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Vibrational communication of subterranean rodents

Ph.D. Thesis

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Annotation

This PhD. thesis focuses on the vibrational communication of subterranean mammals, in particular, vocal communication of bathyergids (*Heliophobius argenteocinereus, Fukomys mechowii, Fukomys darlingi*) and seismic communication of *Tachyoryctes.* We recorded and analyzed the vocalization of three species and discussed the physical parameters of their vocalization in relationship to the special underground acoustic environment. Moreover, social systems of African mole-rats range from solitary to eusocial and thus our results enabled us to discuss the influence of sociality on vocal repertoire richness and its composition. Long distance communication possesses many challenges in underground environments; the only effective mean is seismic communication. We described for the first time seismic signaling in *Tachyoryctes* and proposed its function.

Declaration [in Czech]

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

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List of papers and author's contribution

The thesis is based on the following papers (listed chronologically):

I. Schleich, C.E., Veitl, S., **Knotková, E.**, Begall, S. 2007. Acoustic communication in subterranean rodents, In: Subterranean Rodents: News from Underground. Begall S., Burda H., Schleich C.E., Springer-Verlag, Berlin Heidelberg, pp 113-127 (book chapter).
Ema Knotková participated in recording and evaluating of the vocalization of mole-rats and revision of the manuscript.

II. **Knotková, E.**, Veitl, S., Šumbera, R., Sedláček, F., Burda, H. 2009. Vocalization of the silvery mole-rat: Comparison of vocal repertoires in subterranean rodents with different social systems. Bioacoustics 18(3): 241-257 (IF = 0.895).
Ema Knotková was responsible for recording of the vocalization, evaluating the data, statistical analysis and writing the manuscript.

III. Bednářová R., **Hrouzková-Knotková E.**, Burda H., Sedláček F., Šumbera R. (*in press*): Vocalization of the giant mole-rat (*Fukomys mechowii*), subterranean rodent with the richest vocal repertoire. Bioacoustics (IF = 0.895).
Ema Hrouzková-Knotková designed the experiment and participated in evaluating the data, statistical analysis and writing the manuscript.

IV. Dvořáková, V., **Hrouzková, E**., Šumbera, R. 2012. Vocal repertoire of social Mashona mole-rat (*Fukomys darlingi*). Manuscript in preparation.
Ema Hrouzková designed the experiment and participated in recording of the vocalization, evaluating the data, statistical analysis and writing the manuscript.

V. **Hrouzková, E**., Dvořáková, V., Jedlička, P., Šumbera, R. 2012. Seismic communication in *Tachyoryctes* sp. from Tanzania. Manuscript in preparation.
Ema Hrouzková was responsible for recording of seismic signals, evaluating the data, statistical analysis and writing the manuscript.

Contents

Attached publications

1. Introduction

1.1. Communication

Communication is the process where information is passed from the sender to a receiver through the environment. The information can concern a specific situation the sender is in (e.g. presence of a predator or food) but also it can convey the emotional state (e.g. courtship, aggression) of the sender. The information transmitted by the sender is therefore quite subjective and does not have to be necessarily honest; by studying communication we may be able to reveal internal motivation of an individual (Bradbury and Vehrencamp 1998).

Communication in general is usually directed to other members of the same species (though there are cases of signals directed to predators or members of a differing species, mainly alarm and territorial calls – e.g. Randall 2001, Shelley and Blumstein 2005). Signals can be divided into five main groups according to their content: 1. contact signals –used to coordinate the activities of animals within social groups, to maintain spacing and cohesion during foraging. Recruitment and assembly signals may be used to reduce distances between group members. Greeting and other affiliative signals are often exchanged when the group members reassemble in common location, 2. aggressive and territorial signals - indicate the presence of a territorial owner in a given location, demarcate territorial boundaries, and often include concomitant information about identity and location of the owner. Aggressive calls also occur during escalade violence over ownership of a mate or commodity. Provide information about the likely intentions and levels of commitment of their senders, they may also provide information about relative fighting ability and are produced by dominant animals, 3. distress signals - occur prior to and during an attack of a predator or dominant animal; a victim may also produce these calls. They also occur during handling which simulates attack of a predator, 4. mating signals - provide information on location and availability, that allows members of the two sexes to find and approach each other and determine whether subsequent mating will occur and effects its coordination, 5. alarm signals - indicate the presence of a predator or other threats (Bradbury and Vehrencamp 1998). The richness and composition of the signals repertoire depends on what kind of information is needed the most often and its importance (Schlassburger 1993, Cap et al. 2008, Le Roux et al. 2009).

Communication can be divided by the channel of its dispersal into chemical, vibrational, visual and electrical (Bradbury and Vehrencamp 1998). We will focus on the vibrational communication in more detail. Vibrations can be transmitted by the air (acoustical signals), or by the soil (seismic signals). Vibrations can be produced by the vocal chords (true vocalization) or by any other mean (mechanical sounds – e.g. teeth grinding, thumping, stridulation). Mechanical sounds can also contain seismic parts and vice versa, most of which the seismic signals contain some acoustical part. Seismic signals spread for longer distances through solid environments (Narins et al. 1992, Randal and Lewis 1997, O´Connel-Rodwell et al. 2001).

1.2. Vibrational communication and the environment

The underground environment is very special in sensory way. The walls of tunnels cause collision of short acoustic waves (high frequency sounds), and therefore these waves are absorbed more than long waves (low frequencies). The energy needed for transmission is lowest for the frequency of 440 Hz. Frequencies lower than 440 Hz seems to be weaker due to reflection from the walls and therefore are less intensely transmitted (Heth et al. 1986). The result is the so called stethoscope effect – selective amplification at certain frequencies 200, 400 and less at 800 Hz occurring up to the distance of 1 meter (Quilliam 1966, Heth et al. 1986, Lange et al. 2007). Despite all these effects and with the consideration to the intensity of the vocalization, the calls of the subterranean rodents propagate in the tunnel to the distance of only 5 m (Heth et al. 1986).

The situation of propagation of the airborne sounds between the burrow systems (through the soil) is completely different. Acoustic waves are strongly attenuated by the intervening substrate as well as the soil-air interface, thus vocal communication between the burrows is nearly impossible (Narins et al. 1992, Randall 2001). Vocalization often serves for long-range communication, but it cannot play this role in underground species and they need other forms of signals with which to communicate which are capable of spreading over long-distances through soil. The ideal candidate seems to be seismic waves. They have longer wavelengths, thus they spread better through soil than acoustic waves and are substrate born, and they do not have to overcome the interfaces between two matters (air and soil). Seismic waves spread with at least an order of magnitude better than acoustic waves (Narins et al. 1992, Hill 2008).

1.3. Perceiving of the vibrations

The acoustic waves, which spread through the air, are perceived by the ear. The frequency spectrum perceived by the ear is limited by ear morphology, but at the same time, ear morphology is tuned to the frequencies best transmitted in the environment As stated before, the low frequencies (around 500kHz) spread better in underground environments, so the hearing of its inhabitants are also tuned to these frequencies (Heth et al., 1986, Brückmann & Burda, 1997). Moreover due to the stethoscope effect, which amplifies certain frequencies, the hearing of subterranean mammals tend to be of low sensitivity, otherwise the animal would be over-stimulated by noise (Heffner a Heffner, 1993, Brückmann a Burda, 1997).

Seismic waves spread directly through the soil and therefore they can be perceived by the somatosensory sense or by the ear via bone-conduction. The specialized features in ear morphology have evolved to enhance perception of these very low frequency signals (Nevo et al. 1991, Begall et al. 2007, Mason et al. 2010).

1.4. Vocal communication

Vocal signals of two species of strictly subterranean bathyergids, naked mole-rat (*Heterocephalus glaber*) and Ansel`s mole-rat (*Fukomys anselli*), were described before (Pepper et al. 1991, Credner et al. 1997). Frequency range of all vocalizations is in concordance with the findings about acoustical environment in underground tunnels and their ear morphology (review in Begall et al. 2007).

The effect of underground environment is strong enough to shift also vocalization of fossorial rodents (they spend some time aboveground e.g. for foraging, their eyes are usually fully functional) to lower frequencies in comparison with their ground dwelling relatives as seen in South American hystricognath rodents (Eisenberg 1974, Francescoli 1999, Veitl et al. 2000, Schleich and Busch 2002).

1.5. Seismic communication

Seismic waves spread for quite a long distance through the soil; they seem to be an important source of information about surroundings for underground rodents. Silvery mole-rats (*Heliophobius argeteocinereus*) use seismic waves produced by predators for optimizing their antipredatory strategy (Šklíba et al. 2008), the golden mole (*Eremitalpa granti*) is able to register seismic cues produced by the hummocks of grass preferred by termites (termites are a staple food of golden moles) (Narins et al. 1997). Whereas blind mole-rats use self-generated seismic waves as an echolocation mechanism to determine size and shape of the obstacles (Kimchi et al. 2005).

The most important function of seismic waves in the underground habitat is communication between burrows. Seismic waves are used for communication of the sex of the producer and to lower aggressiveness during mating in solitary species (*Georychus capensis*) (Narins et al. 1992) or coordinate mating in social species (*Fukomys damarensis*) (Jarvis and Bennett 1991), they can be used as territorial signals (*Bathyergus, Georychus, Spalax*) (Heth et al. 1991, Jarvis and Bennett 1991) or even act as an individual signature (*Dipodomys*) (Randall 1994, Randall et al. 2000), seismic signalling is often produced in agonistic interactions (*Microtus*) (Giannoni et al. 1997). Seismic signals can also be used for interspecific communication of subterranean rodent with snakes. Eventually, footdrumming communicates to the snake that the prey is alert and vigilant and not easy prey (Randall and Matocq, 1997).

Generally, there are three means of producing seismic waves by rodents with dominant underground activity: 1. striking the head against the roof of the burrow (Rado et al. 1987), 2. drumming using the legs (Narins et al. 1992, Randall 1997, Randall et. al 2000) 3. using the incisors to tap (Giannoni et al. 1997).

