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Bachelor thesis

Vocalization and sociality of Mashona mole-rat

(*Fukomys darlingi*)

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Annotation:

Vocal repertoire of adult Mashona mole-rat (*Fukomys darlingi*) was described and compared to other subterranean rodents in dependence on social system. Twelve call types have been identified, among them one mechanical sound. Mashona mole-rats vocalize in low frequencies (3,55 kHz) as is usual in subterranean rodents. Mashona mole-rat possess three contact, three aggressive, three distress and two mating calls. This structure of vocal repertoire corresponds to the structure of the vocal repertoire of the Ansell`s mole-rat. Preliminary screening for the individually distinct call type has been performed

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V Českých Budějovicích dne 30. 4. 2010

Veronika Dvořáková

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My thanks belongs to my supervisor Mgr. Ema Knotková for great help and patience while working on this project.

Content:

1. Introduction

1.1. Subterranean rodents

Subterranean rodents are animals living in undeground systems of burrows. They occur all over the world except of Australia and Antarctica. We can distinguish two types of rodents living in underground burrows according to the time they spend aboveground. Strictly subterranean, who mate, breed and forage uderground and come rarely on surface, their burrow entrances are sealed with soil. These are all African mole-rats and blind mole rats (Jarvis and Bennett 1991, Nevo 1999, Šumbera *et al*. 2008). The second type are fossorial rodents (Burda 2003) who also live in underground burrows but they forage aboveground, e.g. *Ctenomys, Arvicola, Spalacopus.* This difference in time spended aboveground influences also an amount of adaptations to subterranean ecotope. Strictly subterranean mammals have number of sensory adaptations; in contrast, fossorial species use to have unmodified sensory system (Begall *et al.* 2007).

1.2. Nonvocal communication

Underground ecotope has a lot of limitations and those affect sensory capabilities and thus communication of subterranean rodents. Because of those special features, some types of communication may be favoured and others restricted.

Chemical communication is transmitted by pheromones – a semiochemicals that acts between individuals of the same species (Dusenbery 1992). Pheromones are presented in urine, feces, vaginal secretions (Bradbury and Vehrencamp 1998), and also in secretions of special glands as in case of harderian gland secretions in blind mole-rat (*Spalax ehrenbergi,* Spalacidae) which serves to inhibit aggression (Shanas and Terkel 1997). The advantage of chemical communications is that scents deposited on the substrate can remain active for relatively long periods (Bradbury and Vehrencamp 1998). Chemical communication in subterranean and fossorial rodents could serve to obtain different information about conspecifics (Menzies *et al*. 1992, Zenuto *et al.* 2004), or to avoid potential predator (Heth and Todrank 1995).

Tactile signals are received by deforming mechanoreceptors wich are distributed all over the body (Dusenbery 1992). Tactile sense is well developed in subterranean rodents and it partly serves as a compensation for vision which is unreliable in dark tunnels (Burda *et al*. 1990, c.f. Park *et al*. 2007).

Visual communication is one of the major communications among mammals. Because of the constant darkness in underground burrows, this statement do not apply for strictly subterranean species and they possess reduced and degenerated eyes (Burda *et al.*1990, Cernuda-Cernuda *et al.* 2003, Němec *et al.* 2004, 2008, Hetling *et al*. 2005). Although they all live underground, visual capabilities differ among strictly subterranean, who are able to distinguish between light and darkness (Burda *et al*. 1990, Hetling *et al*. 2005, Němec *et al.* 2008) and fossorial rodents, who possess better visual capabilites (Peichl *et al*. 2005, Williams *et al*. 2005).

1.3. Acoustic and seismic communication

There are no air currents in underground burrows and so the transport of scent signals is poor. Besides the subterranean ecotope is dark, which means that visual sense is unreliable. Under such conditions, only vibrational communication is effective for middle and long distances. Two types of signals are considered as vibrational, the air-borne acoustic signal and the substratum-born seismic signal (Bradbury and Vehrencamp 1998).

Acoustic communication is propagated along the burrows and disperse to middle distances (Heth *et al*. 1986, Lange *et al*. 2007). It can be use to various purposes such as kin or individual recognition, to distinguish reproductive or dominance status, to synchronize members of colony, to sexually stimulate the mate or to warn against the danger (Schleich *et al*. 2007, Yosida *et al*. 2007, Yosida and Okanoya 2009). Different motivations encoded in vocalization are reflected by different physical structures of the sound (Morton 1977). For example harsh, relatively low-frequency sounds are used during hostile encounters, while higher-frequency, tonelike sounds are used in friendly contexts.

