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Activity pattern of free-living Ansell´s mole-rat (*Fukomys anselli*) as revealed by automatic radio-telemetry

Master thesis

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Annotation:
Social behavior of some species of African mole-rats makes them interesting object of study. Members of multigenerational families were only one pair breeds collectively work on building of their burrow system and obtaining food. Distribution of activity during the day in individual family members may give us a clue of how they manage their work. However, studies monitoring mole-rats in their natural environment are scarce and usually carried out on low number of individuals. Present study deals with outside-nest activity of 16 free-living Ansell´s mole-rats using data obtained by automatic radio-telemetry - method which was used in radio-tracking of mole-rats for the first time. It reveals differences in activity pattern of individual mole-rats and examines how they relate to body mass, sex, reproductive status and affiliation to a family and test whether individuals of the same family tend to be synchronized in their outside nest activity.

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České Budějovice, 13. 12. 2017

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Tereza Hausteinová

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CONTENT

INTRODUCTION

Evolution of animal cooperation and mechanisms maintaining it are intensively studied topics (see for example Dugatkin 1997, Bateson 2000, Smith 2014). Although the cooperation occurs even among non-related individuals it is usually more associated with the kinship of individuals to whom it provides indirect fitness (Hamilton 1964, Clutton-Brock 2002, Dugatkin 2002).

Cooperation between individuals is realized usually on the level of breeding, care for offspring, defense, or obtaining food (Davies et al. 2012). One type of cooperation is so called "cooperative breeding" which is system where group members other than parents (alloparents, usually called helpers) help with care for the offspring (Brown 1983, Lukas and Clutton-Brock 2012). Cooperation is found among many invertebrates as well as vertebrates including several avian and mammalian orders. Well-known examples of cooperatively breeding or hunting species are for instance white-winged choughs *Corcorax melanorhamphos* (Heinsohn and Cockburn 1994), southern ground hornbills *Bucorvus leadbeateri* (Kemp 1980), Harris hawks *Parabuteo unicinctus* (Bednarz 1988), meerkats *Suricata suricatta* (Clutton- Brock et al. 2000), African wild dogs *Lycaon pictus* (Creel and Creel 2002), wolves *Canis lupus* (Macdonald 1983) or killer whales *Orcinus orca* (Visser et al. 2008).

Another example of cooperation among mammals can be found in several species of African mole-rats (Bathyergidae, Rodentia). This family includes three solitary genera as well as three social genera, with advanced cooperative behavior in some species (Bennett and Faulkes 2000). Bathyergids have strictly subterranean lifestyle and thus they have to cope with specific conditions of their underground niche. Among main challenges of their way of life belongs energetically demanding excavation of burrows, uneven distribution of food and limited opportunities of dispersal, which are expected to be particularly difficult in arid environment. Some authors believe that such conditions in arid areas are cause of evolution of sociality in this family (Lovegrove 1991, Jarvis et al. 1994, Faulkes et al. 1997, Faulkes and Bennett 2013). In addition, several mole-rat species are even considered to be eusocial (Jarvis 1981, Jarvis et al. 1994, Burda et al. 2000, Patzenhauerová et al. 2013), which is frequently mentioned as the most complex social system among animals. Eusociality is characterized by division of reproductive labor where only small number of individuals in the multi-generation group breeds and the others help with care for the offspring (Wilson 1971). It can be seen as special case of monogamy (Burda et al. 2000).

Eusociality was first described in insects (Wilson 1971), however it was later described in the naked mole-rat *Heterocephalus glaber* (Jarvis 1981) and in the Damaraland mole-rat *Fukomys damarensis* (Bennett and Jarvis 1988, Jarvis and Bennett 1993). Afterwards it was argued, that more mammalian species fit the definition of eusociality, such as the Ansell´s mole-rat *Fukomys anselli* and the giant mole-rat *Fukomys mechowii* (Burda et al. 2000, Patzenhauerová et al. 2013). To distinguish eusocial (mainly invertebrate) species from other cooperatively breeding species a new criterion - the existence of permanent castes, which represent groups of animals with different morphological development and particular task specialization within the colony, was proposed (Wilson 1971, Gadagkar 1994, Crespi and Yanega 1995).

Considering morphological castes in eusocial mole-rats, there are only two examples provided. One of them is reproductive caste in female naked mole-rats referred to as “queens” (O'Riain et al. 2000, Henry et al. 2007) and the second is so-called dispersive morph (O'Riain 1996, Scantlebury et al. 2006). Nevertheless, validity of both of these morphological castes is in question, because their characteristics - prolonged lumbar vertebrae in queens and large fat reserves in dispersers – are known as common among reproductively active females of mammals or dispersing individuals respectively (see Burda 1999, Vajda et al. 2001).

Some authors tried to define “castes” based on the amount of performed work or alternatively locomotor activity reflecting different “works” (Jarvis 1981, Bennett and Jarvis 1988, Bennett 1990, Jacobs et al. 1991, Bennett 1992, Wallace and Bennett 1998). Such behavioral castes should be permanent discrete categories differing thus from temporal/age polyethism where contribution to colony work of particular individual changes according age of that individual. Many studies focusing on behavioral castes in mole-rats accepted the terms firstly proposed by Jarvis (1981). In her pioneering study she recognized three castes within the colony of the naked mole-rats based on the frequency of various tasks performed by individual members: “frequent workers”, “infrequent workers” and “nonworkers” that usually represented the largest animals in the colony. Breeding males and large non-breeders represented latest group. Nevertheless, following studies have not proven the existence of behavioral castes as permanent discrete categories in this species (Lacey and Sherman 1991, 1997, Jarvis et al. 1991).

Furthermore, there is growing evidence in favor of temporal polyethism than behavioral castes since the system of division of labor is apparently flexible and age-based with possible preferences for diverse tasks in different age groups (Burda 1990, Lacey and Sherman 1991, Mooney et al. 2015, Zöttl et al. 2016a). Recently, mole-rat age has been found to be the most important predictor of an individual´s contribution to cooperative task in the Damaraland mole-rat (Zöttl et al. 2016a). By analyzing a large number of captive individuals, authors found no indication for divergent developmental strategies which would suggest caste system. In addition they neither found any evidence for specialization in cooperative activities. Correspondingly, variation in growth rates of non-breeding Damaraland mole-rats do not support differentiation of individuals into discrete castes associated with specialization for different tasks (Zöttl et al. 2016b).

Almost all findings on polyethism in African mole-rats were discovered under laboratory conditions from behavioral characteristics and activity patterns. Unfortunately, there are only very limited information on this topic from the field. Authors of recent radio-tracking study on spatial-use patterns in Ansell´s mole-rat (Šklíba et al. 2016) found that the large individuals (neglecting their breeding status) spent more time inside the nest than the smaller (and probably younger) animals that were, on the other hand, relatively more often located in greater distances from the nest. No apparent discontinuity in space-use patterns of non-breeders was observed and body mass, turned out to explain a significant part of the variability. Both speak in favor of age polyethism rather than the existence of castes since body mass in this species is most probably related to age with continuous growth as documented by Begall and Burda (1998).

Time investment in cooperative tasks or overall activity in lab was studied mostly in the Damaraland mole-rat (Bennett 1990, Jacobs et al. 1991, Gaylard et al. 1998, Zöttl et al. 2016a), but also in the giant mole-rat (Wallace and Bennett 1998, Dammann et al. 2011), Ansell’s mole-rat (Burda 1990, Shielke et al. 2012), and the common mole-rat *Cryptomys hottentotus hottentotus* (Bennett 1992). In these studies authors noted that the most working members are usually the smaller and younger individuals, whereas large and reproductively active ones performed little work. Exception makes study of Gaylard et al. (1998) where the amount of performed work was higher for larger animals, probably as a result of young and still establishing colony. Burda (1990) found similar results also in Ansell’s mole-rat. The differences in activity between sexes were not consistent among above mentioned studies.

Different authors agree on that social mole-rats spend most of their time in the nest, usually 60 to 90 %, both in laboratory and field studies (field studies: Lovegrove 1988, Lövy et al. 2013, Šklíba et al. 2016; laboratory studies: Bennett 1990, Lacey and Sherman 1991, Desmet et al. 2013), although this time is not necessarily represented only by resting. Nest is also place of pup care, grooming and in case of social species place of social interactions (Lacey et al. 1991). Concerning social species, breeding males usually spend most time in the nest (Jarvis 1981, Bennett 1990, Lövy et al. 2013, Šklíba et al. 2014). Outside-nest activity of breeding females is often comparable with that of non-breeders (Bennett 1990, Dammann et al. 2011, Šklíba et al. 2014) but space-use patterns of Ansell´s mole-rat breeding females imply that they keep their activities close to the nest, which corresponds with their reproductive role (Šklíba et al. 2016). From non-breeders, larger animals are usually those who are found in the nest more often (Jarvis 1981, Lovegrove 1988, Jacobs et al. 1991, Lacey and Sherman 1991, Lövy et al. 2013, Šklíba et al. 2014).

Outside-nest activities primarily include excavation and maintenance of tunnels, foraging, feeding and patrolling, which all take place in the family's complex underground system. Food chambers, where small items of food are stored, and toilet chambers are usually in close vicinity of the nest whereas endings of foraging tunnels may be located several tens of meters far as it is in case of Ansell´s mole-rat (Šklíba et al. 2012). These tunnels are changing over time, because new tunnels are opened while others are backfilled, soil is constantly pushed around and out of the underground system (Šklíba et al. 2009). This activity allows covering area large enough to provide food for the family. Based on the size, food item is transported into food chamber or consumed on the site (Bennett and Faulkes 2000). Mole-rats also transport bedding material into the nest. Foraging tunnels are regularly patrolled and defended in case of intrusion of mole-rat from a different family group or predator (Lacey et al. 1991).

Different individuals may specialize on different activities in the family (Jarvis 1981, Burda 1990, Mooney et al. 2015). Task allocation was discovered in the naked mole-rat where older and larger animals tend to be more aggressive towards unfamiliar conspecifics than others which results in their role as a colony defenders (Lacey and Sherman 1991, O'Riain and Jarvis 1998, Mooney et al. 2015). Large males of mole-rats are also usually among first animals caught during a field trapping and it is suggested that they hold a patrolling function in the colony (Lovegrove 1988, Jacobs et al. 1991). Younger non-breeders of naked mole-rat on the other hand; engage more in a pup care (Mooney et al. 2015). Similarly, Burda (1990) recognizes younger members of family as "babysitters" and the older ones as “workers and soldiers” in Ansell´s mole-rat. What is important, at least in the case of naked mole-rat it seems that individuals are capable of task switching in order to fulfill colony demands (Mooney et al. 2015).

Most typical and energy demanding activity for mole-rats and subterranean mammals generally is digging and transporting of soil. Authors of physiological studies discovered that metabolic rate of burrowing mole-rat is proximately 4-5 times higher compared to its resting metabolic rate (Lovegrove 1989, Zelová et al. 2010). Body temperature rises together with metabolism and animals are forced to make breaks to cool down and prevent overheating (Marhold and Nagel 1995, Buffenstein 1996a). In order to increase efficiency of excavation, social animals may cooperate on the task. Well known example is from the naked mole-rat where animals form so called digging chains (Jarvis and Sale 1971). In these chains, line of individuals help excavate dirt and transport loose soil. Possible cooperation can be indicated from spatial activity pattern of free-living giant mole-rats where non-breeding individuals were repeatedly found accompanied by another family member or replacing one another in area of excavation of new burrows (Lövy et al. 2013).