1.6. Morton`s motivational structural rules

Morton (1977) postulated common rules about the structure of calls depending on the motivation of the animal. Harsh and low frequency sounds indicate hostility whereas tonal and high frequency sounds indicate appeasement or fear. These rules were described on the example of birds, but they apply also to mammals (c.f. Gouzoules and Gouzoules 2000, Compton et al.2001). The Acoustic environment of underground burrows restricts the use of Morton motivational- structural rules, because the high frequencies are attenuated and the hearing of the underground mammals is shifted to the low frequencies.

1.7. Sociality and the communication

In 2003 Dunbar postulated the “grooming” theory: complexity in (human) vocalization evolved to stay in touch with other members of the society, in groups too big to bond by normal grooming. The theory that a sociality drives the evolution of the communicative complexity has occurred before the “grooming” theory (Marler 1977, Waser 1982, Marler and Mitani 1988, Philips and Austad 1990, Hauser 1996), but it has been tested only few times with ambiguous results. Schassburger (1993) suggests that the relationship between sociality measured by the family size - and richness of the vocal repertoire probably depends on more factors than just the number of individuals within a group and suggests to measure social complexity. Indeed, social complexity and stability may be a more relevant measure of sociality than the group size (Blumstein and Armitage, 1997; Burda et al. 2000). The more socially complex the group, the more types of friendly vocalization (sensu Morton 1977) are needed because, friendly vocalization (calls emitted during fearful or appeasing situations) function to enhance group cohesion (Schassburger 1993, Le Roux et al. 2009). The social complexity theory was proved for Canidae (Schassburger 1993) and Herpestidae (Le Roux et al. 2008)

Shelley and Blumstein (2005) studied evolution of vocal alarm communication in rodents and their results did not agree with the theory that increasing social complexity should increase the drive in vocal repertoire size. They hypothesize that alarm calls evolved more likely to communicate to the predator than to the conspecifics and therefore they are not tied to the sociality. Other theories of the cause of the alarm call complexity were stated. The alarm call complexity could be the result of different escape options available to the animal (Macedonia and Evans 1993), different predator hunting methods (Fredericsen and Slobodchikoff 2007) or different needs of group member coordination (Furer and Manser 2009).

1.8. African Mole-rats (Bathyergidae)

African mole-rats of the family Bathyergidae represent a monophyletic group of subterranean rodents endemic to sub-Saharan Africa. They spend their entire life underground (Bennet and Faulkes 2000) with a little above-ground activity in some solitary species (Jarvis and Bennet 1991, Šumbera et al. 2003). Mole-rats are herbivorous; they feed on the underground parts of plants, roots, bulbs and rhyzomes (rewiev in Bennett and Faulkes 2000, Begall et al. 2007). The family of African mole-rats (Bathyergidae, Rodentia) contains species with wide variety of social systems from the solitary to the social with different social group sizes. The genera *Heliophobius, Bathyurgus* and *Georychus* are solitary (Bennett and Jarvis 1988, Bennett et al. 1991, Šumbera et al. 2003, Herbst et al. 2004). Genera *Fukomys* and *Cryptomys* live in social groups of approximately ten members (Bennett 1989, Bennett et al. 1994, Šklíba et al. 2012). The last genus of *Heterocephalus* contains one species, the naked mole-rat (*Heterocephalus glaber*), which forms family groups of 78 members on average (Braude 1991) and is sometimes referred to as eusocial (Jarvis 1981).

1.9. Genus *Tachyoryctes*

The East African genus *Tachyoryctes* belongs to the family Rhyzomyidae together with East Asian genera of *Rhyzomys* and *Cannomys*. Taxonomy status of the genus remains controversial, the number of species described by various researches ranges from two (*T. macrocephalus* and *T. splendens*) (Misonne 1974, Corbet and Hill 1991, Nevo 1999) to fourteen (Allen 1939, Ellerman 1941), because of the confusion the most recent checklist recognizes 11 species (Musser and Carleton 1993). According to morphology and ecology two groups of species can be recognized. *T. macrocephalus* is endemic for the Bale region of Ethiopia and its burrows are not sealed, they show appreciable aboveground activity (Sillero-Zubiri et al. 1995). Whereas the rest of the species are spread throughout East Africa and the eastern part of Central Africa and their burrows are sealed, they show low aboveground activity (Jarvis and Sale 1971). All species of *Tachyoryctes* feed on underground parts of the plants, roots, bulbs and rhyzomes (Kokiso and Bekele 2008).

2. Results

This thesis consists of five manuscripts – two already published (Manuscript No. I and II), one manuscript accepted for publication (Manuscript No. III) and two manuscripts prior to submission (Manuscript No. IV and V).

2.1. Manuscript No. I

Acoustic communication in subterranean rodents

Why study acoustic communication? And why in subterranean rodents? There are several reasons for studying acoustic communication in this particular group of mammals. First, acoustic communication is of great importance to the organization of animal societies. Animals use vocal signals to elicit specific behaviors, initiate contacts with conspecifics, identify individuals or species, signalize status (reproductive, dominance, territorial), solicit food, warn against predators, and coordinate reproductive efforts (courtship, copulation solicitation, physiological synchrony). Beyond the intra-specific level, acoustic signals are also an important factor in reproductive isolation and speciation processes. Furthermore, vocal communication can be a useful instrument for explaining general evolutionary principles. Signal structure and function are shaped by several factors, such as characteristics of the environmental channel in which the signal is transmitted and the physiological and morphological properties of both, the sender and the receiver. Thus, the characteristics of the vocal signals usually demonstrate the kind, intensity and process of natural selection.

Why in subterranean rodents? The answer to this question is intimately linked to the particular environment in which they live. The subterranean ecotope has influenced the evolution of the sensory biology of subterranean rodents. As seen in the previous chapter, the dark and monotonous subterranean environment limits the transmission of most signals and cues, leading to morphological and physiological modifications in the sensory systems of this group. Therefore, studying vocal and seismic communication in subterranean rodents is a useful tool for understanding the adaptive responses of these species to the constraints imposed by life in underground burrows.

In this chapter we review the ecological and evolutionary conditions that shaped the vocal repertoire of subterranean rodents. First, we describe two of the main factors that shape the vocalization characteristics of this group: the underground environment and the social system. Second, we examine seismic signals for long-distance communicationin some species of solitary subterranean rodents, detailing the main hypotheses about the evolution of these signals. Finally, we try to elucidate the role of care-elicitation calls in pups of Ctenomys talarum, in a first attempt to understand the significance of the begging behaviors in this and other species of subterranean rodents.

2.2. Manuscript No. II

Vocalization of the silvery mole-rat: Comparison of vocal repertoires in subterranean rodents with different social systems.

We examined vocalization of solitary subterranean rodent, the silvery mole-rats (*Heliophobius argenteocinereus*, Bathyergidae). Seven true and one mechanical vocalization were identified. The main frequencies of the analysed sounds (0.34 – 13.17 kHz) match to a great extent the frequency range suitable for transmission in underground burrows. Due to narrow frequency range of vocalization, motivation is predominantly expressed by the rate of tonality rather than by frequency changes. The vocal repertoire of the silvery mole-rat perfectly matches to Morton’s MS rules, i.e. that low-frequency and harsh vocalizations indicate hostility whereas high tonal calls signalise appeasement or fear. In comparison with social species, this solitary bathyergid produce fewer calls. They lack contact and alarm calls, but have a rich repertoire of mating calls. Acoustic signals seem to play a major role in lowering natural aggressiveness during the mating period.

2.3. Manuscript No III

Vocalization of the giant mole-rat (*Fukomys mechowii*), subterranean rodent with the richest vocal repertoire. Bioacoustics

In subterranean ecotope, where absence of light and ventilation limits visual and olfactory communication, options for long-range communication are restricted. Vocalization is thus one of the few channels available for transfer of the intraspecific information if the animals are not in direct contact. Nevertheless, even this kind of communication is limited by the acoustic conditions of the burrows. It is known that low-frequency sounds are best propagated here. In our study, we describe a vocal repertoire of the social subterranean rodent, the giant mole-rat (*Fukomys mechowii*, Bathyergidae), from mesic Afrotropics. Its vocal repertoire is shifted to the lower frequencies than in other subterranean rodents. The giant mole-rat has also the richest vocal repertoire among all subterranean rodents studied so far. In four behavioural contexts, we distinguished fourteen single sounds of true vocalization and four types of mechanical communication. Additionally, one seismic (soil-borne) signal of unclear function has been identified. We suggest that the rich vocal repertoire is connected with rich social interactions in giant mole-rats' families.

2.4. Manuscript No. IV

Vocal repertoire of social Mashona mole-rat (*Fukomys darlingi*)

Vocalization plays major role in communication of mammals living in underground burrows, other senses are restricted in its special sensory environment. We recorded vocalization of ten males and ten females of the Mashona mole-rat (*Fukomys darlingi*). Vocalizations were divided into four categories according to behavioural context. We described 11 types of true vocal signal and one mechanic sound. Vocalization is influenced by special acoustical environment underground, lower frequencies propagate the best. According to this finding, the frequency range of Mashona mole-rat calls is shifted towards lower frequencies. Richness and composition of vocal repertoire is influenced by degree of sociality. Vocal repertoire of the Mashona mole-rat agrees with that of other social mole-rats, with the highest diversity in contact and distress calls.

2.5. Manuscript No. V

Seismic communication in *Tachyoryctes* sp. from Tanzania

We described for the first time seismic communication in *Tachyoryctes* sp. from Tanzania. Seismic signals were recorded from six individuals in two experimental settings. In the first experimental setting each mole-rat was left alone in its Plexiglas system and recorded for 24-hours. In the second the two systems were connected, but direct contact was prevented by a wire mash barrier. We found that mole-rats produce seismic pulses by striking their heads against the ceiling of the tunnel. Two types of seismic signals were identified - fast and slow, differing in interpulse distance and behavioural context. The slow signal was produced in both experiments, but the fast signal was produced only in the second experiment in the close proximity of another individual. There is an indication that the seismic signals are individual specific; the success rate of classification according to DFA is 70.4% for the three tested individuals.