Vocalization of subterranean rodents is influenced by the acoustic capabilities of burrows and hearing sensitivity, which is dependent on morphological adaptations of ear. (Burda *et al*. 1990, Burda *et al*. 1992, Mason 2004, Begall and Burda 2006, Begall *et al.* 2007). Studies on acoustics in burrows showed, that low-frequency sounds around 400 Hz are propagated best, that means less attenuated than sounds of lower and higher frequencies (Heth *et al.* 1986). More, the so-called "stethoscope effect" occur in underground burrows, which means that certain sound frequencies (200, 400 and 800 Hz) are amplified at a distance of 1 m (Lange *et al*. 2007). Hearing abilities of subterranean mammals are probably a combination of both degeneration due to lack of stimulation (Heffner and Heffner 1990, 1993) and adaptation to amplified sound in attempt to avoid over-stimulation of the ear (Begall *et al.* 2007, Lange *et al.* 2007). The highest hearing sensitivity of subterranean rodents is in lower frequency range (Heffner and Heffner 1990, 1993, Brückmann and Burda 1997, Begall *et. al.* 2004) than the best hearing sensitivity in similarly sized surface-dwelling rodents (Heffner and Heffner 1985, Heffner *et al.* 1994). Also vocalization shows tunning to lower frequencies (Heth et al. 1988, Pepper *et al.* 1991, Credner *et al.*1997, Veitl *et al.* 2000, Schleich and Busch 2002).

Unlike the accustic communication, seismic signals disperse through substrate to a long distances. (Narins *et al.* 1992). Generating seismic signals vary among species. The blind mole-rat (*Spalax ehrenbergi*) taps its head on the roof of the tunel (Heth 1987, Rado *et al.* 1998). The cape mole-rat (*Georychus capensis,* Bathyergidae) drumming its hind legs on the burrow floor (Narins *et al.* 1992). The giant mole-rat *(Fukomys mechowii,* Bathyergidae) beats with its chest (Bednářová 2008). There are suggested two possible ways how can mole-rats detect seismic signals: by somatosensory reception (Nevo *et al.* 1991) or through the bone conduction system by placing the cheek and lower jaw against the wall of the tube (Rado *et al.* 1998, Mason *et al.* 2010).

Species which use only acoustic communication and species which use combination of acoustic and seismic communication has been described, but the full explanation of the distribution of those two types has not been performed yet.

1.4. Vocalization and sociality

Family Bathyergidae includes species whith both social systems. Some genera are solitary (*Bathyergus, Georhychus, Heliophobius*) and other are social or eusocial (*Heterocephalus, Cryptomys, Fukomys*) (McKenna and Bell 1997). Therefore, they are ideal model for studying of relationships between sociality and vocal repertoire richness and composition. The relationship between amount of vocal signals and sociality was assumed and described in different species (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 degree of social bonding in non-human primates. Not just vocal repertoire size, but also complexity of calls could correlate possitively with group size as in case of Carolina chickadees (Freeberg 2006). Also vocal repertoire composition could be influenced by social system (Bednářová 2008, Knotková *et al.* 2009, Le Roux *et al.* 2009), since social and solitary species use vocalization in different behavioral contexts.

As subterranean rodents differ in a way of life, they also differ in variety and number of calls they use. Normally, social species possess richer vocal repertoire than solitary species. The social species of subterranean rodent with the richest vocal repertoire is *F. mechowii* with total amount of 18 calls (Bednářová 2008), but other social species possess similar amount of sounds. *H. glaber* with the size of the colonies up to 300 individuals (Heffner and Heffner 1993) emit 17 different calls (Pepper *et al*. 1991), *F. anselli* emit 14 different calls (Credner *et al*. 1997) and other studied social rodent from Chile *Spalacopus cyanus* (Octodontidae) possess 12 acoustics calls (Veitl *et al*. 2000). Contrary, solitary species emit fewer amount of sounds. For silvery mole-rat (*Heliophobius argenteocinereus)* eight different acoustics calls has been described (Knotková *et al*. 2009). Solitary species from South America emit three calls in the case of *Ctenomys pearsoni* (Ctenomyidae) (Francescoli 1999) and five calls in the case of *C. talarum* (Schleich and Busch 2002). North American subterranean rodent *Geomys breviceps* has been described to possess four different acoustic calls (Devries and Sikes 2008).

1.5. Individual recognition

Social mole-rats are colony living animals with society divided according to dominance rank. Therefore, it is important to recognize intruders from colony members in attempt to decrease social parasitism and theft of brood or food (Yosida *et al*. 2007). Since they live in hierarchical society it is crucial to distinguish the social status of others (Yosida *et al*. 2007, Yosida and Okanoya 2009). It was described that individuals of naked mole-rats answer more frequently to the call of bigger colony member, and since they are organized hierarchically according to body size, it is suggested as a proof of distinguishing the dominance rank by using vocal signals (Yosida *et al*. 2007). Vocal individual recognition occurs in many social living species, mostly in primates (Rendall *et al*. 1996, Miller *et al.* 2001), but in other social mammals as well (Sayigh *et al*. 1999, Charrier *et al*. 2002, Muller and Manser 2008).