Our knowledge about behavior of African mole-rats originates almost exclusively from laboratory studies. However, laboratory conditions can never fully simulate natural environment. Especially simulation of complex underground systems with natural opportunities for digging is challenging. Moreover, laboratory animals are usually fed *ad libitum*, which reduces their need for foraging. Many types of animals´ behavior are significantly limited in laboratory conditions, field studies are therefore crucial for our understanding of mole-rats´ life.

So far, only seven studies monitoring African mole-rats´ behavior in their natural environment were published. They all involved radio-tracking of collared individuals. Three of them are considering solitary species; a silvery mole-rat *Heliophobius argenteocinereus* (Šklíba et al. 2007, Šklíba et al. 2008, Šklíba et al. 2009), and the other four were focused on social species; Damaraland mole-rat, giant mole-rat and Ansell´s mole-rat (Lovegrove 1988, Lövy et al. 2013, Šklíba et al. 2014, Šklíba et al. 2016). With exceptions of studies done by our team on Ansell’s mole-rats (Šklíba et al. 2014, 2016) analyzing individuals from five family groups, the main disadvantage of those studies is sample size restricted to small number of individuals or one family group.

Ansell´s mole-rat lives in family groups with one exclusive breeding pair where family members contribute to the care for the offspring and maintaining of their underground system. According some authors this species is considered as eusocial (Burda 1990, Sichilima et al. 2011, Šklíba et al. 2012, Patzenhauerová et al. 2013). Studies of Šklíba et al. (2014) and Šklíba et al. (2016) have brought new information about daily life of this species including activity pattern and spatial-use pattern. Authors discovered that daily activity of Ansell´s mole-rats has unimodal distribution with one prominent peak corresponding to fluctuations of daily temperature in depth of foraging tunnels, probably as a way of behavioral thermoregulation. Individuals from the same family groups were found to be more similar in their activity patterns then individuals across the families (Šklíba et al. 2014). Similarly, affiliation to a family group explains great proportion of variability in space-use patterns of individuals. After the removal of the effect of family, great proportion of variability can be explained by body mass of the individuals. Larger individuals and breeders tend to spent more time inside the nest and in its close vicinity than smaller members of their families (Šklíba et al. 2016). Finally, authors of the last mentioned study propose that differences in individuals´ space-use patterns in Ansell´s mole-rats are the consequence of age polyethism rather than the existence of castes (see above).

All field studies including those of Šklíba et al. (2014) and Šklíba et al. (2016) are based on the data obtained by manual radio-telemetry. Disadvantage of this method is relatively scarce record with usually one fix of animal per hour and disturbances of individuals during their localization by approaching observer. In this context, using more advanced technology such as automatically recording radio-telemetry receiver with stationary antenna placed above the communal nest could provide more detailed time record of radio-collared individuals without need for physically approaching them.

In my master thesis, I analyzed outside-nest activity of cooperatively breeding Ansell´s mole-rat in nature using automatically recording radio-telemetry. Aims of my study are: 1) to describe pattern of their outside-nest activity in natural conditions. 2) To reveal the frequency distribution of activity bouts according to their duration. 3) To test if there are individual differences in the length of activity bouts between mole-rats and if they are related to body mass, sex, reproductive status and affiliation to a family. 4) To reveal whether individuals of the same group are synchronized in their outside nest activity beyond the level given by general similarity of their daily activity patterns.

MATERIALS AND METHODS

Study site and animals

The study was conducted in the Lusaka East Forest Reserve in Zambia (15°28′S, 28°25′E, altitude 1320 m). It is a mesic area with annual precipitation of 900 mm and regular changes of rainy (October/November to March/April), dry cold (April to July) and dry hot (August to October) season. Vegetation is formed by miombo woodland (Fig. 11) characterized by species of *Brachystegia*, *Isoberlinia*, *Julbernardia*, and *Marquesia macroura* (Fanshawe 1971).

The Ansell’s mole-rat is one of the smallest species of genus *Fukomys*. Body mass of adult individuals in captivity reaches approximately up to 130 g for males and 100 g for females (Burda et al. 1999). Mean weight of captured individuals in this study was 72 ± 14 g (maximum 96 g) in adult males and 62 ± 8 g (maximum 83 g) in adult females which is slightly more than weight of free-living Ansell´s mole-rats is study of Sichilima et al. (2011). It is a highly social species living in groups of 5-16 individuals with only one breeding pair (Sichilima et al. 2011, Šklíba et al. 2012, Patzenhauerová et al. 2013). It builds extensive, complexly branched underground burrow systems consisting on average of 1.2 km of tunnels (Šklíba et al. 2012; Fig. 12). The foraging tunnels are located mostly in a depth of around 10 cm, nest is situated deeper (around 50 cm) with a tangle of adjoin tunnels (Fig. 13). Food stores and toilet chambers are usually found in a close proximity of the nest (within 2 m). Only one communal nest is used at a time (Šklíba et al. 2014).

Field work

Mole-rats were trapped by Hickman traps from 17 April to 6 May 2010, in the beginning of dry the season. Ansell´s mole-rats from five different family groups were captured, weighted and their sex and reproductive status was determined. Individuals weighting more than 45 g were shortly anesthetized by ketamine and xylazine and equipped with radio-collars (Brass collar, Pip transmitter; Biotrack Ltd, Dorset, UK; Fig. 14). Weight of collars was less than 5% of the body mass of the smallest animal under study. All animals were released back into their burrow systems within 48 hours from their capture. Radio-tracking started three days after the release of last individual at least.

In total, seven males and nine females were analyzed (for further details see Tab. 1). Each individual was continuously monitored for the 96-h period using an automatic receiver (ATS R4500S Receiver/Datalogger with Digital Signal Processing; Fig. 15) with stationary antenna placed above the communal nest of the respective family. Incoming signal and the number of detected pulses from radio-collars were recorded in one (family P02, P04, P05) or two min intervals (family P01, family P10). Female F217 from family P01 has an incomplete record of only 24 hours, due to the loss of radio collar during monitoring.

Simultaneously with collecting of data for this study animals were followed with manual radio-tracking. Results of manual radio-tracking were published in other studies (see Šklíba et al. 2014 and Šklíba et al. 2016). After the end of radio-tracking all animals were captured and transferred into captivity. Their burrow systems were excavated and mapped as a part of another study (see Šklíba et al. 2012).

All animals were handled with approval of the Institutional Animal care and use committee and Ministry of Education of Czech Republic (7942/2010-30) and the Zambian Wildlife Authority.

Data processing

An additional measuring of signal reach was conducted in order to decide what rate of signal decrease indicates that a radio-tracked individual left the nest. To do so, radio-tracking collar was buried into the depth of 20, 45 and 90 centimeters and incoming signal from the collar was measured in several distances horizontally from the antenna; distances were from zero to seven meters. Measuring signal strength revealed that in the distance of one meter, regardless of the depth, incoming signal decrease on average to 72.8±0.8 % of signal detected right above the collar (zero distance). Based on these findings, it was decided that individual with value of signal lower than 72 % of its maximum recorded signal would be considered as being outside the nest area (beyond one meter radius from communal nest). Individuals within the nest area (less than one meter from the nest) were denoted as inside the nest.

To unify 1 and 2 min intervals of record and to avoid possible errors of data recording caused by short loss of incoming signal, the data were pooled into 10 min intervals. For each of the 10 min interval it was assigned whether the animal was inside the nest (when more than half of the 1 or 2 min intervals forming pooled 10 min interval were rated inside the nest based on the signal strength) or likely outside the nest (when less than half of the 1 or 2 min intervals forming pooled 10 min interval were rated inside the nest based on the signal strength). Resulting dataset was used for testing and an actogram was created for each animal based on pooled data.

For subsequent analyses, the number and duration of activity bouts (comprising of 10-min intervals) of each individual were counted up. Activity bout was defined as period of successive 10 min intervals rated as outside the nest. Activity bouts separated by single 10 min interval of presence in the nest were considered as continuous activity bout since in such short period of time the individual was most probably staying active even in the nest. All activity bouts were sorted into four categories based on their duration (10-20 min, 30-60 min, 70-220 min, 230-860 min) according to that they upper limits created geometric row and numbers of activity bouts in these categories were approximately comparable. Into category “10-20 min” were included activity bouts long 10 and 20 minutes, into category “30-60 min” were included activity bouts long from 30 to 60 minutes, into category “70-220 min” were included activity bouts long from 70 to 220 minutes, and into category “230-860 min” were included activity bouts long from 230 to 860 minutes. The mean numbers of activity bouts in all categories per 24 hours were calculated for each individual. For each activity bout it was noted if its middle value lies within the period of main activity or out of this period. The period of main activity was determined for all studied mole-rats as time when more than half of all radio-tracked individuals were active at least in two observing days, which is the time between 11:20 and 16:20.

Results of this study were compared with the results of study of Šklíba et al. (2014). To test the concordance between the manual and automatic radio-tracking data, I used a generalized least-squares (GLS) model using the NLME package (Pinheiro et al., 2015) and Tukey´s HSD tests. Compared was the proportion of outside-nest activity transformed by an arcsine transformation in each individual based on data obtained by manual radio-telemetry from the first four days of radio-tracking (see Šklíba et al. 2014) with row and pooled data obtained by automatic radio-telemetry. In the model, animal identity was included as random factor to avoid pseudoreplications since each individual was represented by three values. Proportion of outside-nest activity obtained by manual radio-telemetry differs significantly from the proportion of that individuals´ activity based on the row data obtained by automatic radio-telemetry (Tukey´s test: p=0.024), yet it does not differ when based on pooled data obtained by automatic radio-telemetry (Tukey´s test: p=0.983). Although proportion of outside-nest activity based on raw data obtained by automatic radio-telemetry differed from results obtained by manual radio-telemetry, the difference is marginal and disappears when using pooled data (Fig. 1). Both methods (manual and automatic radio-telemetry) therefore provide comparable results.

Statistical analyses

In order to visualize differences in mean number of activity bouts of defined length categories (10-20 min, 30-60 min, 70-220 min, 230-860 min) among individuals across all families, I used a principal component analyses (PCA) plot with body mass, sex*breeding status (combination of individual´s sex and whether it was breeder or non-breeder) and family affiliation as explanatory variables. Using the variance partitioning technique (Šmilauer and Lepš 2014) based on redundancy analysis (RDA), I calculated the partial effect of these three variables on the mean number of activity bouts of defined length categories. PCA plot and RDA with variance partitioning were computed both for data undifferentiated and differentiated according to occurrence of activity peak (i.e. within the period of main activity, out of the period of main activity). All multivariate analyses (PCA, RDA) were carried using CANOCO software, version 5.