3. General discussion

3.1. Vocal communication

We described vocalization of three more species of mole-rats, so now vocalization for five species of mole-rats from three genera is known: naked mole-rat - *Heterophalus glaber* (Pepper et al. 1991), silvery mole-rat - *Heliophobius argenteocinereus* (**Manuscript No. II**), giant mole-rat – *Fukomys mechowii* (**Manuscript No. III**), Ansell´s mole-rat – *Fukomys anseli* (Credner et al. 1997) and Mashona mole-rat – *Fukomys darlingi* (**Manuscript No. IV**). Vocalization of all these species is shifted towards lower frequencies and is consistent with Morton`s MS rules (**Manuscript No. I, II, III, IV**).

3.2. Sociality and the communication

If we compare the group size and richness of the vocal repertoire of the mole-rats (Tab. 1), we could see that the only studied solitary species – silvery mole-rat – has the lowest number of the calls and also the portion of friendly vocalization is quite low (37.5 %). The more interesting finding is the relatively low number of friendly vocalization and lower number of total calls of the naked mole-rat compared to the giant mole-rat. Naked mole-rat lives in groups containing seventy members while giant mole-rat families consist of only ten members, but the total number of calls of the naked mole-rat is only 11, whereas the total number of calls of the giant mole-rat is 18. Portion of friendly vocalization is also higher in the giant mole-rat (55.6%) but the difference is not so prominent. This findings suggest that the naked mole-rats, despite their huge colonies, might have less or comparably socially complex colonies as giant mole-rats. The large colony size of the naked mole-rats could be only a by-product of extreme fecundity, unmatched by other bathyergids.

Table 4: Colony size, total number of calls and ration of a friendly vocalization among different species

	Colony members (mean ± SD) (range)	Total no. of calls	Friendly vocalization	Percentage of friendly vocalization
Heterocephalus glaber[1]	78.3±55.3 (25–204) [2]	12	6	50
Fukomys mechowii[3]	9.9±2.49 (7-16)[4]	18	10	55.6
Fukomys anselli[5]	9.2±2.5[6] (5-13)	14	5	35.7
Fukomys darlingi[7]	7.4±1.7 (5-9)[8]	12	5	41.6
Heliophobius argenteocinereus[10]	solitary	8	3	37.5

1. Pepper et al. 1991, 2. Braude 1991, 3. **Manuscript No. III**, 4. Šumbera et al. 2012, 5. Credner et al. 1997, 6. Šklíba et al. (2012), 7. **Manuscript No. IV**, 8. Bennett et al. 1994, 10. **Manuscript No. II**.

Despite their different degree of sociality, all mole-rats inhabit same sense environment: systems of underground tunnels. Therefore, theories explaining the complexity of the alarm vocalization by the different escape options or different predator hunting methods (Macedonia and Evans 1993, Fredericsen and Slobodchikoff 2007) could be omitted. Only the “group coordination method” theory (Furer and Manser 2009) and the “social complexity” theory (Blumstein and Armitage 1997) could be taken in account. The solitary species of mole-rat – the silvery mole-rat has no alarm calls. The social species of the genus *Fukomys*, the Ansel´s, Mashona and giant mole-rats, have one alarm call each. Only the naked mole-rat has three types of alarm calls (Pepper et al. 1991, Credner et al. 1997, **Manuscript No. II, III, IV**). The higher number of alarm calls in naked mole-rat could show higher social complexity, but the problem is more complicated as shown in Shelley and Blumstein (2005). The more likely the bigger alarm call diversity of the naked mole-rats is caused by the higher need of coordination of the group movements as long as the naked mole-rats live in large family group. Moreover, its tunnels are not sealed and they also “volcano” during disposing of soil aboveground exposing themselves to higher predation risk. (Brett 1991). (Furer and Manser 2009).

3.3. Seismic communication

Whereas *Georychus, Bathyergus* and *F. damarensis* produce seismic signals by drumming with their foot, we described new way of producing seismic signals by giant mole-rat (*Fukomys mechowii*) – chestbeating (**Manuscript No. III)**. Production of seismic signals is more frequent in solitary species, but surprisingly, *Heliophobius argenteocinereus* lacks this type of communication (**Manuscript No. II**). Seismic signals can carry wide variety of information, solitary *Georychus capensis* convey via this type of communication information about sex of the animal and its willingness to mate (Narins et al. 1992) and solitary *Bathyergus* use it as territorial signal (Jarvis and Bennett 1991). Social *F. damarensis* coordinate mating by seismic communication (Jarvis and Bennett 1991), while *F. mechowii* produce it in aggressive situations (**Manuscript No. III**).

Among subterranean mammals seismic communication is best known in the spalacid. *Spalax ehrenbergi* uses seismic signals in the context of territorial behaviour and also during mating (Rado et al. 1987, Heth et al. 1991). Since seismic communication has been described also for the zokor (*Eospalax* *fontanierii*) (Li et al. 2001), we assumed that other spalacids such as *Tachyoryctes* may also use seismic signals for communication. We recorded two types of seismic signals produced by *Tachyoryctes* – fast and slow, differing mainly in interpulse distance (**Manuscript No. V**). Slow signal is probably used as warning. Either for conspecific or predator – snake as in other fossorial rodents (review in Randall 2001 and Hill 2008). Fast signal shows individual specifity and is produced in close proximity of other individual only. Therefore we categorized it as territorial signal, which is very frequent use of seismic signals (Rado et al. 1987, Randall et al. 1984, 1989, 1994, and 1997, Jarvis and Bennett 1991).

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Manuscript No. I

Schleich EC, Veitl S, **Knotková E**, Begall S. 2007. Acoustic communication in subterranean rodents, In: Subterranean Rodents: News from Underground. Begall S., Burda H., Schleich C.E., Springer-Verlag, Berlin Heidelberg, pp 113-127

10 Acoustic Communication in Subterranean Rodents

Cristian E. Schleich, Silke Veitl, Ema Knotková, Sabine Begall

10.1 Introduction

Why study acoustic communication? And why in subterranean rodents? There are several reasons for studying acoustic communication in this particular group of mammals. First, acoustic communication is of great importance to the organization of animal societies. Animals use vocal signals to elicit specific behaviors, initiate contacts with conspecifics, identify individuals or species, signalize status (reproductive, dominance, territorial), solicit food, warn against predators, and coordinate reproductive efforts (courtship, copulation solicitation, physiological synchrony). Beyond the intra-specific level, acoustic signals are also an important factor in reproductive isolation and speciation processes.

Furthermore, vocal communication can be a useful instrument for explaining general evolutionary principles. Signal structure and function are shaped by several factors, such as characteristics of the environmental channel in which the signal is transmitted and the physiological and morphological properties of both, the sender and the receiver. Thus, the characteristics of the vocal signals usually demonstrate the kind, intensity and process of natural selection.

Why in subterranean rodents? The answer to this question is intimately linked to the particular environment in which they live. The subterranean ecotope has influenced the evolution of the sensory biology of subterranean rodents. As seen in the previous chapter, the dark and monotonous subterranean environment limits the transmission of most signals and cues,

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leading to morphological and physiological modifications in the sensory systems of this group. Therefore, studying vocal and seismic communication in subterranean rodents is a useful tool for understanding the adaptive responses of these species to the constraints imposed by life in underground burrows.

In this chapter we review the ecological and evolutionary conditions that shaped the vocal repertoire of subterranean rodents. First, we describe two of the main factors that shape the vocalization characteristics of this group: the underground environment and the social system. Second, we examine seismic signals for long-distance communication in some species of solitary subterranean rodents, detailing the main hypotheses about the evolution of these signals. Finally, we try to elucidate the role of care-elicitation calls in pups of *Ctenomys talarum*, in a first attempt to understand the significance of the begging behaviors in this and other species of subterranean rodents.

Manuscript No. II

Knotková E, Veitl S, Šumbera R, Sedláček F, Burda H, 2008. Vocalization of the silvery mole-rat: comparision of vocal repertoires in subterranean rodents with different social systems. Bioacoustics 18(3):241-257.

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VOCALISATIONS OF THE SILVERY MOLE-RAT: COMPARISON OF VOCAL REPERTOIRES IN SUBTERRANEAN RODENTS WITH DIFFERENT SOCIAL SYSTEMS

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ABSTRACT

We examined vocalisations of a solitary subterranean rodent, the Silvery Mole-rat *Heliophobius argenteocinereus* (Bathyergidae). Seven true vocalisations and one mechanical vocalisation were identified. The main frequencies of the analysed sounds (0.34-13.17 kHz) match to a great extent the frequency range suitable for transmission in underground burrows. Due to the narrow frequency range of vocalisations, motivation is predominantly expressed by the rate of tonality rather than by frequency changes. The vocal repertoire of the Silvery Mole-rat perfectly matches to Morton's MS rules, i.e. that low-frequency and harsh vocalisations indicate hostility whereas high tonal calls signalise appeasement or fear. In comparison with social species, this solitary bathyergid produces fewer calls. It lacks contact and alarm calls, but has a rich repertoire of mating calls. Acoustic signals seem to play a major role in lowering natural aggressiveness during the mating period.

Manuscript No. III

Bednářová R, **Hrouzková-Knotková E**, Burda H, Sedláček F, Šumbera R. 2012. Vocalization of the giant mole-rat (*Fukomys mechowii*), subterranean rodent with the richest vocal repertoire. Bioacoustics. – *in press*.

Vocalization of the giant mole-rat *(Fukomys mechowii)*, subterranean rodent with the richest vocal repertoire

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Abstract

In subterranean ecotope, where absence of light and ventilation limits visual and olfactory communication, options for long-range communication are restricted. Vocalization is thus one of the few channels available for transfer of the intraspecific information if the animals are not in direct contact. Nevertheless, even this kind of communication is limited by the acoustic conditions of the burrows. It is known that low-frequency sounds are best propagated here. In our study, we describe a vocal repertoire of the social subterranean rodent, the giant mole-rat (*Fukomys mechowii,* Bathyergidae), from mesic Afrotropics. Its vocal repertoire is shifted to the lower frequencies than in other subterranean rodents. The giant mole-rat has also the richest vocal repertoire among all subterranean rodents studied so far. In four behavioural contexts, we distinguished fourteen single sounds of true vocalization and four types of mechanical communication. Additionally, one seismic (soil-borne) signal of unclear function has been identified. We suggest that the rich vocal repertoire is connected with rich social interactions in giant mole-rats' families.

