis was to explore two aspects of the ecology of a peculiar fossorial rodent species, the giant root-rat (*Tachyoryctes macrocephalus*), in its natural environment and to discuss the results in relation with available ecological data on other fossorial/subterranean rodents. The two aspects were: 1) impact of the giant root-rat on the Afroalpine ecosystem, and 2) its temporal and spatial activity. The main findings of this thesis based on three studies can be summarized as follows:

In **study I** we analysed the giant root-rat's impact on various ecosystem features to evaluate its ecosystem role that has remained largely unknown to date. We evaluated the impact of root-rats' activity on plant species composition, vegetation cover, fresh plant biomass, and soil characteristics (hardness and soil nutrient contents). We have demonstrated a significant effect of giant root-rats' activity on various ecosystem features. Firstly, root-rats changed plant composition by reducing the dominant species of the Afroalpine grassland, the forb *Alchemilla abyssinica*, while enhancing the presence/abundance of other species, such as *Salvia merjame*. Secondly, they reduced vegetation cover, but not fresh plant biomass. And finally, as a result of their extensive burrowing activity, we detected a decrease of soil hardness along with an increase in soil nutrients. All these factors consequently created a dynamic microhabitat heterogeneity in our study locality.

We also regularly observed some rodents utilizing their abandoned tunnel systems and several predators, especially the Ethiopian wolf (*Canis simensis*), preying on root-rats. Hence, mammals also apparently benefit from the root-rats' presence and conservation plans for the whole Afroalpine ecosystem should unfold from the fact that the giant root-rat is one of the main agents in the ecosystem functioning. In fact, based on our data we can conclude that the giant root-rat acts as an ecosystem engineer in the Afroalpine ecosystem. Still, some questions about root-rats' ecosystem role remained unanswered and our study opened new horizons for future research that should focus for example on the likely interaction of the giant root-rat's activity with the grazing of domestic livestock, which is not yet well understood.

The general objective of **study II** was to determine daily activity patterns of the giant root-rat in its natural habitat and to reveal how these patterns are affected by environmental conditions, to see if the giant root-rat adjusts its activity to them in order to save energy, similarly to other rodent species from climatically challenging environments. Our findings revealed several trends in root-rats' daily activity patterns that likely

represent the way of coping with adverse climatic (cold temperature and its large daily amplitude) and ecological (high risk of predation in a habitat lacking cover) conditions of the Afroalpine ecosystem. Firstly, we detected that root-rats spent only a small proportion of time outside their nests (21.4% of a day) and aboveground (5.4% of a day). Secondly, the activity was tightly related to the temperature on the soil surface. Root-rats displayed unimodal pattern of activity with its peak around midday when the mean daily surface temperature was the highest. And thirdly, we registered increased aboveground activity during warm hours in the cold season that can be attributed to basking according to our assumption. The detected small amounts of activity, its synchronization with the aboveground temperature cycle and occasional basking can be regarded as the main energy-saving behavioural strategies to cope with the harsh Afroalpine environment used by the giant root-rat.

Our results contributed to the understanding of the interspecific variation in activity timing among subterranean rodents with different degrees of underground lifestyle. While in strictly subterranean rodents, activity timing is usually shaped by temperature changes in underground burrows according to many recent field studies, fossorial rodents' activity seems to be influenced rather by the aboveground temperature cycle, despite the fact they spent only a relatively short time on the surface. The aboveground conditions possibly place much higher thermoregulatory demands on them, thus in this respect, they are rather similar to rodents with more pronounced aboveground activity than to strictly subterranean rodents.

The main objective of **study III** was to analyse space-use patterns of the giant root-rat with respect to the environmental conditions and their seasonal changes. Based on radio-tracking data, we provided the first empirical evidence of root-rats' spatial behaviour; we quantified home-range sizes of individual root-rats, and evaluated their seasonal change and overlap. According to our results, root-rats occupied surprisingly small home ranges of only around 100 m² which is approximately 200 times less than expected for a mammalian herbivore of the same body mass. Even though home ranges were tightly packed at some sites with high population density, we found only little home-range overlaps between neighbouring individuals. These data confirm the assumption that giant root-rat is solitary. Contrary to the expectations that root-rats will increase their home-range size as a response to a decreasing food supply, we did not record considerable change of home-range size between seasons. On the

other hand, we found that a great number of root-rats relocated their home ranges or at least shifted them in some direction. This behaviour can be viewed as a strategy preventing depletion of food resources within the home range while reducing the cost of maintaining and defending a large territory.