To test individual differences in the lengths of activity bouts (approximated by the Gamma distribution), generalized linear mixed models (GLMM) with the geeglm function from the GEEPACK package was used (Højsgaard et al. 2006). Animal identity was included as random factor to avoid pseudo-replications, as several activity bouts for each individual in each model were involved. I used two different models. In the first one, the effects of 1) occurrence of activity bouts – if they occurred within or outside the period of main activity (IN, OUT), 2) affiliation to a family (P01, P02, P04, P05, and P10) and 3) their interaction was tested. In the second model, I analyzed the effects of 1) activity bout occurring within or out of the period of main activity (IN, OUT), 2) combination of sex and breeding status (bF = breeding female, bM = breeding male, nF = non-breeding female, nM = non-breeding male) and 3) their interaction. Both models were performed with R statistical software (R Core Team, 2017).

To test the synchronization between individuals, I used simple permutation test (see Šklíba et al. 2014). In this test, score x was computed for each dyad of individuals from every family. Score x represents the total number of cases when both individuals of the dyad were located outside the nest at the same time. Next, for each 10 min interval of the 4-day activity record of both individuals of the particular dyad, the order of the four observing days was randomly exchanged yet with daytime preserved and new score was computed (xp). P was calculated as the proportion of cases out of 1000 permutations where $xp \geq x$. As significant synchronization of activity in particular dyad above the general similarity of their activity patterns was considered $p < 0.05$, whereas $p > 0.95$ was considered as significant desynchronization. Female with incomplete record was excluded from this test.

All means in this study are presented ±SD.

Table 1. Characteristics of Ansell´s mole-rats and their family groups used in this study.

Family ID	Family size	Family HR size (m^2)	Animal ID	Sex and reproductive status	Body mass (g)
P01	10	960	M038	breeding M	86
-||-	-||-	-||-	M150	non-breeding M	84
-||-	-||-	-||-	M203	non-breeding M	57
-||-	-||-	-||-	F217*	breeding F	69
P02	5	2109	F138	non-breeding F	56
-||-	-||-	-||-	M967	breeding M	90
P04	13	6070	F027	non-breeding F	64
-||-	-||-	-||-	F465	non-breeding F	68
-||-	-||-	-||-	F485	non-breeding F	83
P05	> 7	6565	F419	non-breeding F	57
-||-	-||-	-||-	F443	non-breeding F	49
-||-	-||-	-||-	F532	breeding F	54
P10	9	6832	F015	non-breeding F	62
-||-	-||-	-||-	M062	breeding M	87
-||-	-||-	-||-	M092	non-breeding M	58
-||-	-||-	-||-	M352	non-breeding M	47

F = female; M = male; asterisk marks the female with incomplete record. Family and home range (HR) sizes with minimum convex polygons (MCP) adopted from Šklíba et al. (2016).

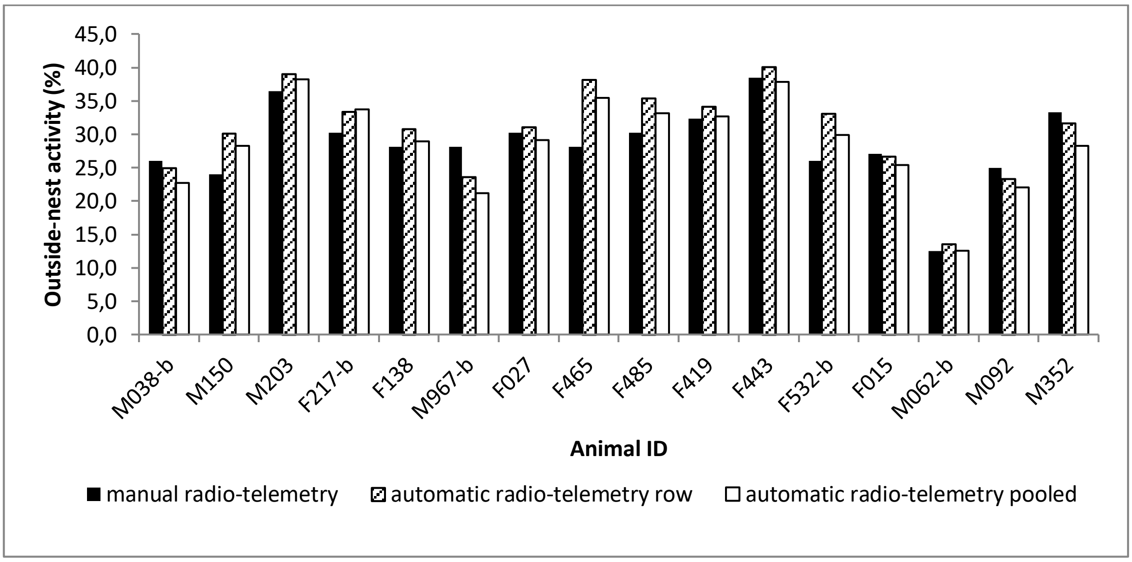

Figure 1. Outside-nest activity based on manual and automatic radio-telemetry data. Manual radio-telemetry represents data obtained during first four days of radio-tracking in study of Šklíba et al. (2014). Automatic radio-telemetry represents data used in this study, both without pooling (raw) and pooled into 10-min intervals.

RESULTS

Apart of breeding male M967, activity of each individual was concentrated into afternoon hours (Fig. 2). Except the period of main activity, which was approximately between 11:00 and 16:00, individuals had some additional activity bouts throughout the day. Breeders and non-breeders of both sexes performed one peak of activity around 14:00 (Fig. 3). Average proportion of outside-nest activity in all mole-rats reached 28.7±6.8 % of the monitored time and differed markedly in breeding males (Tab. 2).

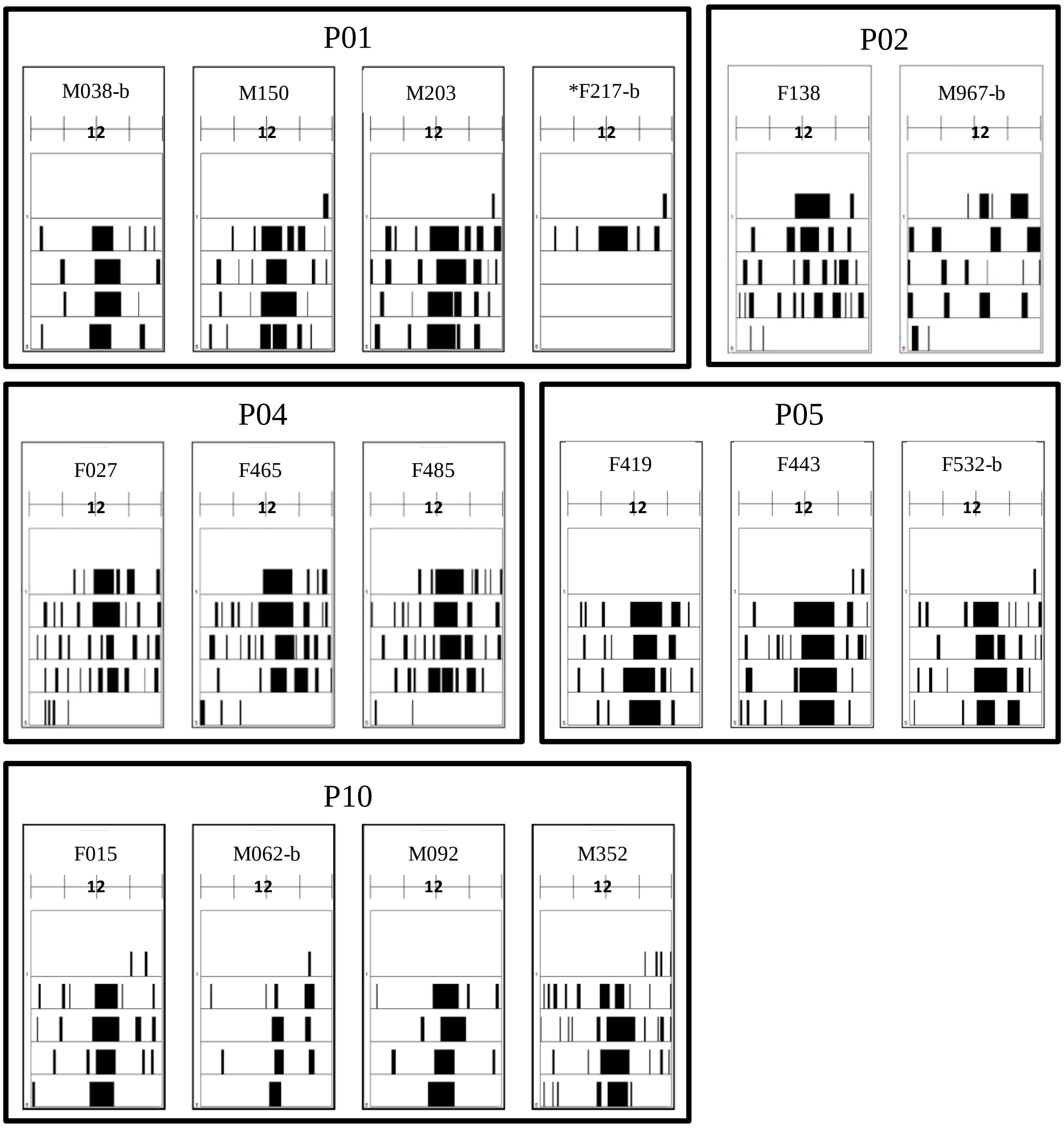

Figure 2. Actograms of radio-tracked Ansell´s mole-rat individuals. Black bars mark the outside-nest activity. Every row of activity represents the 24-h period of radio-tracking from midnight to midnight. Time scale is marked every six hours. Breeding individuals are labeled with –b, asterisk marks female with incomplete record.

Table 2. Average proportion of outside-nest activity in individuals of different sex and reproductive status.

Individual sex*breeding status (n)	Mean of outside-nest activity proportion %
Breeding male (3)	18.8 ± 5.5
Breeding female (2)	31.7 ± 2.8
Non- breeding male (4)	29.2 ± 6.7
Non-breeding female (7)	31.8 ± 4.2
All (16)	28.7 ±6.8

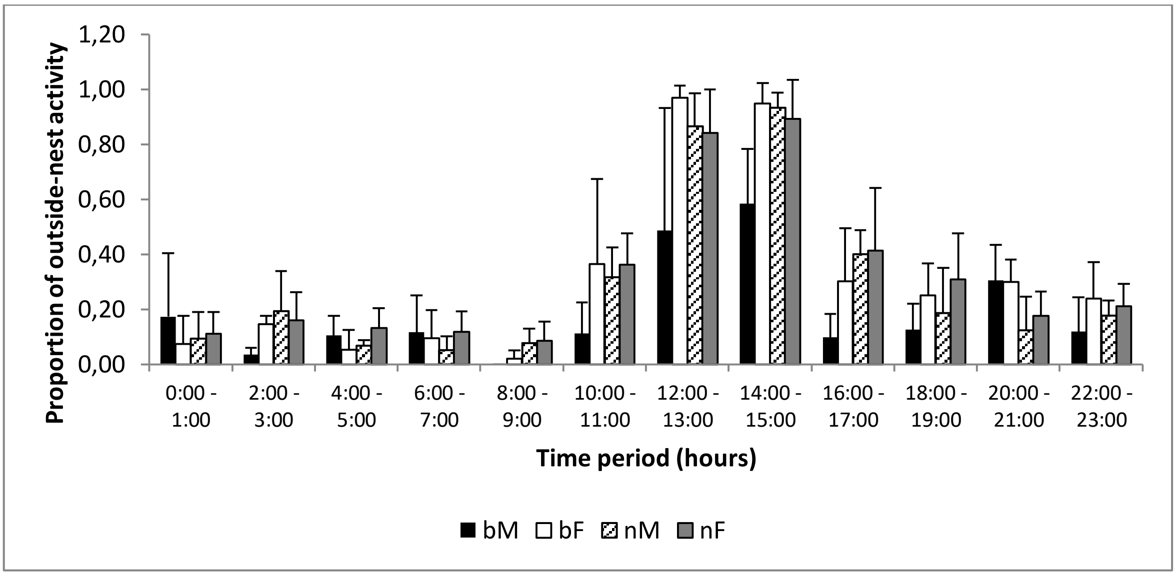

Figure 3. Outside-nest activity of the radio-tracked mole-rats during 24 hours according to their sex and breeding status. Mean ± standard deviation is depicted for the proportions of outside-nest activity. bM = breeding male; bF = breeding female; nM = non-breeding male; nF = non- breeding female.