Manuscript No. IV

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Vocal repertoire of social Mashona mole-rat (*Fukomys darlingi*).

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Abstract

Vocalization plays major role in communication of mammals living in underground burrows, other senses are restricted in its special sensory environment. We recorded vocalization of ten males and ten females of the Mashona mole-rat (*Fukomys darlingi*). Vocalizations were divided into four categories according to behavioural context. We described 11 types of true vocal signal and one mechanic sound. Vocalization is influenced by special acoustical environment underground, lower frequencies propagate the best. According to this finding, the frequency range of Mashona mole-rat calls is shifted towards lower frequencies. Richness and composition of vocal repertoire is influenced by degree of sociality. Vocal repertoire of the Mashona mole-rat agrees with that of other social mole-rats, with the highest diversity in contact and distress calls.

Key words

Mashona mole-rat, *Fukomys darlingi*, Bathyergidae, vocalization, communication.

Introduction

The Mashona mole-rat faces a special sensory environment, due to the limited amount of light, and lack of light stimuli below ground in its burrow. Their eyes are specialized to distinguish between light and dark (review in Burda 2006). Tactile sense is well developed in these rodents and in partly probably serves as a form of compensation for its poor vision. However, tactile sense reaches only on very short distance (Burda et al. 1990, Park et al. 2007). The absence of air currents in underground burrows limit transport of scent signals. Under such conditions, only vibrational communication is effective for middle and long distances. Two types of signals are considered as vibrational, air-borne acoustic signals and substrate-born seismic signals (Bradbury and Vehrencamp 1998).

Acoustic signals are propagated within the burrows over middle distances (Heth et al. 1986, Lange et al. 2007). Subterranean rodents probably use this method of communication for various purposes, such as kin and individual recognition, to distinguish reproductive or dominance status, to sexually stimulate a mate or to warn against danger (Schleich et al. 2007, Yosida et al. 2007, Yosida and Okanoya 2009). Further, vocalization may encode different motivations, which are reflected in different physical structures of the sound. For example, harsh, relatively low-frequency sounds are used during hostile encounters, while higher-frequency, tone-like sounds are used in friendly contexts (Morton 1977).

Vocalization in subterranean rodents is influenced by the acoustic parameters of their burrows and hearing sensitivity, which in turn is dependent on the morphological adaptations of the ear (Burda 2006, Begall et al. 2007). Studies on acoustics in burrows have shown that low-frequency sounds around 400 Hz are propagated best, inidicating that they are less attenuated than sounds of lower and higher frequencies (Heth et al. 1986, Lange et al. 2007). Moreover, the so-called “stethoscope effect” exists, which means that certain sound frequencies (200, 400 and 800 Hz) are amplified at a distance of 1 m (Lange et al. 2007). The best hearing sensitivity of subterranean rodents is in the lower frequency range compared with similarly sized surface-dwelling rodents. Consequently, vocalization in subterranean rodents shows tuning to lower frequencies (Schleich et al. 2007, Devries and Sikes 2008, Knotková et al. 2009, Bednářová et al. *in press*).

The African mole-rats (Bathyergidae, Rodentia) includes species with diverse social systems. Some genera are solitary (*Bathyergus, Georhychus, Heliophobius*) and other are social (*Heterocephalus, Cryptomys, Fukomys*) (McKenna and Bell 1997). Therefore, they are an ideal model to study relationships between sociality, vocal repertoire richness and composition. The relationship between thenumber of vocal signals and sociality of particular species was described in different taxa (Veitl et al. 2000, McComb and Semple 2005, Knotková et al. 2009, Le Roux et al. 2009). McComb and Semple (2005) provide evidence that vocal repertoire size correlates positively with the degree of social bonding in non-human primates. Not just vocal repertoire size, but also complexity of calls could correlate positively with group size as in the case of Carolina chickadees (Freeberg 2006). Also, vocal repertoire composition could be influenced by species social system (Knotková et al. 2009, Le Roux et al. 2009 Bednářová et al. *in press*), since social and solitary species use vocalization in different behavioural contexts. Social species possess richer vocal repertoires than species that are solitary (Schleich et al 2007).

Materials and methods

Studied animals

The Mashona mole-rat (*Fukomys darlingi*), formerly known as *Cryptomys darlingi* (Kock et al. 2006) is herbivorous, socially living subterranean bathyergid. They occur in shrub habitats and miombo woodland (Bennett and Faulkes, 2000). They live in families containing approximately seven animals (5–9) where reproduction is restricted to one breeding pair (Bennett et al.1994). It is supposed that this species occurs in Eastern and Northern Zimbabwe, and is believed to also occur in Western Mozambique (c.f. Bennett and Faulkes, 2000). Based on karyology and cytochrome b analysis, a mole-rat population from southern Malawi originally assigned to *Cryptomys hottentotus* is actually *F. darlingi* (Van Daele, unpublished results).

Vocalizations were recorded in 10 adult males and 10 females of the Mashona mole-rat. Studied animals were kept in breeding facility at the Faculty of Science in České Budějovice, Czech Republic. Families or pairs were kept in open terrariums with horticultural peat and supplemented with plastic tubes as imitation of tunnels and flowerpots as nest boxes. The room was lit in 12D/12L (lights on at 0700 h). The temperature was kept on 25 ± 1^{o}C. Animals were fed *ad libitum* with carrots, potatoes, apples and cereals.

Data collecting

Vocalization was recorded in four experimental settings. 1. Home terrariums – the mole-rat families were recorded in their home terrarium without any manipulation using an ad libitum sampling method. 2. Perspex tunnels with two home boxes - filled with peat to simulate natural burrows, the whole family was kept there for two months. For purpose of recording, parts of the tunnels were opened. 3. Open plastic boxes with peat - open boxes were used for quick separation of unfamiliar animals during aggressive encounters. The first animal was placed in the open box and left to explore. After ten minutes of resting, the second animal was added. The tested pairs were always composed of strangers and they were male-male, female-female and male-female. 4. A Perspex tunnel 170cm in length, with two home boxes on each side, divided in the middle by a perforated partition and supplemented with strap-on dividers on each side - animals were placed into opposite home boxes and left to explore their surroundings. After they calmed down (i.e. animal rested on one place), the strap-on dividers were opened and animals were allowed to reach the middle perforated partition. Both familiar and unfamiliar animals were used in this experiment.

The sampling sessions took place at different times of the day to enhance the possibility to record all call types. The microphone was held at a distance of 15-20 cm, the distance being far enough away to ensure that the animals were not disturbed. The duration of a single recording was 10 to 30 minutes and ended after five minutes of vocal inactivity. For detailed description of the behaviour, an ethogram for naked mole-rats published in Sherman *et al*. (1991) was used.

All vocalization was divided into five groups, based on their behavioural context: (1) contact, (2) aggressive and territorial, (3) distress, (4) mating, (5) alarm. Categories have been defined according to Bradbury and Vehrencamp (1998). Special category - mechanical sounds, contains all sounds produced by any means except vocal cords.

1. <u>Contact calls</u> are generally used to coordinate activities of animals within groups to maintain spacing and cohesion during foraging. Recruitment and assembly signals may be used to reduce distances between group members. Greeting and other affiliative signals are often exchanged, when group members reassemble in a common location.

2. <u>Aggressive and territorial calls</u> indicate the presence of a territorial owner in a given location, demarcate territorial boundaries, and often include concomitant information about identity and location of the owner. Aggressive calls also occur during escalated violence over ownership of a mate or commodity. Providing information about the likely intentions and levels of commitment of their senders, they may also provide information about relative fighting ability. They are produced by animals dominant in actual interaction.

3. Distress calls occur in stressful situations aroused during the encounter of animals, such as food competition or movement restriction.

4. Mating calls provide information on location and availability that allows members of the two sexes to find and approach each other and determine whether subsequent mating will occur and effects its coordination.

5. Alarm calls indicate the presence of a predator or other threats. They also occur during handling which may simulates attack of a predator.

The records were taken with a MD 735 Senheiser dynamic microphone (frequency range 50-18.000 Hz) and recorded using a SONY digital audio tape-recorder TCD-D8 (sample frequency 44.1 kHz, resolution 16 bit) on a DAT cassette. Part of recording was taken with a MD 431 II Senheiser dynamic microphone (frequency range 40-16.000 Hz) and recorded using a Marantz card audiorecorder PMD660 (sample frequency 44.1 kHz, resolution 16 bit). During recordings, animals were filmed on camera (Canon DVD camcorder PAL DC 40).

Data analysis

Recordings were transferred to a computer and evaluated usinf the Avisoft-SAS Lab Pro Software, version 5.0.01 (2010) program, where the sampling rate was changed from 44.1 to 22.05 kHz. The following spectrogram parameters were used: Hamming Window, Fast-Fourier-Transformation (FFT) of 256 points, frame size 100% and overlap 50%. We measured the following variables: minimum and maximum frequency of the sound, the most intensive frequency, 25%, 50% and 75% quartile, the beginning and the end of fundamental frequency, minimum and maximum of the fundamental frequency, range of the fundamental frequency and duration of the sound. The most intensive frequency of the sound was found by bound reticule cursor. Other variables were measured in point, where the frequency was lower by 20dB. For fundamental frequency variables the most intensive frequency was measured on fundamental frequency and from this point the same procedure was used as in case of whole sound.

Separate analysis was computed in the STATISTICA StatSoft, Inc. (2010), version 9.0 program. The descriptive statistics was used to characterize basic parameters of the sounds. The classification into categories was done with the Discriminant Functional Analysis (DFA) with *a priori* classification probabilities proportional to group size. The results were visualized using Principal Component Analysis (PCA) based on a correlation matrix.

Results

In total 932 true vocalization sounds and 80 mechanical sounds were evaluated. Calls were divided into four groups according to behavioural context: contact, distress, aggressive and mating calls. A separate category for was created, which was the only mechanical sound recorded.