With providing the primary data on spatial behaviour of the giant root-rat in its natural habitat, this study fundamentally contributed to the knowledge of the ecology of this unique endemic fossorial rodent. Furthermore, it has opened new chapters for future research. Since spatial framework of animals is driven by many environmental factors including competition and accessibility of mates, spatial behaviour has consequences not only for individual fitness but also for population structure and dynamics. Thus, our data can serve as a springboard for studies concerning population ecology of the giant root-rat.

Appendix I

Supplementary material for Chapter III

Early dry season 29. 10. – 7. 12. 2013									
Animal ID	Body mass	sex	Capture date	Status / behaviour / fate	HR size (m2)			Dispersal distance (m)	
					GC	100% MCP	95% MCP		
M802	753	M	20.10.2013	Successfully radio-tracked	112	209	200	-	
F272	920	F	20.10.2013	Successfully radio-tracked	56	38	30	-	
F392_1	754	F	20.10.2013	Lost collar	-	-	-	-	
F964	808	F	20.10.2013	Successfully radio-tracked	88	94	92	-	
F832	827	F	21.10.2013	Successfully radio-tracked	64	38	35	-	
F574	1040	F	21.10.2013	Successfully radio-tracked	80	60	54	-	
M334	1045	M	21.10.2013	Successfully radio-tracked	?	194	184	-	
F723	980	F	21.10.2013	Predated by a wolf	-	-	-	-	
F633	925	F	21.10.2013	Successfully radio-tracked	84	57	43	-	
F233	523	F	22.10.2013	Successfully radio-tracked	60	51	44	-	
F302	500	F	22.10.2013	Successfully radio-tracked	72	66	44	-	
M161	311	M - subadult	22.10.2013	Likely predated	-	-	-	-	
M532	705	M	23.10.2013	Successfully radio-tracked	108	130	75	-	
F424	465	F	24.10.2013	Successfully radio-tracked	92	73	65	-	
F045	559	F	24.10.2013	Successfully radio-tracked	88	75	42	-	
F504	679	F	24.10.2013	Likely predated by a wolf	-	-	-	-	
F143	657	F	24.10.2013	Not radio-tracked after a successful dispersal	-	-	-	326	
F674	672	F	25.10.2013	Successfully radio-tracked	96	144	69	-	
M603	657	M	25.10.2013	Successfully radio-tracked	112	156	148	-	
F362	460	F	27.10.2013	Successfully radio-tracked	132	141	124	-	
M022	507	M	27.10.2013	Successfully radio-tracked	68	52	36	-	
F774	600	F	28.10.2013	Successfully radio-tracked	104	111	98	-	
M203	658	M	28.10.2013	Successfully radio-tracked	92	120	104	-	
F451	624	F	28.10.2013	Successfully radio-tracked	124	232	202	-	
M175	562	M	29.10.2013	Successfully radio-tracked	64	39	29	-	
F392	590	F	29.10.2013	Successfully radio-tracked	116	127	105	-	
F882	715	F	29.10.2013	Successfully radio-tracked	80	82	58	-	
M083	621	M	29.10.2013	Predated by a wolf during a dispersal attempt	-	-	-	77 (then predated)	