Out of all activity bouts the highest frequency has the shortest once (Fig. 4). Activity bouts shorter than one hour account for 76 % of all bouts performed by all radio-tracked mole-rats. Individuals differ in distribution of their activity bouts in defined length categories and in proportion of outside-nest activity (Tab. 3).

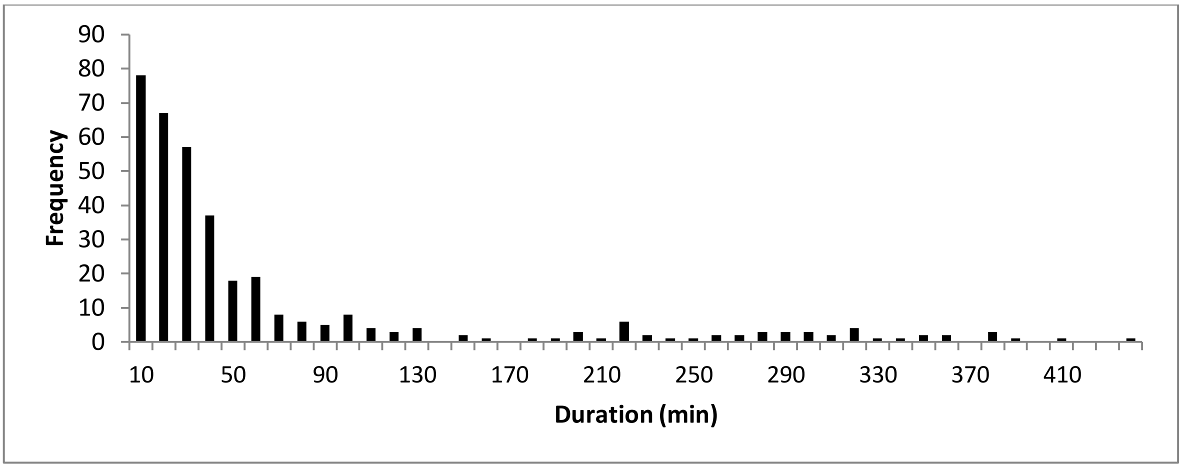

Figure 4. Frequency distribution of activity bout lengths in Ansell´s mole-rats during whole period of recording.

Table 3. Mean number of activity bouts according to their length categories and proportion of outside-nest activity of each radio-tracked Ansell´s mole-rat per 24 hours. Breeding individuals are marked with –b, asterisk marks female with incomplete record.

Family ID	Animal ID	10 – 20 min	30 – 60 min	70 – 220 min	230 – 860 min	Proportion of outside-nest activity (%)
P01	M038-b	1.5±0.6	1±0	0±0	1±0	22.8
-‖-	M150	2.5±0.6	1.5±0.6	1.5±1.3	0.25±0.5	28.2
-‖-	M203	1.75±1.5	2.5±1	1±0.8	1±0	38.2
-‖-	*F217-b	2±0	3±0	0±0	1±0	33.7
P02	F138	2.25±2.6	3±1.2	1.5±1	0.25±0.5	29.0
-‖-	M967-b	1.25±1	1.5±1.3	1.75±1.3	0±0	21.2
P04	F027	4.5±1	3.75±0.5	1±0.8	0.25±0.5	29.2
-‖-	F465	3±0.8	3.5±1.9	1±0.8	0.5±0.6	35.4
-‖-	F485	4±2.4	2.75±1.3	1±1.4	0.75±0.5	33.2
P05	F419	1.75±1	2±1.2	0.5±0.6	1±0	32.6
-‖-	F443	2.5±1.7	2.25±0.5	0.5±0.6	1±0	37.8
-‖-	F532-b	2.5±1.3	2±1.8	1.25±1.5	0.5±0.6	29.7
P10	F015	1.5±1.9	2.5±1.3	0.25±0.5	0.75±0.5	25.4
-‖-	M062-b	0.5±1	1.25±1	1±0.8	0±0	12.5
-‖-	M092	0.25±0.5	1.25±1.3	0.25±0.5	0.75±0.5	22.1
-‖-	M352	6±1.4	1.25±0.6	0.75±1	0.5±0.6	28.3

PCA plot shows some trends between breeders and non-breeders of both sexes and between family groups on activity bouts of different length categories (Fig. 5). Whereas non-breeding females incline to activity bouts of 10-20 min and 30-60 min, breeding females incline to activity bouts of 230-860 min which means that hey leave nest for longer periods. Low number of all activity bouts (indicating low overall activity) is very remarkable in breeding males. Out of all families, individuals of family P04 were found to be very close to each other. Body mass is negatively related to 10-20 min and 30-60 min activity bouts. Short activity bouts, i.e. those of 10-20 min and 30-60 min are highly correlated.

Variance partitioning technique using RDA (Fig. 6) revealed that the highest amount of variability in individual activity pattern represented by mean number of activity bouts in different length categories was explained by affiliation to a family group although the result is not significant (17 %; p=0.148; Tab. 4).

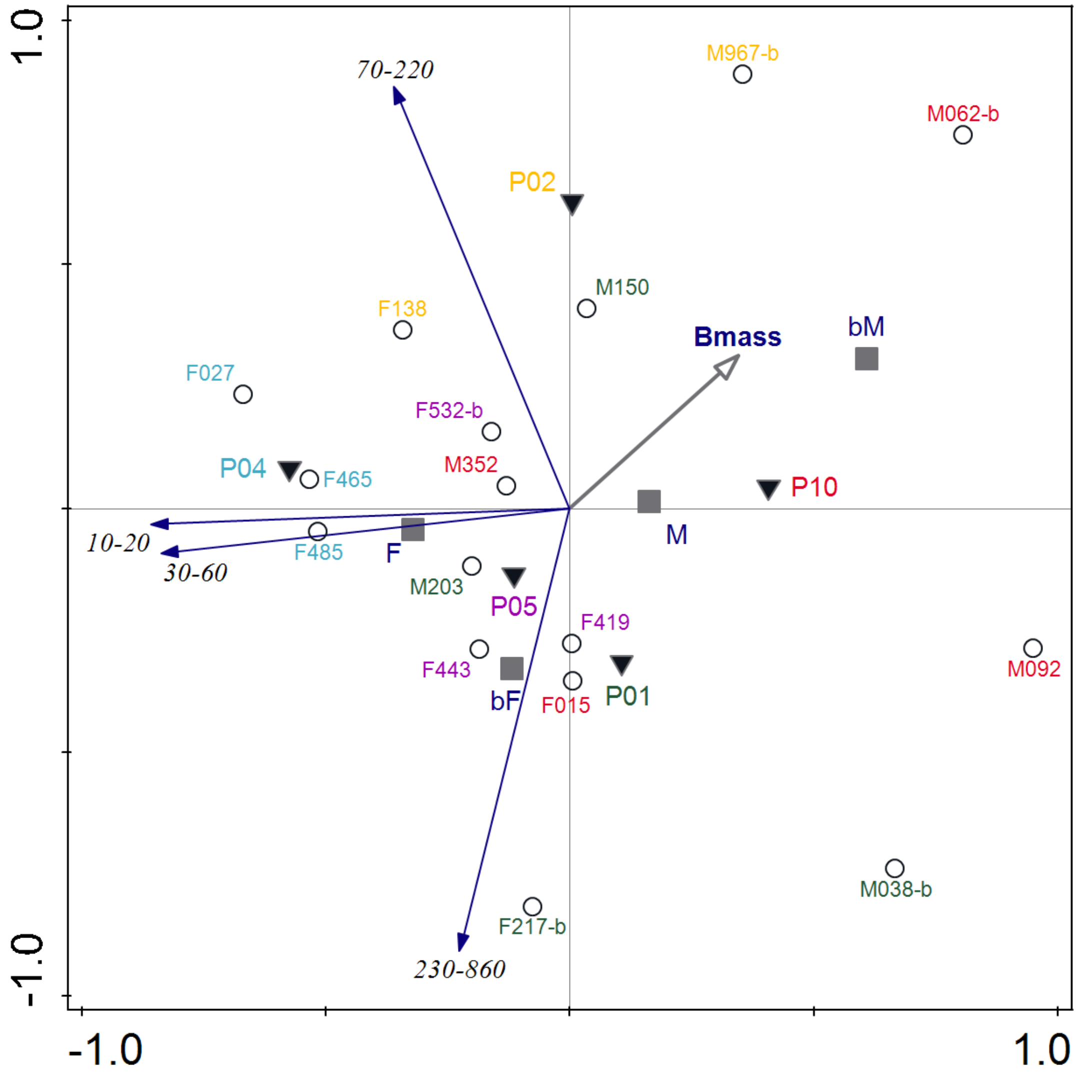

Figure 5. PCA plot showing individual mole-rats in a multidimensional space defined by mean number of activity bouts in different length categories per 24h. Explanatory variables are passively projected into the diagram as gradient (body mass) or centroids (categorial variables). Bmass = body mass; bM = breeding male; bF = breeding female; M = non-breeding male; F = non-breeding female.