Mechanical sounds

The only mechanical sound – *teeth grinding* (n=80) – is classified into a special category, its basic characteristics are in Table 1. *Teeth grinding* (Figure 1) is produced by rubbing the upper and lower incisors together. Teeth grinding has a broad frequency range and is usually produced when the animals relax, but also during aggressive encounters.

True vocalizations

Contact calls

Contact calls (n = 116) were classified into three categories. The basic characteristics are depicted in Table 1, classification success then in Table 2. Their separation by PCA is showed in Figure 3.

Cheep2 (Figure 2a)

Cheep2 is the only atonal contact call. This sound has broad frequency range and relatively high main frequency. Cheep2 was produced by a female in a nest or plastic tube when a male approached (experiment 1 and 2). It was also recorded when two familiar animals were placed into the Perspex tunnel divided by a barrier (experiment 4), the subordinate animal vocalized to the breeding member of his family.

Cheep1 (Figure 2b)

The Cheep1 is similar to cheep2 and was recorded under the same behavioural context. The main difference between these two sounds is that cheep1 is not atonal and has a lower minimal frequency.

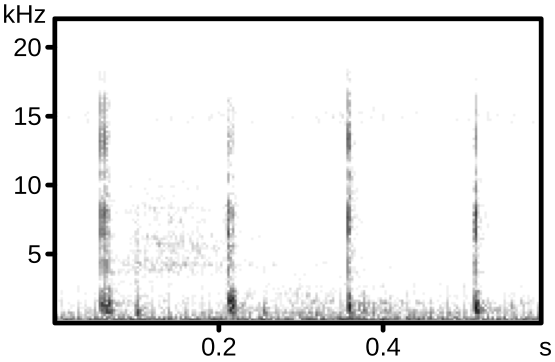

Figure 1.: Spectrogram of the teeth grinding.

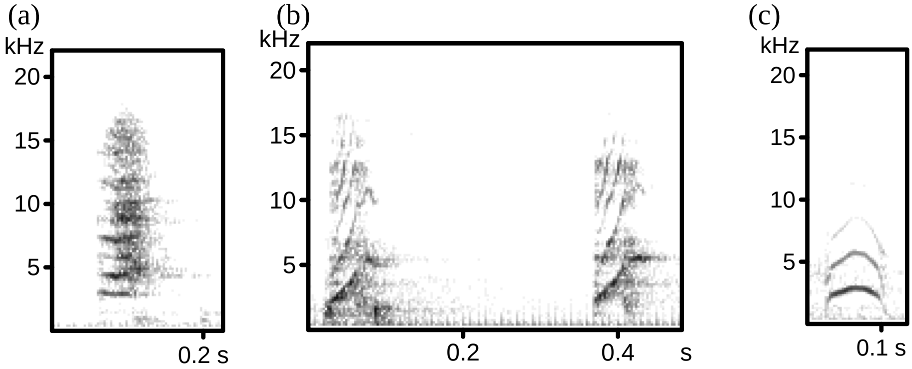

Figure 2.: Spectrogram of the sounds: a) cheep2, b) cheep1, c) twitter.

Twitter (Figure 2c)

The last type of contact call is twitter; this sound has a markedly lower frequency range than Cheep2 and Cheep1. This sound was recorded in families kept in a Perspex system (experiment 2). The sound was produced when animals passed each other in tunnels.

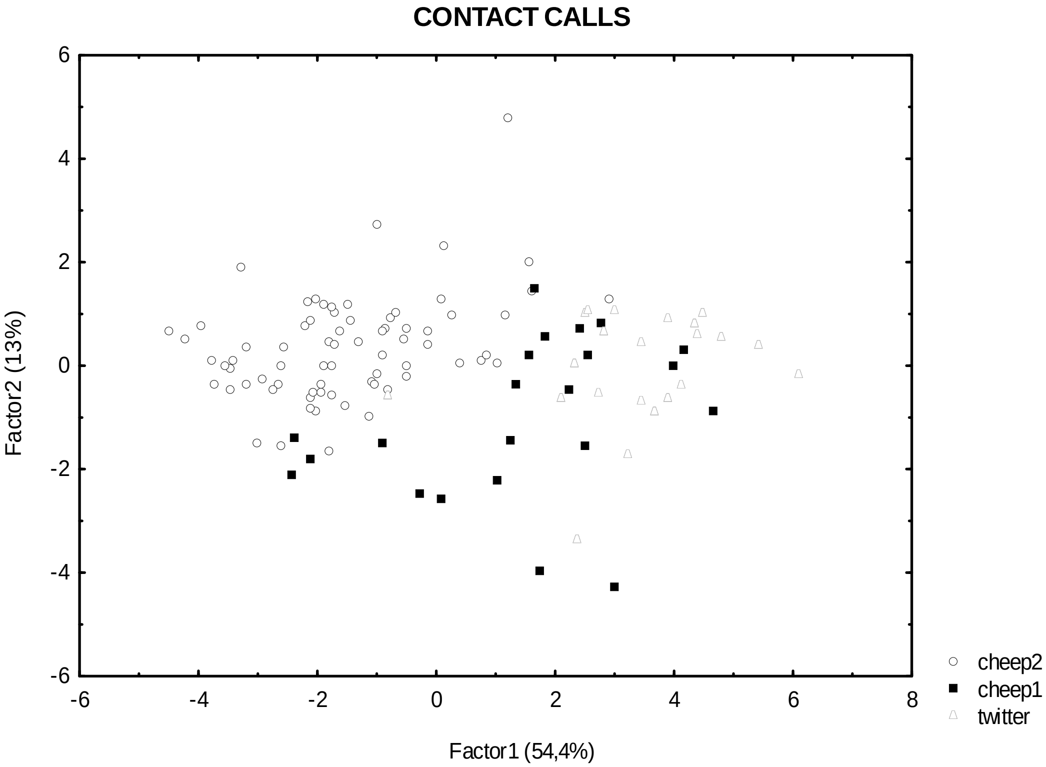

Figure 3.: Separation of contact calls showed by plot of two factors gained in PCA. (N=116)

Aggressive and distress calls

Aggressive and distress calls (n = 306) were classified into six categories. The basic characteristics are depicted in Table 1, classification success then in Table 2. Their separation by PCA is showed in Figure 5.

Whistle (Figure 4a)

Whistle is the shortest sound of all aggressive calls. This tonal sound has the most intensive frequency around 4.58 kHz. This sound was recorded during experiment 4. with two unfamiliar animals and was emitted by the attacker.

Squeak (Figure 4b)

Squeak is a tonal sound similar to whistle, but with a longer duration. It also differs in inclination of the curve when maximal fundamental frequency reaches higher, around 5.68 kHz. This sound was also emitted by the aggressor.

Table 1: Basic characteristics of the sounds

Category	**Name of sound**	**N**	**Frequency range (kHz)**	**Fundamental frequency (kHz)**	**Main frequency (kHz) mean ± SD**	**Duration of sound (s) mean ± SD**
Mechanical sound	teeth grinding	80	0.43 – 13.98	0.44 – 2.62	1.34 ± 1.17	0.03 ± 0.02
Contact calls	cheep2	72	2.59 – 14.48	3.50 – 5.09	6.43 ± 2.93	0.05 ± 0.01
	cheep1	22	1.82 – 13.72	1.91 – 4.69	4.20 ± 2.71	0.07 ± 0.01
	twitter	22	1.52 – 7.26	1.53 – 3.65	3.55 ± 2.06	0.06 ± 0.02
Aggressive calls	whistle	39	3.50 – 10.41	3.60 – 4.81	4.58 ± 1.46	0.04 ± 0.01
	squeak	9	3.28 – 11.00	3.29 – 5.68	4.57 ± 0.81	0.06 ± 0.01
Distress calls	squeal	167	1.96 – 12.45	2.03 – 5.33	3.80 ± 1.57	0.07 ± 0.02
	harsh	35	1.51 – 10.35	2.09 – 4.94	3.77 ± 1.48	0.06 ± 0.02
	snort	45	0.14 – 6.57	0.14 – 0.94	0.48 ± 0.18	0.08 ± 0.02
	Cry	11	2.85 – 16.06	3.73 – 5.48	5.21 ± 1.76	0.07 ± 0.02
Mating calls	cluck	291	0.66 – 3.73	0.67 – 1.90	1.50 ± 0.76	0.03 ± 0.01
	shriek	219	0.50 – 2.81	0.50 – 1.39	0.98 ± 0.34	0.03 ± 0.01

Table 2: The Success rates of a classification of the sounds according to DFA.

Count	Category	Sound	Success rates (%)	Total classification success (%)	Wilk's Lambda
116	Contact calls			92.2	0.099
		Cheep 2	98.6		
		Cheep 1	81.8		
		Twitter	81.8		
306	Aggressive and distress calls			79.7	0.053
		Whistle	87.2		
		Squeak	33.3		
		Squeal	86.8		
		Harsh	25.7		
		Snort	100.0		
		Cry	72.7		
510	Mating calls			82.9	0.54
		Cluck	81.8		
		Shriek	84.5		

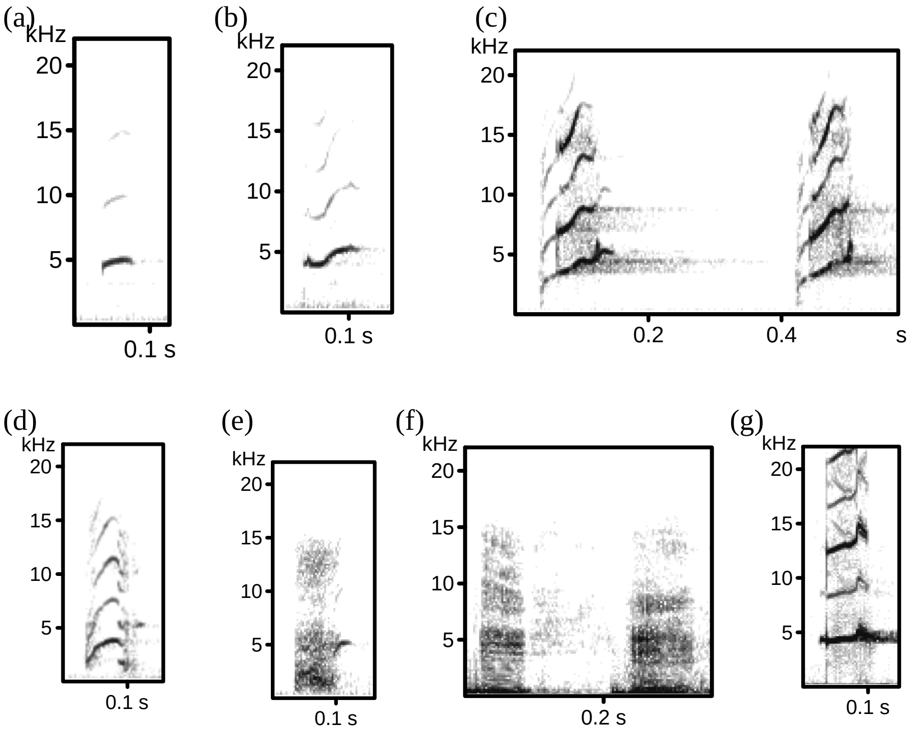

Figure 4.: Spectrogram of sounds: a) whistle, b) squeak, c, d) squeal, e) harsh, f) snort, g) cry.