The vocal individual recognition is possible thanks to the timbre. The sound is produced by vocal cords and before it clangs, it has to go through several body cavities such as larynx, oral cavity or nasal cavity. Resonance in these cavities causes, that certain frequencies are absorbed and others are reinforced and so the distortion of original sound come up. As the body cavities differ among individuals, the timbre differs too (Bradbury and Vehrencamp 1998).

Vocalization used for individual recognition should be some frequent call with antiphonal nature (Yosida *et al*. 2007), it has to show a strong individual stereotypy, such as weak intra-individual and high inter-individual variability (Trillmich 1981, Charrier *et al*. 2002, Yosida *et al*. 2007). To identify the acoustic parameters of call, that may encode individual identity, is determined the potential of individual coding (PIC) as the ratio of intra-individuals and inter-individuals variability (Robisson *et al*. 1993).

1.6. Mashona mole-rat

The Mashona mole-rat (*Fukomys darlingi*), formely known as *Cryptomys darlingi* (Kock *et al*. 2006.) is herbivorous, socially living subterranean rodent from family Bathyergidae (Rodentia). The Mashona mole-rat occurs in Zimbabwe, Mozambique and southern Malawi in small familial colonies of between five and nine animals (Bennett *et al*. 1994, Gebathuler *et al.* 1996, Benntett and Faulkes 2000)

2. The aim of this paper

1. To record and describe vocalization of social African mole-rat *Fukomys darlingi.*
2. To compare richness and composition of vocal repertoire of social and solitary subterranean rodent species.
3. To find a type of call appropriate for individual recognition.

3. Materials and methods

3.1. Studied animals

Vocalizations were recorded in adult social Mashona mole-rat (*F. darlingi*). Studied animals were kept in breeding stock at the Faculty of Science in České Budějovice, Czech Republic. Six of Mashona mole-rats were trapped in Nsanje, southern Malawi, the rest of animals was born in captivity. Families or pairs were kept in open glass-boxes littered with horticultural peat and supplemented with plastic tubes as imitation of tunnels and flowerpots to simulate the nest. The room was lighted 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. In total, vocalization from 20 animals was taken, 10 males and 10 females.

3.2. Data collecting

Vocalization was recorded in four experimental setings. 1. Home terrariums (Fig. 1) - colony of the mole-rats were recorded in their home terrarium without any manipulation. Usually contact calls have been recorded by the method of *ad libitum* sampling. 2. Perspex tunnels with two home boxes filled with horticultural peat to stimulate natural burrows (Fig. 2) - for purpose of recording part of the tunnels has been opened, mainly contact calls have been recorded. 3. Opened plastic boxes littered with horticultural peat – opened boxes were used to eneable quick dividing of unfamiliar animals during experiments. Animal has been put into the terrarium and let to explore, after ten minutes when it rested on one place the other animal has been added. Mating calls were recorded while making new pairs; aggressive and distress calls were recorded during same sex encounters. 4. Perspex tunnel 168cm in length, in the middle divided by perforated partition and supplemented with strap-on dividers on each side (Fig. 3) - animals have been put into the opposite home boxes and let to explore, when they calmed down (rested on one place), the strap-on dividers were opened and animals were allowed to reach the middle perforated partition. It was used for recording aggressive and distress calls (unfamiliar individuals) or contact calls (familiar individuals)

Figure 1.: Home terrarium

Figure 2.: Perspex tunnel simulating natural burrows

Figure 3.: Perspex tunnel, in the middle divided by perforated partition

The sampling sessions took place in different times of the day to enhance possibility of recording all types of calls. The microphone was held in a distance of 15-20 cm, it was far enough to ensure that animals were not disturbed. Duration of 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) has been used.

All vocalization has been divided into five groups, based on the 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 are mechanical sounds, which contains all sounds produced by any means except vocal cords.

1. Contact calls are used to coordinate 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 group members reassemble in a common location.

2. Aggressive and territorial calls 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 occur also 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 dominant animal.