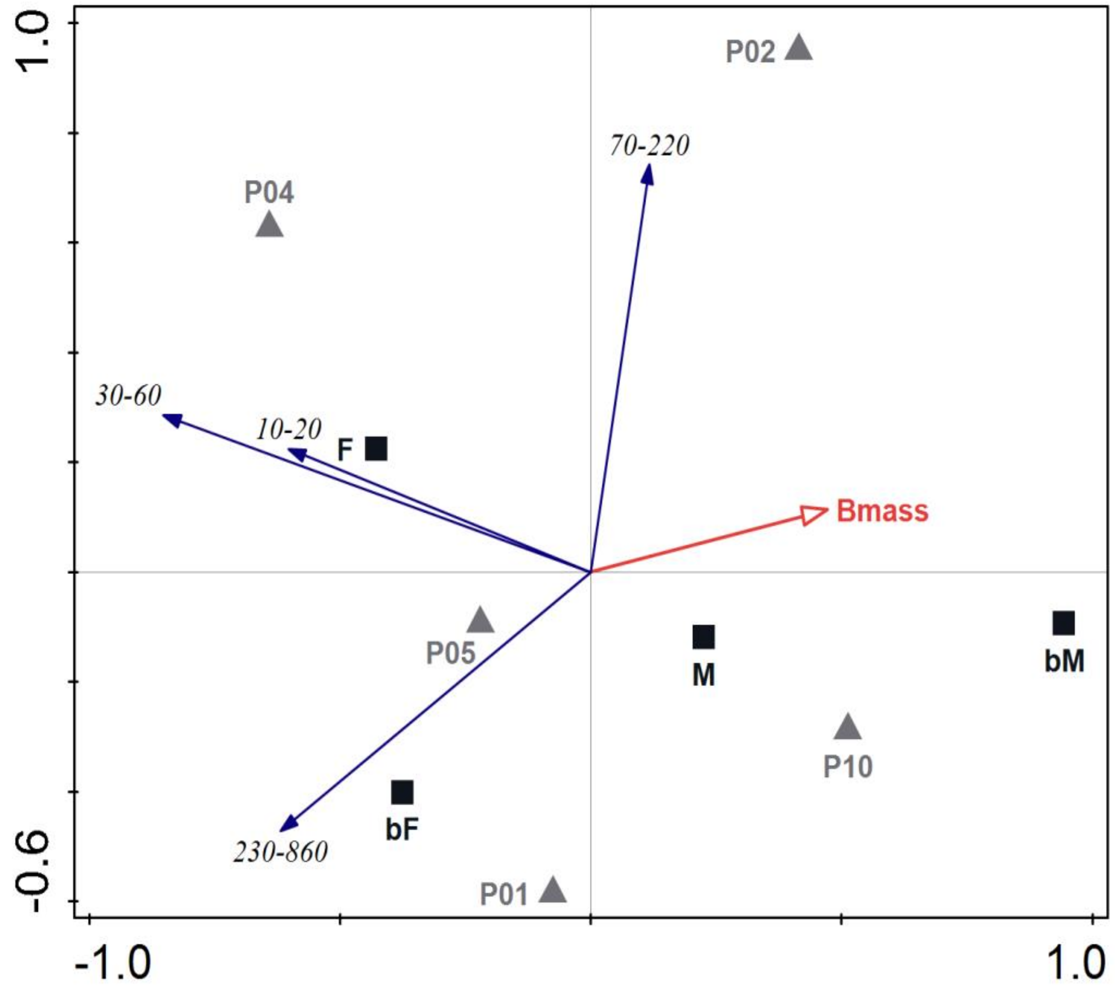

Figure 6. RDA plot of mean number of activity bouts in different length categories. Bmass = body mass; bM = breeding male; bF = breeding female; M = non-breeding male; F = non-breeding female.

Table 4. Proportion of explained variability by three explanatory variables on mean number of activity bouts of radio-tracked Ansell´s mole-rats.

Fraction	% of Explained	% of All	DF	F	P
Body mass	-5.8	-1.7	1	0.8	0.466
Sex*repr. status	5.9	1.7	3	1.1	0.416
Family	57.8	17.0	4	1.7	0.148
Total Explained	100.0	29.4	8		

PCA revealed that individual mole-rats are different in term of their association with activity bouts of different length according the period when they activity occur (during or outside of the main activity, Fig. 7). Non-breeding females are characteristic of more short activity bouts (10-20 min and 30-60 min) performed outside of the period of main activity; breeding females tend to have more activity bouts in category 230-860 min within the period of main activity. Non-breeding males incline mainly to activity bouts of 230-860 min out of the period of main activity. Breeding males have generally low number of activity bouts, both within and out of the period of main activity. Body mass correlates negatively with activity bouts of 10-20 min and 30-60 min performed out of the period of main activity and activity bouts of 230-860 min performed within this period and correlates positively with 10-20 min activity bouts performed during activity peak. Although family members are variable in their activity patterns, they are more similar to each other than to individuals from other families.

Amount of variability in individual´s activity pattern represented by mean number of activity bouts in different length categories according their occurrence performed during the period of main activity and out of this period was mostly explained by individual´s affiliation to a family group (20.9 %; p=0.052; Tab. 5) as revealed by variance partitioning technique using RDA (Fig. 8).

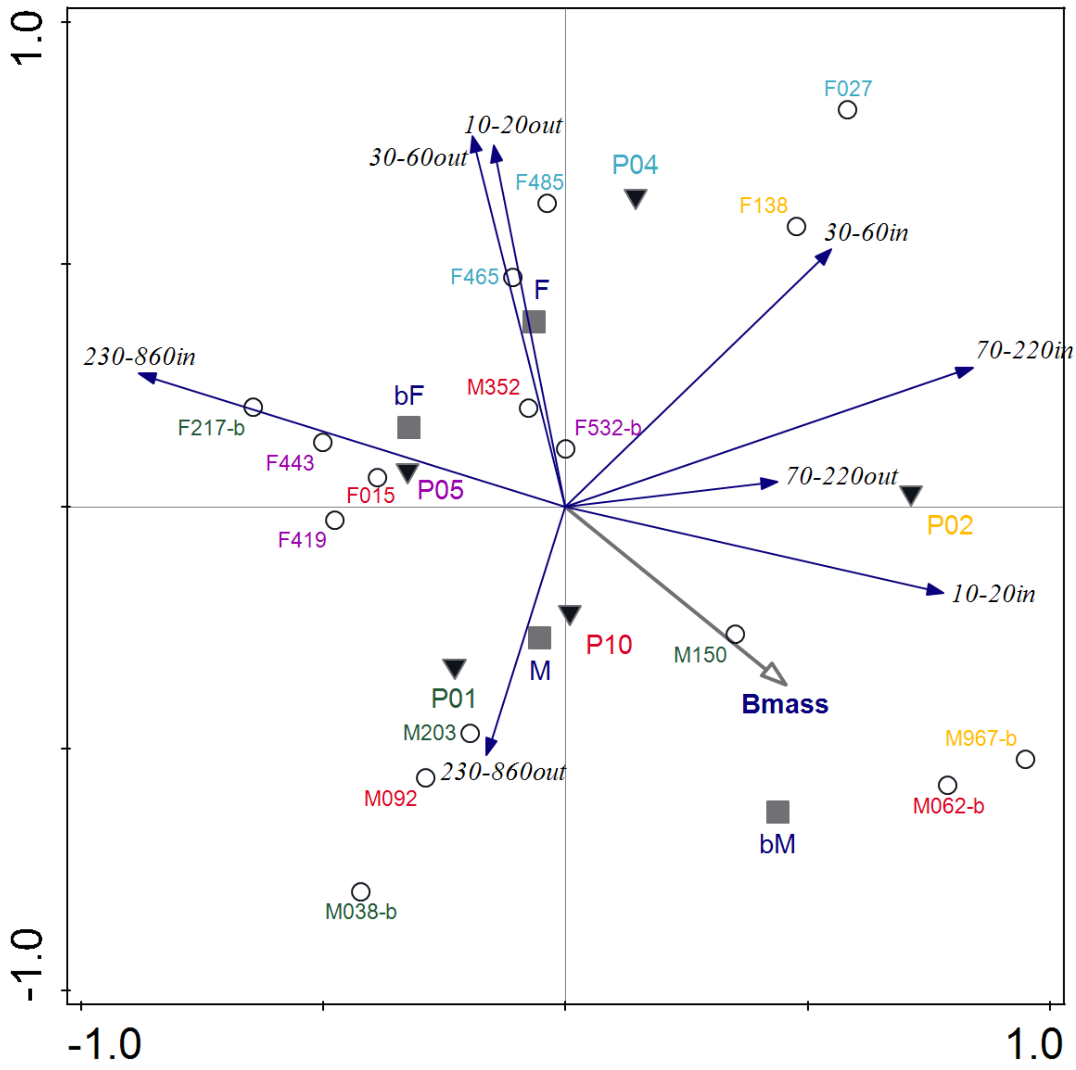

Figure 7. PCA plot showing individual mole-rats in a multidimensional space defined by mean number of activity bouts in different length categories divided on those performed within (marked with in) and out of main activity (marked with out) period. Explanatory variables are passively projected into the diagram as gradient (body mass) or centroids (categorical variables). Bmass = body mass; bM = breeding male; bF = breeding female; M = non-breeding male; F = non-breeding female.

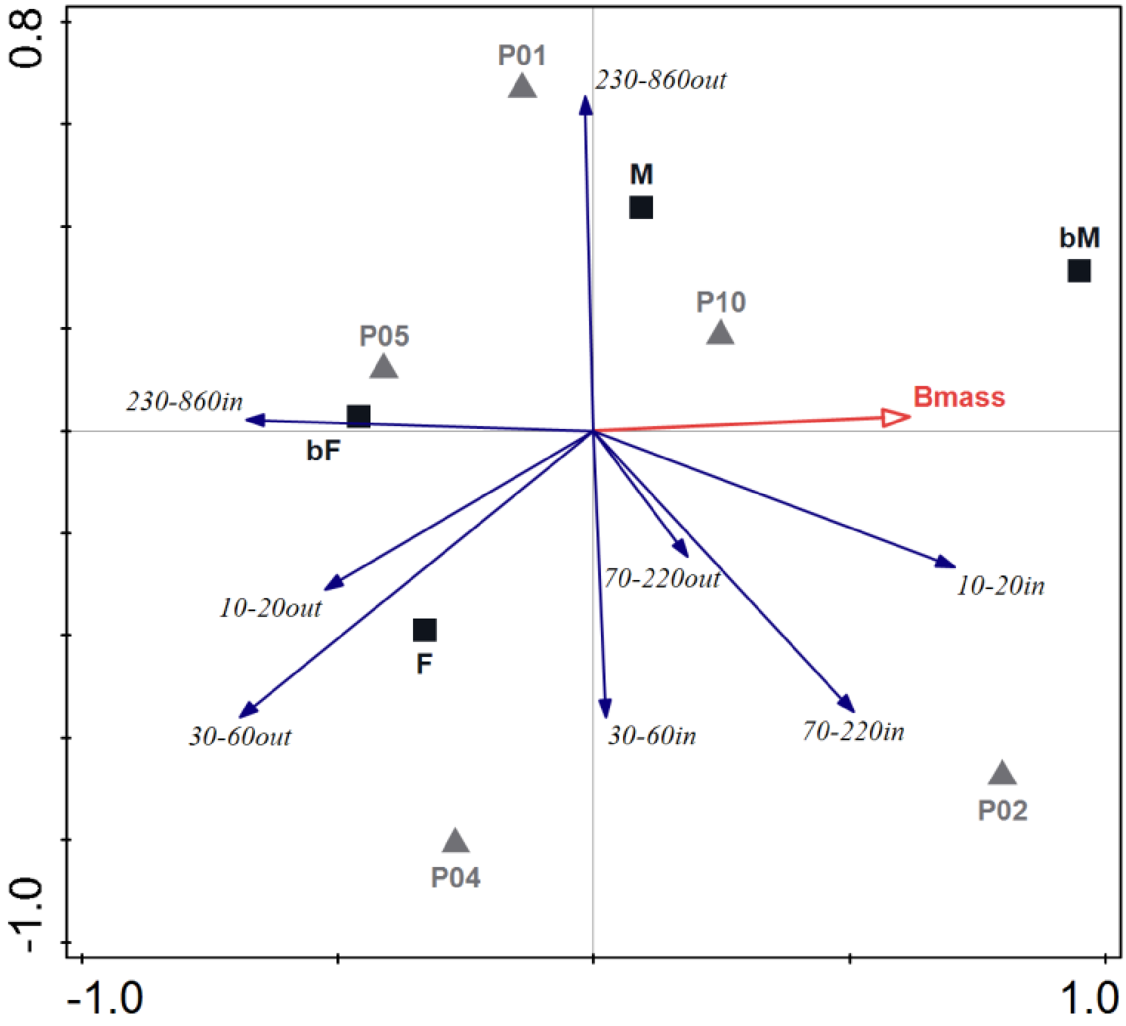

Figure 8. RDA plot of mean number of activity bouts in different length categories divided on those performed within and out of main activity period. Bmass = body mass; bM = breeding male; bF = breeding female; M = non-breeding male; F = non-breeding female.