Squeal (Figure 4c, d)

Squeal is often produced sound during aggressive encounters. This sound has together with harsh quite low minimal frequency. The frequency range of squeal is higher than the frequency range of remaining aggressive calls except cry. Squeal has two subtypes which differ in openness of the curve (Fig. 10, c,d). This sound was recorded when unfamiliar animals were put together and was emitted by the defending animal.

Harsh (Figure 4e)

Harsh is an atonal sound with low minimal frequency. This is distress call emitted by defending animal.

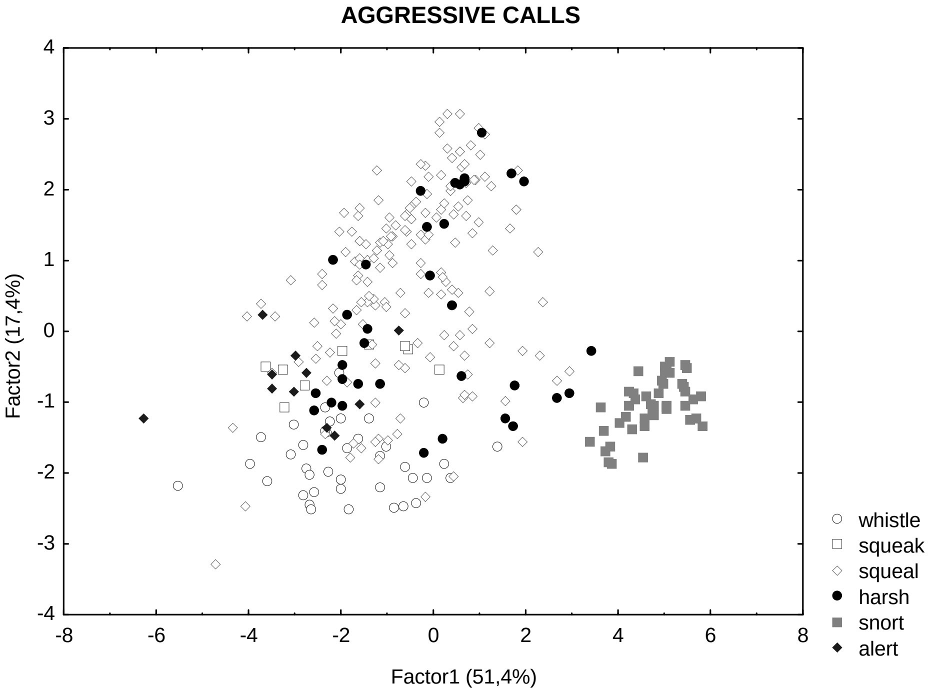

Figure 5.: Separation of aggressive calls showed by plot of two factors gained in PCA. (N=306)

Snort (Figure 4f)

Snort is atonal sound with a very low fundamental frequency. This sound has a noticeably lower frequency range than other aggressive calls. It is produced by an acute exhalation. Animals produced this sound while being handled

Cry (Figure 4g)

Cry is very loud and high tonal sound. The main frequency of cry is located much higher than in other aggressive calls. The cry is produced by animals probably as a reaction to pain during attack or when one animal restricts the movement of the other.

Mating calls

Mating calls (n = 510) were classified into two categories. The basic characteristics are depicted in Table 1, classification success then in Table 2. Their separation by PCA is showed in Figure 7.

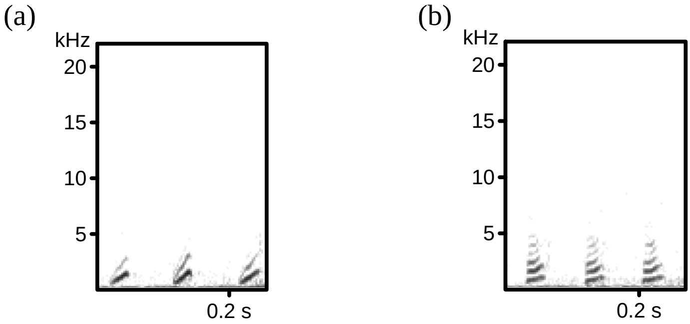

Figure 6.: Spectrogram of the sounds: a) cluck, b) shriek

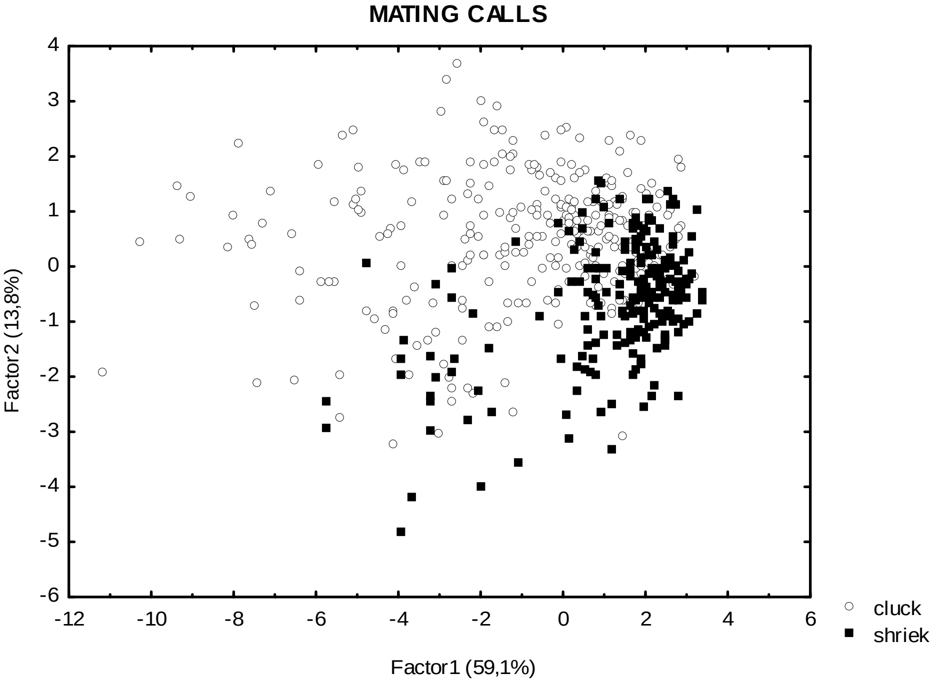

Figure 7.: Separation of mating calls showed by plot of two factors gained in PCA. (N=510)

Cluck (Figure 6a)

Cluck is a very short vocalization. The range of frequency is very low; it usually does not exceed 5 kHz. Clucks were mostly emitted in a series together with shrieks. This sound was recorded during courtship, when animals were sniffing each other's anogenital area, emitted predominantly by the female.

Shriek (Figure 6b)

The Shriek is similar to the cluck but with many interstages between shriek and cluck. Shriek has a main frequency lower than cluck and does not rise in frequency towards the end.

Discussion

Similarly to all subterranean rodents studied so far, the vocalization of *F. darlingi* is also shifted to lower frequencies. We described 12 types of vocal signals consisting of 11 sounds of true vocalization and one mechanically produced sound. This amount of calls corresponds to the acoustic repertoire of other social subterranean rodents. *F. anselli* possess 14 different calls (Credner et al. 1997) and *S. cyanus* 12 acoustic calls (Veitl et al. 2000). The remaining two social species, in which vocalization has been studied, possess a larger range of sounds. *Heterocephalus glaber* emit 17 different calls (Pepper et al. 1991), and *F. mechowii* 18 calls (Bednářová et al. *in press*). Solitary subterranean rodents possess markedly lower amounts of vocalizations, since they do not usually come in contact with conspecifics otherwise than during mating. The widest vocal repertoire amongsolitary species is attributed to *Heliophobius argenteocinereus* with eight types of calls (Knotková et al. 2009).

Teeth grinding is a mechanical sound described in all studied subterranean rodents and probably even in all rodents. This sound is not a true vocalization but may have a communicative purpose (c.f. Schleich and Busch 2002). Mashona mole-rats emitted this sound when at rest and also during aggressive encounters. A similar behavioural context was observed in other social mole-rats by Bednářová et al *in press*, and Credner et al. 1997. In the case of solitary *C. talarum* or *Heliophobius argenteocinereus* teeth grinding was accompanied by fighting behaviour (Schleich and Busch 2002, DeVries et al. 2008, Knotková et al. 2009).