Animal ID	Body mass	sex	8.12.2013 – 22.2.2014		Late dry season 23.2. – 3.4.2014			
			Status / behaviour / fate	Dispersal distance (m)	Status / behaviour / fate	GC	100% MCP	95% MCP
M802	753	M	Undertook a successful dispersal	80	Successfully radio-tracked	52	39	33
F272	920	F	Shifted HR to wetland	-	Successfully radio-tracked	76	51	46
F392_1	754	F	-	-	-	-	-	-
F964	808	F	Shifted HR to wetland	-	Successfully radio-tracked	112	135	126
F832	827	F	Shifted HR to wetland	-	Successfully radio-tracked	112	142	62
F574	1040	F	Shifted HR to wetland	-	Successfully radio-tracked	100	113	105
M334	1045	M	Likely predated	-	-	-	-	-
F723	980	F	-	-	-	-	-	-
F633	925	F	Shifted HR to wetland	-	Successfully radio-tracked	84	74	69
F233	523	F	Undertook a successful dispersal	137	Predated by an eagle	-	-	-
F302	500	F	Remained sedentary	-	Successfully radio-tracked	120	105	104
M161	311	M - subadult	-	-	-	-	-	-
M532	705	M	Remained sedentary	-	Successfully radio-tracked	56	40	38
F424	465	F	Remained sedentary	-	Successfully radio-tracked	84	95	57
F045	559	F	Remained sedentary	-	Successfully radio-tracked	64	37	31
F504	679	F	-	-	-	-	-	-
F143	657	F	Remained sedentary	-	Lost collar	-	-	-
F674	672	F	Remained sedentary	-	Died of unknown reason	-	-	-
M603	657	M	Remained sedentary	-	Successfully radio-tracked	48	35	23
F362	460	F	Undertook a successful dispersal	294	Died of unknown reason	-	-	-
M022	507	M	Undertook a successful dispersal	272	Successfully radio-tracked	60	25	23
F774	600	F	Remained sedentary	-	Successfully radio-tracked	72	61	60
M203	658	M	Undertook a successful dispersal	428	Not radio-tracked	-	-	-
F451	624	F	Remained sedentary	-	Successfully radio-tracked	72	78	45
M175	562	M	Undertook a successful dispersal	132	Successfully radio-tracked	100	104	77
F392	590	F	Remained sedentary	-	Successfully radio-tracked	100	126	70
F882	715	F	Shifted HR to wetland	-	Successfully radio-tracked	116	87	86
M083	621	M	-	-	-	-	-	-

Appendix II

Curriculum vitae

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PhD. student in Zoology

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University of South Bohemia, Faculty of Science

Dissertation title: Ecology and behaviour of an enigmatic fossorial rodent, the giant root-rat (*Tachyoryctes macrocephalus*), endemic to the Afroalpine habitat in the Bale Mountains, Ethiopia

Mgr. in Zoology

2010-2013

University of South Bohemia, Faculty of Science

Thesis: Roosting ecology of three cryptic whiskered bats: Alcatthoe Whiskered Bat (*Myotis alcathoe*), Brandt's Bat (*Myotis brandtii*) and Whiskered Bat (*Myotis mystacinus*)

Bc. in Biology

2007-2010

University of South Bohemia, Faculty of Science

Thesis: Bats in cottages in surroundings of České Budějovice: species diversity and roost preferences.

WORK EXPERIENCE

Camp counsellor

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Website Vertebratus.cz

CONFERENCES

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Lučan, R. K., Bartonička, T., Březinová, T., Jahelková, H., Šálek, M., **Vlasatá, T.** (2010). Spatial activity and habitat preference of the Alcatthoe Whiskered bat (*Myotis alcatthoe*). ZOOLOGICKÉ DNY Praha, Czech Republic, p. 143 (talk)

TEACHING EXPERIENCE

Field Work I. and II., Faculty of Science, University of South Bohemia

Practical Courses in Zoology, Faculty of Agriculture, University of South Bohemia

PUBLICATIONS

Vlasatá, T., Šklíba, J., Lövy, M., Meheretu, Y., Sillero-Zubiri, C. & Šumbera, R. (2017). Daily activity patterns in the giant root rat (*Tachyoryctes macrocephalus*), a fossorial rodent from the Afro-alpine zone of the Bale Mountains, Ethiopia. *Journal of Zoology*. 302(3). 157-163.

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Volf, M., Redmond, C., Albert, Á. J., Le Bagousse-Pinguet, Y., Biella, P., Götzenberger, L., Hrázský, Z., Janeček, Š., Klimešová, J., Lepš, J., Šebelíková, L. **Vlasatá, T.**, & de Bello, F. (2016). Effects of long- and short-term management on the functional structure of meadows through species turnover and intraspecific trait variability. *Oecologia*, 180(4), 941-950.

DOI: 10.1007/s00442-016-3548-y

POPULARIZATION

Vlasatá, T. (2017). Life as a Root Rat in the Bale Mountains of Ethiopia? A Telemetric Study on Unique Fossorial Rodent. *Živa* 2017, 6: 318.

RELEVANT SKILLS

Advanced user of Microsoft Office

Intermediate user of programme Statistica, R, Canoco 5, and QGIS

Upper-intermediate English

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