Table 5. Proportion of explained variability by three effects on mean number of activity bouts of radio-tracked Ansell´s mole-rats when divided on those performed within and out of the period of main activity.

Fraction	% of Explained	% of All	DF	F	P
Body mass	-11.6	-3.2	1	0.6	0.690
Sex*status	-1.2	-0.3	3	1.0	0.492
Family	75.8	20.9	4	1.8	0.052
Total Explained	100.0	27.6	8		

The interaction of the activity timing (whether it occurred within or out of the period of main activity of all individuals) and the family affiliation significantly affected the lengths of activity bouts in studied mole-rats (GLMM: χ^2=20.8, p<0.001; Fig. 9). In the second model (Fig. 10), neither the interaction between the activity timing and the combination of sex and breeding status (GLMM: χ^2=4.8, p=0.186) nor a simple effect of the sex and breeding status alone (GLMM: χ^2=1.5, p=0.679) affected the length of the activity bouts significantly. In both models, variability was significantly affected by the timing of activity bout – whether it occurred within or outside the period of main activity (GLMM: χ^2=159.2, p<0.001; χ^2=147.2, p<0.001, Tab.7).

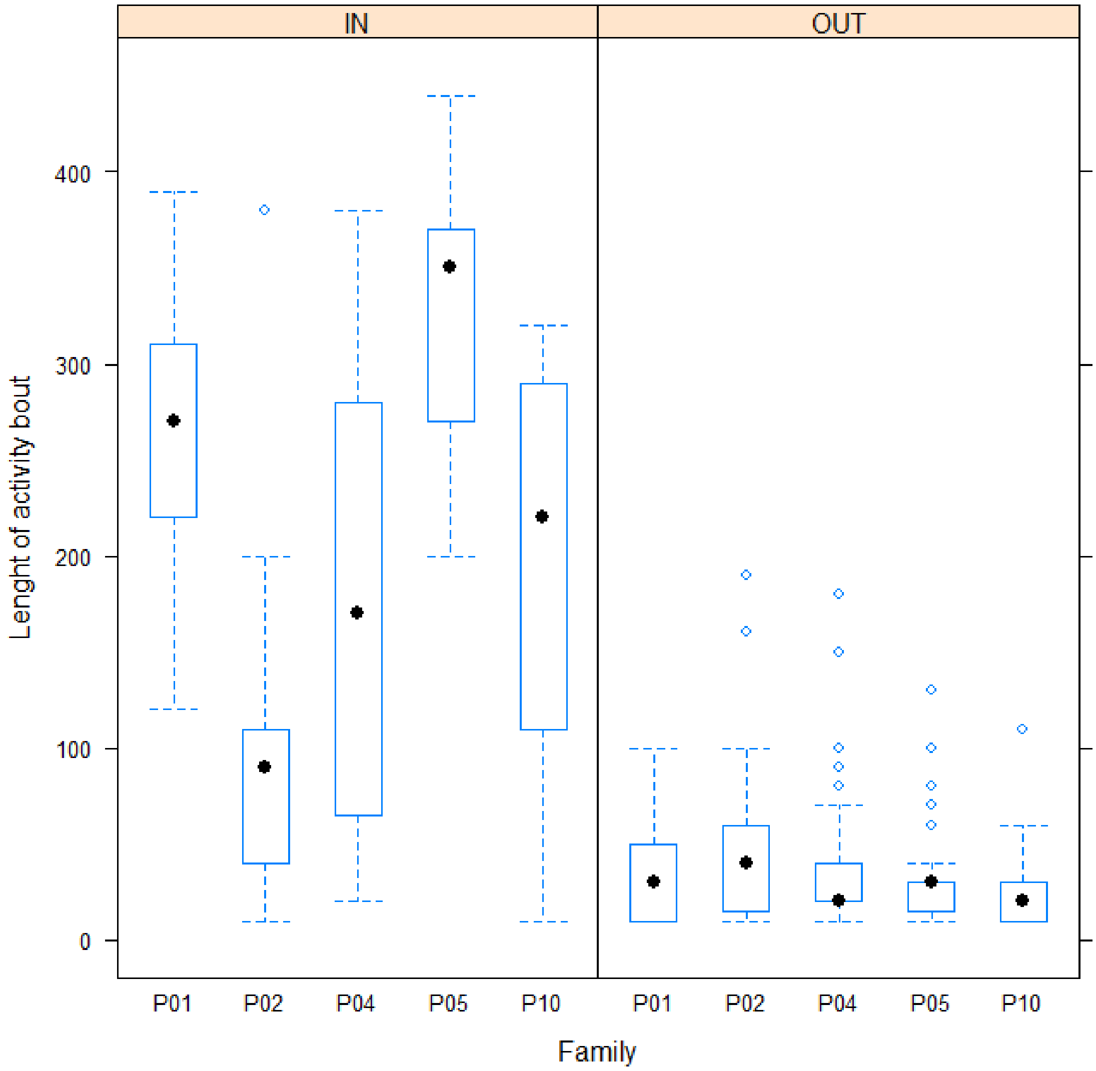

Figure 9. Differences in lengths of activity bouts in mole-rats recorded both during and out of the period of main in relation to affiliation of a family group. Medians, quartiles, non-outlier ranges and extremes are depicted.

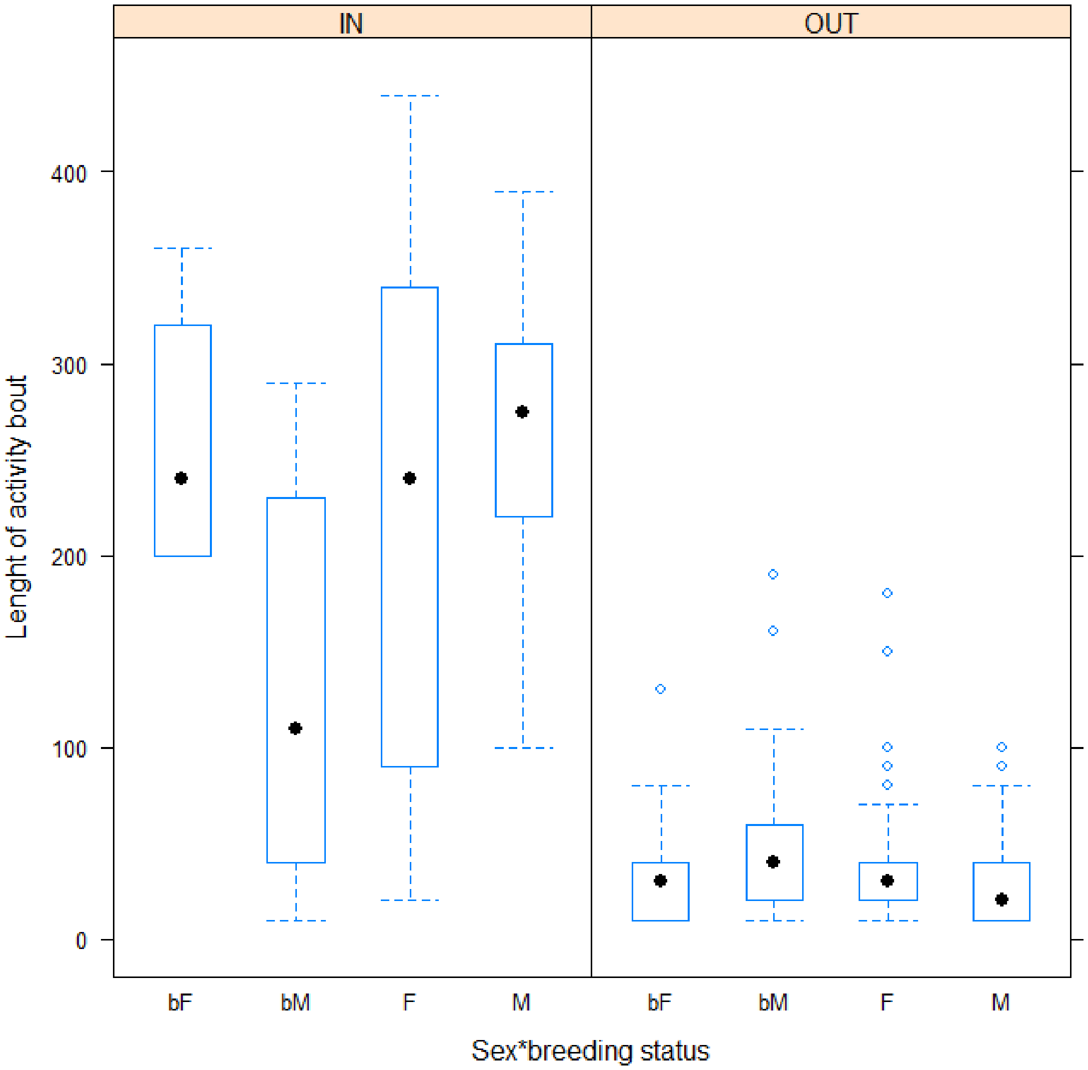

Figure 10. Differences in lengths of activity bouts in mole-rats recorded both during and out of the period of main activity in relation to the combination of sex and breeding status. Medians, quartiles, non-outlier ranges and extremes are depicted. bF = breeding female; bM = breeding male; F = non-breeding female; M = non-breeding male.

Out of 16 possible dyads of individuals of the same family, almost half tended to be synchronized in their outside-nest activity beyond the level given by a general similarity of their daily activity patterns over the four days of monitoring (Table 6). Synchronization was significant ($p<0.05$) in 7 of these dyads. Two dyads, both involving one breeder and one non-breeder, were highly desynchronized in their activity ($p>0.95$). Family groups differed in synchronization between their members. For example, while all dyads of the family P10 tended to be synchronized, female F419 of the family P5 was significantly synchronized with another non-breeding female but desynchronized with the breeding female (Table 6).

Table 6. Synchronization in dyads of radio-tracked animals. For each possible dyad of family members, synchronization is expressed as proportion of time spend outside the nest simultaneously from the time spend outside the nest by one of the animals in the dyad. BON (both out of the nest) represents the number of 10-min intervals from the 96-h radio-tracking period when both animals of the dyad were outside the nest simultaneously. BIN (both in the nest) represents the number of 10-min intervals from the 96-h radio-tracking period when both animals of the dyad were inside the nest simultaneously. ION (in/out of the nest) represents the number of 10-min intervals from the 96-h radio-tracking period when one animal of the dyad was inside the nest while the other one was outside the nest. For BON, BIN and INON are presented proportions (Prop.). P is the result of permutation test expressing the level of dyad´s synchronization.