Tonal vocalizations can be divided into four behavioural categories (contact, aggressive, distress, mating and alarm calls). *Fukomys darlingi* emits three different types of contact calls, two tonal and one atonal sound with a broad frequency range 1.52 – 14.48 kHz, with twitter only posing a markedly lower maximal frequency 7.26 kHz. *Fukomys anselli* (Credner *et al*. 1997) and *Heterocephalus glaber* (Pepper *et al*. 1991) possess two types of contact calls each. The remaining studied social subterranean rodents exhibit more of contact

Table 4: Colony size and ration of a friendly vocalization among different species

	Colony members (mean ± SD) (range)	Total no. of calls	Friendly vocalization	Percentage of friendly vocalization
Heterocephalus glaber[1]	78.3±55.3 (25–204) [2]	12	6	50
Fukomys mechowii[3]	9.9±2.49 (7-16)[4]	18	10	55.6
Fukomys anselli[5]	9.2±2.5[6] (5-13)	14	5	35.7
Fukomys darlingi[7]	7.4±1.7 (5-9)[8]	12	5	41.6
Heliophobius argenteocinereus[10]	solitary	8	3	37.5

1. Pepper et al. 1991, 2. Braude 1991, 3. Bednářová et al. *in press*, 4. Šumbera et al. 2012, 5. Credner et al. 1997, 6. Šklíba et al. (2012), 7. Present study, 8. Bennett et al. 1994, 10. Knotková et al. 2009.

calls, *S. cyanus* four types (Veitl *et al*. 2000) and *F. mechowii* five contact calls, (Bednářová et al. *in press*). *Spalacopus cyanus* and *F. mechowii* contact calls represent the richest group of their true vocalization Portion of friendly vocalization (sensu Morton 1977) within species repertoire may represent degree of sociality. However, do not fit without exceptions in bathyergids (Table 4). In this context it is interesting that social *F. anselli* possess within its vocal repertoire comparable percentage of friendly vocalization as solitary *Heliophobius*

Tonal aggressive calls of *F. darlingi* are whistle and squeak. Both are emitted by dominant animals when an unfamiliar animal encountered. In addition, one more aggressive call has been observed in *F. darlingi*. This call, the snort, is atonal sound with quite long duration 0.08s ± 0.02 and very low minimal frequency around 0.14 kHz in comparison with other aggressive calls. This sound was produced by animals during handling and usually was followed by attempts to bite. The same snort sound was observed in *F. mechowii* (Bednářová et al. *in press*), and the“grunt“ sound in *H. glaber* (Pepper et al. 1991) and “grunt“ sound *H. argenteocinereus* (Knotková et al. 2009) was accompanied by the same behaviour. The richest amount of aggressive sound has been described in the social *F. anselli* which possess six different aggressive vocalizations followed by *Heterocephalus glaber* with four types and *F. darlingi* and *F. mechowii* with three types (Pepper et al. 1991, Credner et al. 1997, Bednářová et al. *in press*). Richness of the aggressive calls in *F. anselli* could suggest its aggressiveness, which corresponds with low number of contact calls and small portion of friendly vocalizations within their repertoire.

Subterranean rodents usually possess one or two types of distress calls (Pepper et al. 1991, Credner et al. 1997, Francescoli 1999, Veitl et al. 2000, Schleich and Busch 2002, Knotková et al. 2009, Bednářová et al. *in press*). In *F. darlingi* three types of distress calls were observed. Squeal is an often produced tonal sound emitted by subordinate animal during aggressive encounters. Squeal has two subtypes which differ in ending of the call. A similar sound, also called squeal, has been described in *F. mechowii* (Bednářová et al. *in press*). A second type of distress call observed in *F. darlingi* is a harsh, atonal sound with quite a low minimal frequency around 1.51 kHz. This sound was emitted by a subordinate and/or attacked animal during aggression. The last type of distress vocalization in *F. darlingi* is cry. Cry is a very loud sound (frequency range: 2.85 – 16.06 kHz) with a high main frequency around 5.21 kHz emitted as a reaction to pain or alternatively, when one animal restricts the movement of another. A similar sound has been described in many others subterranean rodents. *F. mechowii* emits a cry during food competition and also when an animal restricts the movement of another (Bednářová et al. *in press*), “squeal“ is produced by *S. cyanus* in potentially dangerous, stressful situations (Veitl et al. 2000), and the same sound has been described as “scream“ in *F. anselli*, being produced as a reaction to pain or fright (Credner et al. 1997).

Mating calls are considered a primary type of vocalization in solitary species because the need to find another animal of the same species only arises during the mating season and so their vocalization serves mainly to lower agresivity or to sexually stimulate the mate (Francescoli 1999, Schleich and Busch 2002, Knotková *et al*. 2009). The quantity of mating calls across subterranean taxa corresponds with this suggestion. For solitary *C. talarum* and *Heliophobius argenteocinereus* mating calls present the most extensive group of vocalizations (Schleich and Busch 2002, Knotková *et al*. 2009). social subterranean rodents also emit several different types of mating calls, the amount of these sounds vary from two as in case of *S. cyanus* (Veitl *et al*. 2000) or *F. darlingi* (present study) to three in *F. anselli* and *F. mechowii* (Credner *et al*. 1997, Bednářová et al. *in press*). But in none of the social species do mating calls represent the most extensensive group of sounds. Interestingly, in *Heterocephalus glaber* only one type of this call has been described (Pepper *et al*. 1991).

Most of the social subterranean rodents emit at least one type of alarm call (Veitl *et al*. 2000, Bednářová et al. *in press*). In *F. darlingi* and in *F. anselli* none alarm sound has been observed (Credner *et al*. 1997, present study). In contrary, *Heterocephalus glaber* possess three different types of alarm calls (Pepper *et al*. 1991). High richness of the alarm calls in this species may be a consequence of higher predation risk compared to other bathyergid, because, its tunnels are not sealed and they also “volcano” during disposing of soil aboveground exposing themselves to higher predation risk. (Brett 1991).

Acknowledgement

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Manuscript No. V

Hrouzková E, Dvořáková V, Šumbera R. 2012. Seismic communication in *Tachyoryctes* sp. from Tanzania

Seismic communication in *Tachyoryctes* sp. from Tanzania

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Abstract

We described for the first time seismic communication in *Tachyoryctes* sp. from Tanzania. Seismic signals were recorded from six individuals in two experimental settings. In the first experimental setting each mole-rat was left alone in its Plexiglas system and recorded for 24-hours. In the second the two systems were connected, but direct contact was prevented by a wire mash barrier. We found that mole-rats produce seismic pulses by striking their heads against the ceiling of the tunnel. Two types of seismic signals were identified - fast and slow, differing in interpulse distance and behavioural context. The slow signal was produced in both experiments, but the fast signal was produced only in the second experiment in the close proximity of another individual. There is an indication that the seismic signals are individual specific; the success rate of classification according to DFA is 70.4% for the three tested individuals.

Key words

Seismic communication, *Tachyoryctes*, East African mole-rat, substrate borne vibration.

Introduction

The subterranean environment presents many challenges for its mammalian inhabitants, especially regarding their sensory ecology. The use of traditional senses such as vision and hearing is highly restricted in subterranean burrows (Burda et al. 1990, Francescoli 2000). However, other types of senses used for orientation or communication are highlighted .One of the most peculiar being the use of substrate born vibrations (Hill 2008). Mole-rats were able to use these vibrations - seismic waves to transfer various information through the soil. The perception of substrate born vibration is for example useful in gathering information from their surroundings which may be relevant for example in the antipredatory context (Šklíba et al. 2008). The desert afrosoricid golden mole (*Eremitalpa granti*) make use of use of vibration in foraging, being able to register seismic cues produced by the hummocks with grass where there is a greater chance of encountering termites, the golden mole's staple food (Narins et al. 1997). In addition, the blind mole-rat (*Spalax ehrenbergi*) use self-generated seismic waves as an echolocation mechanism to determine the size and shape of an obstacle (Kimchi et al. 2005).

The best known use of seismic waves by subterranean and fossorial mammals is for intraspecific communication. In burrow systems it is very difficult to communicate effectively over long distances using traditional communication channels such as vocalization. Vocalization is almost excluded if burrow systems of different individuals/families are not in direct contact, because the sound waves are attenuated by the soil. It is expected that seismic signals propagate in the subterranean environment at least an order of magnitude better than auditory signals (Narins et al. 1992). Among subterranean mammals this type of communication is best known in the spalacid. *Spalax ehrenbergi* uses seismic signals in the context of territorial behaviour and also during mating (Rado et al. 1987, Heth et al. 1991) Such seismic communication has also been described in several African mole-rat species (Bathyergidae, Rodentia) (Jarvis and Bennett 1991, Narins et al. 1992, Bednářová *in press*). For example, in solitary *Georychus capensis* it was found that seismic signals can carry information about the sex of its producer and its mate attractiveness (Narins et al. 1992). In the Damaraland mole-rat (*Fukomys damarensis)* the seismic signals are used for the coordination of mating behaviour (Jarvis and Bennett 1991). In the giant mole-rat (*Fukomys mechowii*) substrate borne vibrations are produced during aggressive encounters (Bednářová *in press*). However, seismic communication is not known only in strictly subterranean rodents, i.e. rodents which breed and forage underground and rarely come to the surface, but was also described in several fossorial species. In these species the seismic signals reach the burrows of receivers with a higher probability than acoustic signals (Randall 1994, Giannoni et al. 1997, Randall et al. 2000).

The methods used for generating seismic signals vary from species to species suggesting that this type of communication has evolved independently in phylogenetically unrelated lineages. Thus, blind mole-rats strike their heads against the roof of their burrows (Rado et al. 1987), while Cape mole-rats (Narins et al. 1992), great gerbils (Randall et. al 2000) and kangaroo rats (Randall 1997) drum their hind legs against the burrow floor. In addition, several vole species tap their incisors on the burrow floor (Giannoni et al. 1997). It is suggested that Eastern African mole-rats *Tachyoryctes* (Kenya) also produce seismic signals by tapping their incisors in a similar way to voles ((Jarvis (1969) in Mason (2010)).

Among rodents with dominant subterranean activity genus *Tachyoryctes* (Spalacidae*)* is one of the least understood groups. This genus is distributed mainly in East Africa, from Ethiopia to northern Tanzania (Nowak 1999). These rodents are generalist herbivores feeding on underground as well as aboveground parts of the plants (Kokiso and Bekele 2008). They use their teeth to dig and their heads to push the soil (Jarvis and Sale 1971). In contrast to its phylogenetically related genus *Spalax*, members of genus *Tachyoryctes* poses functional eyes. This genus is solitary and of fossorial habit i.e. it spends some time above ground while foraging (Sillero-Zubiri 1995, Kokioso and Bekele 2008). Interestingly, in the recent study of Mason et al. (2010), a specialized middle ear structure used in the perception of seismic waves has been described. Therefore, we might expect that *Tachyoryctes* is able to perceive and use substrate born vibrations for communication.

Materials and methods

In our study we tested four males and two females of *Tachyoryctes sp.* from Tanzania (Arusha area). According to their body mass, all individuals were adult (210 ± 82g) (see Kokiso 2006 for adult body mass). All animals were kept in an animal room at the University of South Bohemia, Faculty of Science in České Budějovice, Czech Republic. Each individual was kept in a system of Plexiglas tubes (4 m long) filled with horticultural peat. The room was lit on a 12L/12D regime (lights on at 0700 h). The room temperature was kept at 25 ± 1°C. They were fed ad libitum on potatoes, carrots, lettuce, apples, and cereals.

Seismic waves were measured using a Vistec Gaia 2 with three seismometers ViGeo 4.5d1. The production of seismic waves was recorded in two experimental settings. In the first each animal was transferred to a home Plexiglas system quiet isolated room and monitored continuously for the occurrence of spontaneous seismic signals for 24 hours. Each animal was recorded for two 24-hours periods, animal ID 4 was recorded one more additional day. In the second, two mole-rat Plexiglas home systems were connected by a Plexiglas tunnel with wire mesh as a barrier. Animals were thus in direct contact, but could not injure each other. Each individual was tested with all the remaining individuals in this setting. Each session was monitored and the occurrence of seismic waves recorded. Sessions where terminated after ten minutes if the mole-rats displayed no activity. A video record using a Panasonic SDR- H69 camera was made. Records of seismic activity were processed using the Seismic Waves Interpretation Programme (SWIP) version 3.2.4. Statistical analysis was performed using STATISTICA Statsoft, Inc (2010) version 9.0. Interpulse distance, number of pulses within each bout, and distance between bouts were measured in both tests. Inter-individual differences in seismic signalling in all measured parameters were evaluated using a DFA test.

Results

In our study we found that the tested animals produced substrate born vibrations (seismic pulses) by striking their heads against the ceiling of the tunnel. The pulses were produced in bouts i.e. sets of pulses divided by pauses at least two times longer than the mean interpulse distance. We identified two types of seismic signals, slow and fast, differing mainly in interpulse distance. The slow signal has an interpulse distance (0.12 s) of twice the length of the fast signal (0.05 s). The slow signal was predominantly produced in the first experiment, when the individual was monitored alone for 24 hours (parameters of slow signals are shown in Tab. 1 and Fig.1). The slow signal was produced when the animal was disturbed or agitated (presence of the keeper, activity of other individual in the same room). Each animal produced slow signals at an average of 83.01±37.84 bouts per day (11 - 155 bouts), especially during the morning hours when they are usually fed. The bouts were produced in series containing 18 bouts on average. These series were interspersed with periods of silence of differing length (see Table 1 for details).

Tab. 1 Physical parameters of the slow and fast signal.

	Slow signal		Fast signal	
	n	mean±S.D.	n	mean±S.D.
Interpulse distance (s)	7607	0.12 ± 0.02	755	0.05 ± 0.01
Interbout distance (s)	573	3.89 ± 6.27	18	18.44 ± 23.14
Number of pulses within each bout	892	9.53 ± 4.22	35	22.54 ± 7.81
Interseries distance (s)	33	9104.13 ± 12792.89	-	-
Number of bouts within each series	34	17.79 ± 14.55	-	-

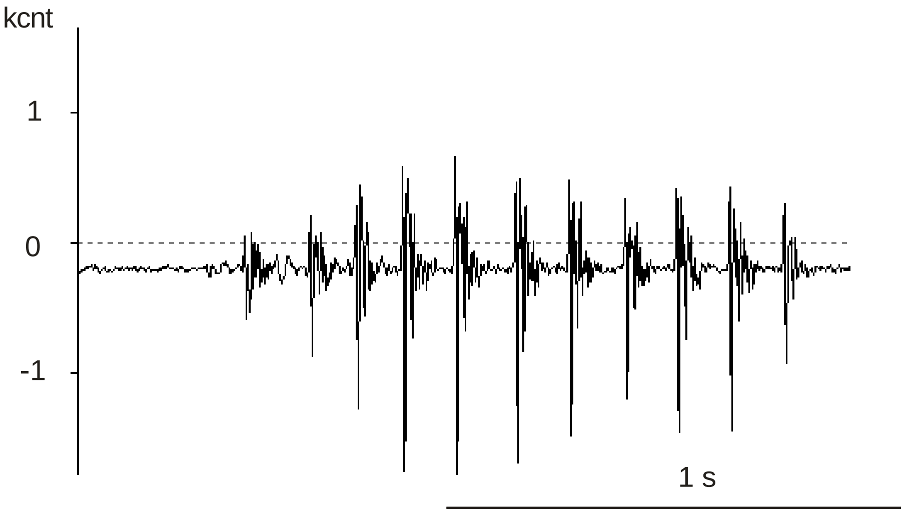

Fig. 1 Oscilogram of one slow signal bout containing 11 pulses.

The fast signal was recorded mainly in the second experiment. It has a shorter interpulse distance compared to the slow signal (Parameters of the fast signal are shown in Tab. 1 and Fig. 2.). The fast signal was recorded in the close presence of other individual. The fast signal is individually variable. Overall the DFA correctly classified 70.4% of call to the particular individual (Wilks' lambda = 0.46) (Tab. 3). Signals of the animal ID 1 were classified with 87.5% success, animal ID 2 with 57.2%, animal ID 3 66.7%. The most useful variable in differentiating individuals was interpulse distance. The fast signals were not produced in series.

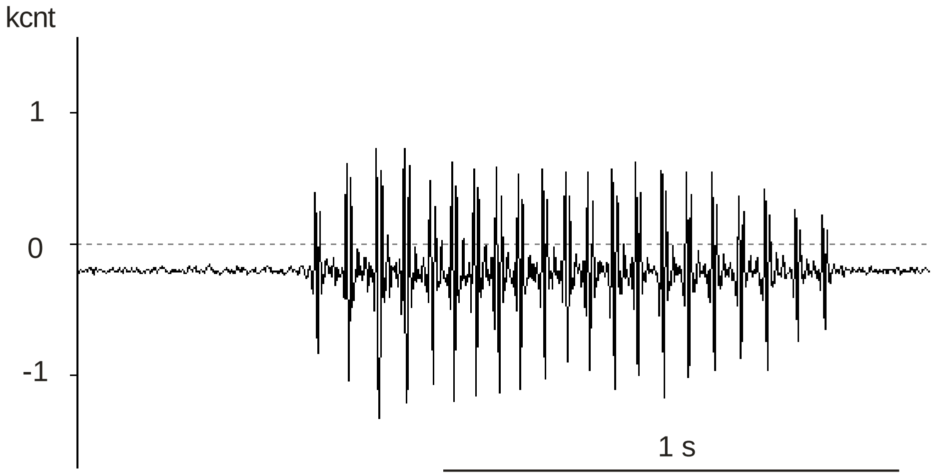

Fig.2 Oscilogram of one bout of the fast signal containing 21 pulses.

Tab. 3 The Success rates of a classification of the sounds according to DFA.

	Percent correct	1 (p=0.30)	2 (p=0.26)	3 (p=0.44)
1	87.5	7	0	1
2	57.2	0	4	3
3	66.7	2	2	8
Total	70.4	9	6	12

Discussion

Our results showed that this species is able to generate substrate born vibration. We thus assume that it is also capable of seismic communication as indicated by its middle ear morphology (Mason et al. 2010). Although J.U.M Jarvis noted that *Tachyoryctes* produces seismic signals by use of its upper incisors (Jarvis 1969 in Mason (2010)), we recorded only the thumping of its head on the burrow roof similarly as in *Spalax*. Since seismic communication has been described also for the zokor (*Eospalax fontanierii*) (Li et al. 2001), we assume that other spalacids such as *Rhizomys and Cannomys* may use seismic signals for communication, or at least they should be able to perceive them, because all those species are closely related.

Substrates borne vibrations are used by solitary subterranean and fossorial species mainly in the territorial and mating contexts (review in Randall 2001). The advantage of seismic signals is in communication over long distances (Hill 2008). In our study we recorded two types of seismic signals; however more experiments need to be done to recognize its specific functions. Seismic signalling during courtship is common in solitary living rodents; seismic communication is used to minimize agonistic behaviour between potential sexual partners in e.g. *Spalax, Rhombomys, Dipodomys* (Butterworth et al. 1961, Rado et al. 1987, Heth et al. 1991, 1994, Randall et al. 2000).

In our study, the slow signal was produced mainly in situations where the animal was disturbed. We suppose it may serve as a warning either for the conspecific to minimize direct conflict between neighbours (Randall et al. 1984, 1989, 1994, 1997) or as a signal towards a predator. Seismic signals as a communication signal towards a predator, especially snakes, were found in a variety of mammals (review in Randall 2001 and Hill 2008).

Randall (2001) proposes that ritualized seismic communication in kangaroo rats has evolved from the intention movement of fleeing. In *Tachoryctes* and spalacids it probably has evolved from the pushing of the soil with the head during the disposal of excavated soil. In contrast to the substrate born vibration produced during the simple sealing of the tunnel, the seismic signal in *Tachyoryctes* has a more periodic structure, the interpulse distance and number of pulses within each bout is constant (our unpubl. results).

The fast signal was produced mainly in close contact with other conspecifics. Our results suggest that fast seismic signals are individually specific, so they are thus suitable for territorial signals and spacing behaviour. Many solitary fossorial and subterranean rodents use substrate borne vibrations as territorial signals. Seismic signals in the subterranean environment spread better than vocalisations (Narins et al. 1992, 1997) and are often used as a signature (Randall et al. 1984, 1989, 1994, and 1997).

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