	Combination of animals		**Synchronization (%)**								
Family	**Animal A**	**Animal B**	**from A**	**from B**	**BON**	**Prop. of BON (%)**	**BIN**	**Prop. of BIN (%)**	**ION**	**Prop. of ION (%)**	**p**
P01	M038-b	M150	74.8	60.5	98	17.0	97	16.8	381	66.1	0.046
-||-	M038-b	M203	78,6	47.0	103	17.9	144	25.0	329	57.1	0.414
-||-	M150	M203	73.5	54.3	119	20.7	143	24.8	314	54.5	0.073
P02	F138	M967-b	15.0	20.5	25	4.3	239	41.5	312	54.2	0.997
P04	F027	F465	59.5	49.0	100	17.4	172	29.9	304	52.8	0.035
-||-	F027	F485	56.0	49.2	94	16.3	171	29.7	311	54.0	0.686
-||-	F465	F485	56.9	60.7	116	20.1	163	28.3	297	51.6	0.011
P05	F419	F443	76.6	66.1	144	25.0	118	20.5	314	54.5	0.005
-||-	F419	F532-b	56.4	61.6	106	18.4	148	25.7	322	55.9	0.996
-||-	F443	F532-b	56.4	71.5	123	21.4	144	25.0	309	53.6	0.500
P10	F015	M062-b	34.7	70.8	51	8.9	117	20.3	408	70.8	0.011
-||-	F015	M092	65.3	76.2	96	16.7	81	14.1	399	69.3	0.006
-||-	F015	M352	65.3	58.9	96	16.7	118	20.5	362	62.8	0.062
-||-	M062-b	M092	59.7	34.1	43	7.5	112	19.4	421	73.1	0.028
-||-	M062-b	M352	59.7	26.4	43	7.5	149	25.9	384	66.7	0.128
-||-	M092	M352	70.6	54.6	89	15.5	111	19.3	376	65.3	0.108

DISCUSSION

Analyses of activity pattern of free-living Ansell´s mole-rat based on data obtained by automatic radio-telemetry showed that on average mole-rats spent about 29 % of the time outside of the nest and breeding males turned out to be the least active individuals from radio-tracked mole-rats. Outside-nest activity of all but one individual was concentrated into afternoon hours culminating around 14:00. In addition to this prominent peak, several bouts of different length occurred also throughout the whole day in all individuals. Most common were shorter activity bouts (10 and 20 minutes long), which is the information that could not be obtained by usual way of radio-tracking. Frequency of activity bouts of particular length differed markedly between individuals and inter-individual variability in activity patterns was best explained by affiliation to a family group. Most individuals had the tendency to synchronize or, on the other hand, desynchronize in their outside-nest activity with other members of their families.

My approach using automatic recording of activity allow to evaluate daily activity pattern in more detail and more precisely. Similarly to other studies, mole-rats spent most of their time inside the nest with only 28.7±6.8 % of time located outside the nest area (Tab. 2). This corresponds with finding of both laboratory (Bennett 1990, Lacey and Sherman 1991, Schielke et al. 2012, Desmet et al. 2013) and field (Lovegrove 1988, Šklíba et al. 2007, Lövy et al. 2013, Šklíba et al. 2016) studies carried out on variety of African mole-rat species where studied animals spent inside the nest 60 - 90 % of time. It should be noted that activity is here defined as activity outside the nest therefore period when mole-rats were active is probably underestimated since some activities, including grooming, pup care and some social interactions, occur also in nests (Lacey et al. 1991). On the other hand, we cannot exclude that mole-rats could rest also outside of nests while in periphery of burrow system. Nevertheless, due to fact, that Ansell´s mole-rats has only one active nest per burrow system (Šklíba et al. 2012) and that mole-rats generally prefer to rest in their nests (Šklíba et al. 2007), I suppose that it is not very relevant in this species.

Among mole-rats categories distinguished in my study, the breeding males were least active (i.e. spending least time outside the nest), whereas activity of breeding females and both non-breeding males and females was higher with almost no differences among them (Tab. 2). Although Schielke et al. (2012) found no difference in activity of breeding males in Ansell´s mole-rat, they usually tend to be least active in other social species of mole-rats (Jarvis 1981, Bennett 1990, Lövy et al. 2013). This was found to be extreme in breeding male of free-ranging *Fukomys mechowii*, whose home range was extremely small and who spent most of its time inside the nest making only short trips to food stores (see Fig. 1 in Lövy et al. 2013). Thus, my finding confirms this anecdotal observation done only on one individual in another species of genus *Fukomys* in nature. Considering breeding females of other mole-rats, their activity is usually comparable to non-breeders (Bennett 1990, Dammann and Burda 2006, Dammann et al. 2011) which is consistent with my result of study. Although breeding status of females had no influence on amount of their outside-nest activity in my study, work of Šklíba et al. (2016) carried out on the same individuals, but with position spatially located, found that most activities of breeding females took place close to the communal nest. Although only two breeding females were monitored, this finding is in agreement with their reproductive role. Breeding females probably concentrate on activities in close distance from the nests and do not participate much in risky and energy demanding activities in distant part of burrow systems such as defense against intruders and predators and digging of new burrows.

As previously discovered by manual radio-telemetry (Šklíba et al. 2014, Fig. 16a), the radio-tracked Ansell´s mole-rats concentrated their activity into afternoon hours with one distinctive peak of activity around 14:00 (Fig. 2 and 3). This activity peak correlates with fluctuations of daily temperature in depth of foraging tunnels (Fig. 16b) meaning that radio-tracked individuals concentrated their outside-nest activity into the warmest part of the day. Authors of the study argue that this behavior is probably part of energy-saving strategy caused by high thermoregulatory requirements in Ansell´s mole-rat (Šklíba et al. 2014).

Thermoregulation may be one of crucial factors responsible for distribution of activity bouts in the mole-rats during day. Lovegrove (1988) argued that division of outside-nest activity into several shorter time periods per day in Damaraland mole-rats may be adaptation to avoid overheating during hot daylight hours in Kalahari semi-desert. He found that the radio-tracked mole-rats spent outside the nest most often periods lasting around 55 min (Fig. 17) with relatively small variance in their length and no distinct concentration during the whole day. According to the author, Damaraland mole-rat preferred such periods of activity because their body temperature increased during the foraging and burrowing (remarkable increase of body temperature during digging activity is known in African mole-rats, see Lovegrove 1989, Zelová et al. 2010, Okrouhlík et al. 2015) and they were forced to return into their nest to cool down after some time. However, this is likely not the case in the Ansell´s mole-rat, because individuals exhibited activity bouts of diverse length per day from which most frequent were those long 10 and 20 minutes, but activity bouts long up to several hours also occurred. Data collected for this study were gathered during the period when temperatures in foraging tunnels of Ansell´s mole-rats were deep below their lower critical temperature (i.e. 10˚C, Šklíba et al. 2014) which is in remarkable contrast to the study of Lovegrove (1988), who followed activity of the Damaraland mole-rats in period when temperature in burrows was above the upper limit of their thermoneutral zone. Moreover, compared to the Damaraland mole-rat, the Ansell´s mole-rat is a small species with relatively high value of thermal conductance (Marhold and Nagel 1995) minimizing risk of overheating. On the other hand, due to small body size and high thermal conductance they probably reduce their outside-nest activity on necessary minimum manifested only in short activity bouts in order to minimize heat losses to colder environment and concentrate their activity into the warmest part of the day.

Similarly as the Ansell´s mole-rats in present study, free-living the giant mole-rats perform their activities in temperatures below their thermoneutral zone (Lövy et al. 2013). Nevertheless, activity pattern of the giant mole-rat was still more similar to that of the Damaraland mole-rat with frequent but short activity bouts on average 54 minutes long distributed during the day with no apparent peak. Lövy et al. (2013) supposed that the similarities in length and distribution of activity bouts in these two species are the consequence of social behavior rather than thermoregulatory aspects and that the high number of short activity bouts might be a by-product of disturbances by many individuals in communal nest or consequence of cooperation on work task. On the other hand, one dispersing female of giant mole-rat, living alone in time of radio-tracking, concentrated her activity into the time of temperature maximum in foraging tunnels (Lövy et al. 2013) similarly as did the Ansell´s mole-rats and the solitary silvery mole-rats (Šklíba et al. 2007). Ansell´s mole-rat is therefore more similar in its activity pattern to solitary living individuals in which temperature works as important clue of daily activity.

Nevertheless, even under such thermoregulatory constraints individuals of monitored Ansell´s mole-rat differed in distribution of activity bouts in distinct length categories (Tab. 3). Number of activity bouts of all categories negatively correlated with body mass which was most remarkable in the breeding males since they belong to largest individuals in my study. It corresponds with the fact that breeding males were generally less active than other individuals as mentioned above. Surprising are the tendencies observed in breeding and non-breeding females. While breeding females tended to perform long activity bouts, the non-breeding females inclined to perform short activity bouts, even though amount of their overall activity was comparable. Again, such result might be affected by small sample size in case of breeding females but also by the fact, that breeding females improve their thermostability during pregnancy (Buffenstein 1996b) which may allow them to stay longer in inconvenient temperature conditions in burrow. Interestingly, distribution of activity bouts in non-breeding females does not match the expectances derived from their space-use patterns. Due to fact, that non-breeding females were located in greater distances from the nest more often than other individuals (Šklíba et al. 2016) we might expect longer stay outside the nest. Surprisingly, exactly the opposite was found. Nevertheless, if these individuals carry energetically consuming activities such as digging and transport of soil during their stay in periphery of burrow system, I may speculate that such activities are short term and mole-rats return relatively soon to burrow to rest.

Although breeders and non-breeders showe different tendencies to activity bouts of specific length in their activity patterns, sex in combination with breeding status turned out to have low explaining power. Variability in individuals´ activity patterns in outside-nest activity was best explained by the affiliation to a family group (Tab. 4, 5). Families of highly social Ansell´s mole-rats are therefore very likely maintaining daily regimes specific particularly for them. This is understandable since the activity budget of each family is probably influenced by the unique micro-environmental conditions of its occupied system (food supply and soil characteristics, which determine also length of burrow systems) as well as the size and composition of family itself (Tab. 1). Family affiliation also explained great proportion of variability in spatial-use patterns of manually radio-tracked mole-rats (Šklíba et al. 2016) showing that specific family routine is pronounced even on the level of space use. What is interesting is that the greatest variability in activity patterns occurs during the activity peak, whereas individuals across sexes and families are relatively uniform in distribution of activity bouts during rest of the day (Fig. 12, 13). This is probably the result of thermoregulatory restrictions in Ansell´s mole-rat as discussed above.

Social species of African mole-rats use the advantages of cooperative foraging, which allows them to reduce time spend on searching for food (Spinks and Plaganyi 1999). Yet the excavation of burrows is energetically demanding (Zelová et al. 2010), therefore synchronization of such activity between family members could be profitable. In my study, considerable differences in synchronization between some family members are apparent (Tab. 6). It seems that individuals tend to synchronize they outside-nest activity with some of their family members and desynchronized with others. For example, breeding male from family P10 synchronized with two non-breeders, but desynchronizes with another non-breeder. Similarly in family P04, two non-breeding females were highly synchronized with each other, but neither of them synchronized with breeding female. Moreover, one of those non-breeding females was highly desynchronized with the breeding female. These results may suggest that sex in combination with breeding status could be important for activity synchronization of family members but larger dataset would be needed to test that.

It seems that individual preferences for outside-nest activity with particular family member(s) exist, although we have no evidence that individuals spend time of their activity together. Synchronization between mole-rats may as well reflect an inside-nest social interactions rather than outside-nest cooperation. Synchronization of stay in the nest in Ansell´s mole-rats may be the result of affiliative relationships which can be found among group members of other social species such as bottlenose dolphins *Tursiops sp.* (Connor et al. 2006), feral horses *Equus caballus* (Cameron et al. 2009), free-ranging dogs *Canis familiaris* (Bonnani et al. 2010), Bonnet macaques *Macaca radiate* (Adiseshan et al. 2011), or African elephants *Loxodonta africana* (Archie et al. 2011).

Studying of subterranean mammals in their natural environment is extremely challenging task and radio-tracking is probably only useful tool in revealing details of their hidden lives. This study represents important contribution to studying behavior of social living African mole-rat. Compared to other similar research, the advantage of this study from methodological point of view lies in the using of automatically recording radio-telemetry which provides more detailed record than traditionally used manual radio-telemetry. In the future, researches should concentrate on discovering daily activity patterns in other free-living African mole-rat species, exploration of mole-rats´ daily behavior in different temperature conditions, revealing the influence of family characteristics on activity pattern of its members and discovering the influences on synchronization of family members.

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SUPPLEMENTARY

Figure 11. Miombo woodland, Lusaka, Zambia. The radio-tracking locality.

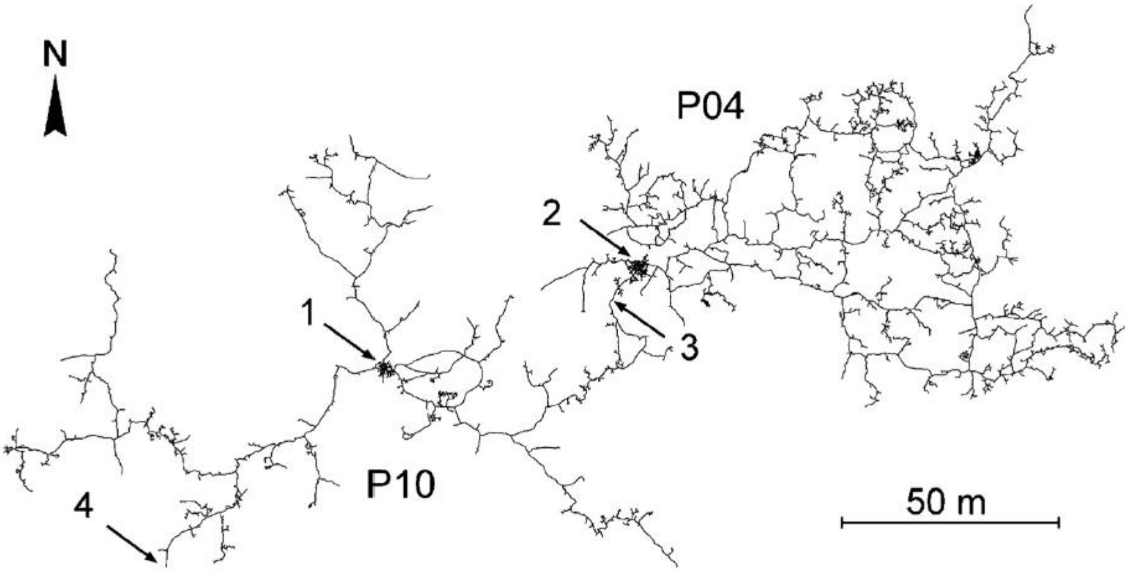

Figure 12. Burrow systems of two family groups (P10 and P04) of the Ansell´s mole-rat. 1,2 – nests of the respective burrow systems; 3 – connection between burrow systems blocked by a short soil plug; 4 – connection between burrow systems P10 and P05 (freely passable). Adopted from Šklíba et al. 2012.

Figure 13. Communal nest (in the center) with a tangle of adjoin tunnels.

Figure 14. Anesthetized Ansell´s mole-rat equipped with radio-collar.

Figure 15. Automatic receiver used in radio-tracking.

Table 7. Results of GLMM testing the individual differences in the lengths of activity bouts in Ansell´s mole-rats.

Model	Explained variable	Explanatory variable	χ^2	P
1	Length of activity bouts	Affiliation to a family	25.7	<0.001
	-‖-	Occurrence of activity bout	159.2	<0.001
	-‖-	Interaction	20.8	<0.001
2	Length of activity bouts	Sex*breeding status	1.5	0.679
	-‖-	Occurrence of activity bout	147.2	<0.001
	-‖-	Interaction	4.8	0.186

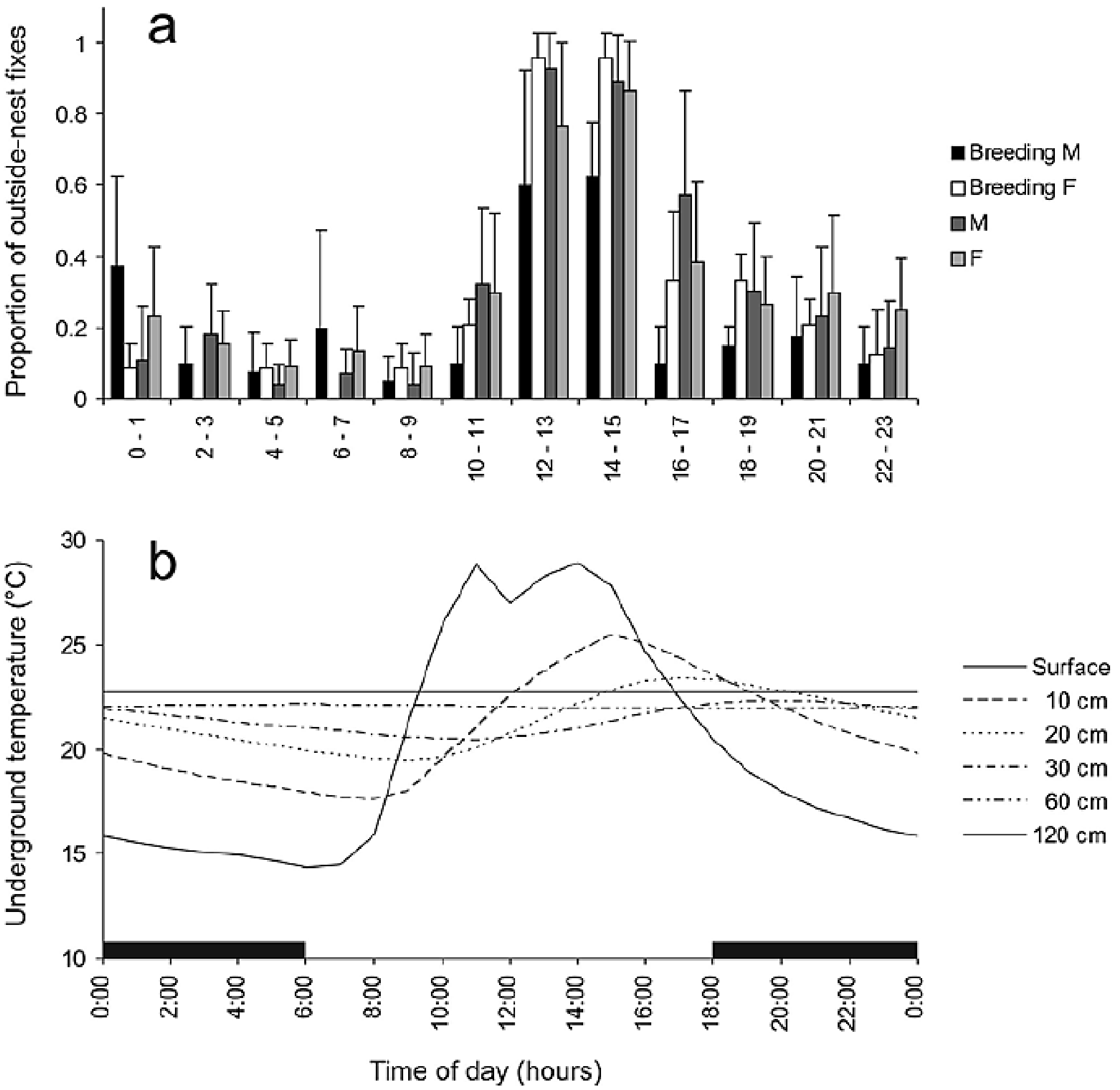

Figure 16. Outside-nest activity of the radio-tracked Ansell´s mole-rats (a) and underground temperature fluctuations (b) during a 24-h day. Means ± standard deviations are presented for the proportions of outside-nest fixes. Black horizontal bars indicate the dark phase of the day. F = female; M = male. Adopted from Šklíba et al. 2016.

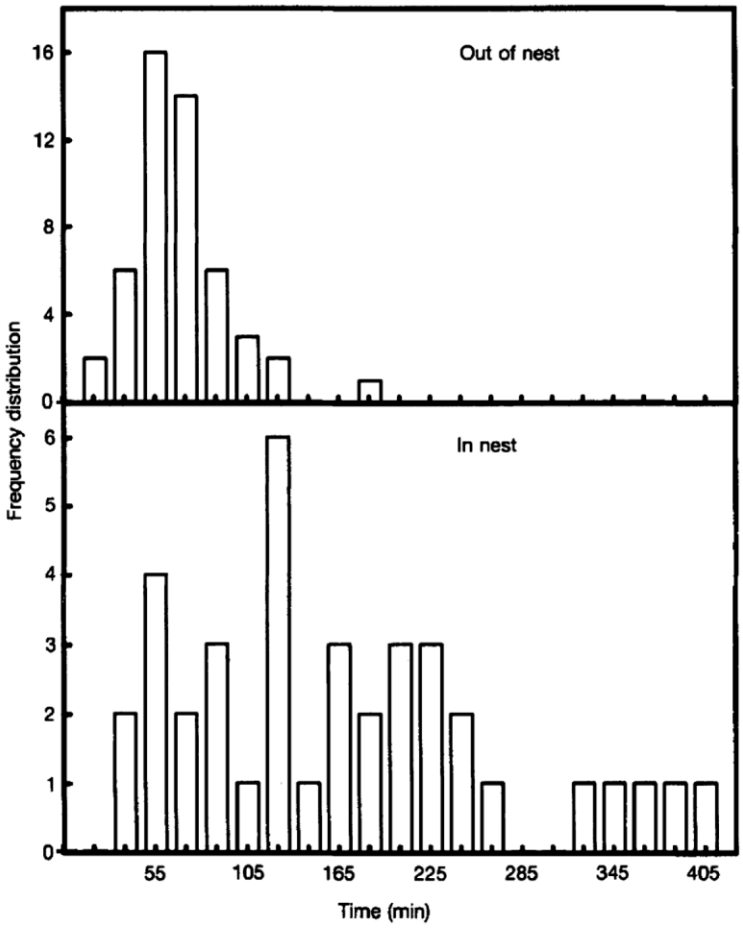

Figure 17. Frequency distribution of the time periods spent in the nest, and out of the nest in Damaraland mole-rat. Adopted from Lovegrove 1988.