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

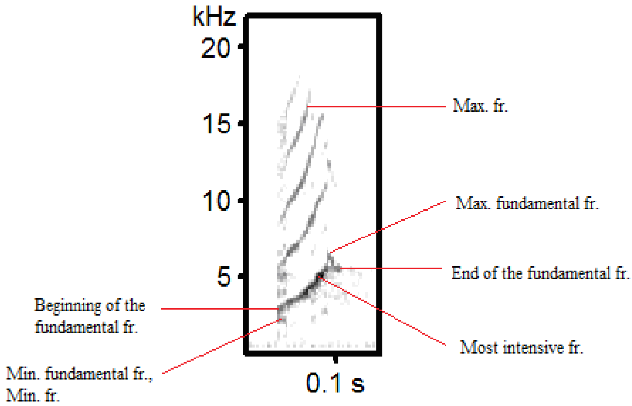
4. Mating calls provide information on location and availability that allows members of the two sexes to find and approach each other and determine whether subsequent mating will occur and effects its coordination.

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

The records were taken with dynamic microphone MD 735 Senheiser (frequency range 50-18.000 Hz) and recorded with 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 dynamic microphone MD 431 II Senheiser (frequency range 40-16.000 Hz) and recorded with Marantz card audiorecorder PMD660 (sample frequency 44,1 kHz, resolution 16 bit). During recordings, animals were also filmed on camera (Canon DVD camcorder PAL DC 40).

3.3. Data analysing

Recordings were transferred to the computer and evaluated in Avisoft-SAS Lab Pro Software, version 5.0.01 (2010) programme, where the sampling rate was changed from 44.1 to 22.05 kHz. Following spectrogram parameters were used: Hamming Window, Fast-Fourier-Transformation (FFT) of 256 points, frame size 100% and overlap 50%. We measured 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 (Fig. 5). 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.



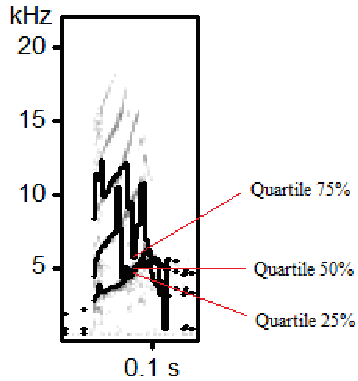


Figure 4.: Measuring variables

Figure 5.: Measuring quartiles

Separate analysis was computed in the STATISTICA StatSoft, Inc. (2010), version 9.0 programme. 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 was proportional to group size. The results were visualized using Principal Component Analysis (PCA) based on correlation matrix.

4. Results

In total 932 sounds of the true vocalization and 80 mechanical sounds have been evaluated. Calls were divided into four groups according to behavioural context: contact, distress, aggressive and mating calls. The separate category is created by teeth grinding, which is the only mechanical sound.

4.1. Mechanical sounds

Teeth grinding

Table 1.: Characteristic physical features of teeth grinding in adult Mashona mole-rat.

Name of sound	N	Frequency range (kHz)	Fundamental frequency (kHz)	Main frequency (kHz) mean ± SD	Duration of sound (s) mean ± SD
Teeth grinding	80	0,43 – 13,98	0,44 – 2.62	1,34 ± 1,17	0,03 ± 0,02

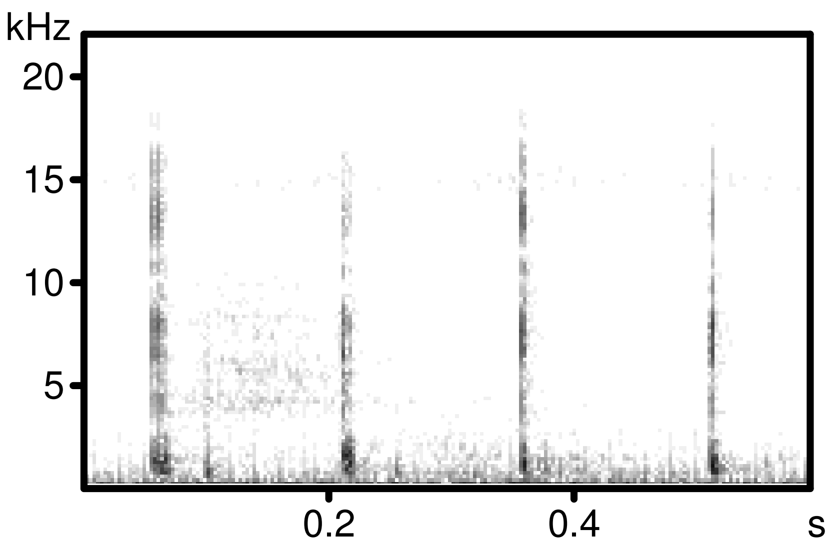


Figure 6.: Spectrograph of the teeth grinding sound.

Teeth grinding does not belong to the true vocalization because this sound is not produced by vocal cords. This mechanical sound is produced by rubbing the upper and lower incisors together. Teeth grinding has broad frequency range 0,43 – 13,98 kHz and it is usually produced when the animals relax, but could be also produced during aggressive encounters.

4.2. True vocalization

Contact calls

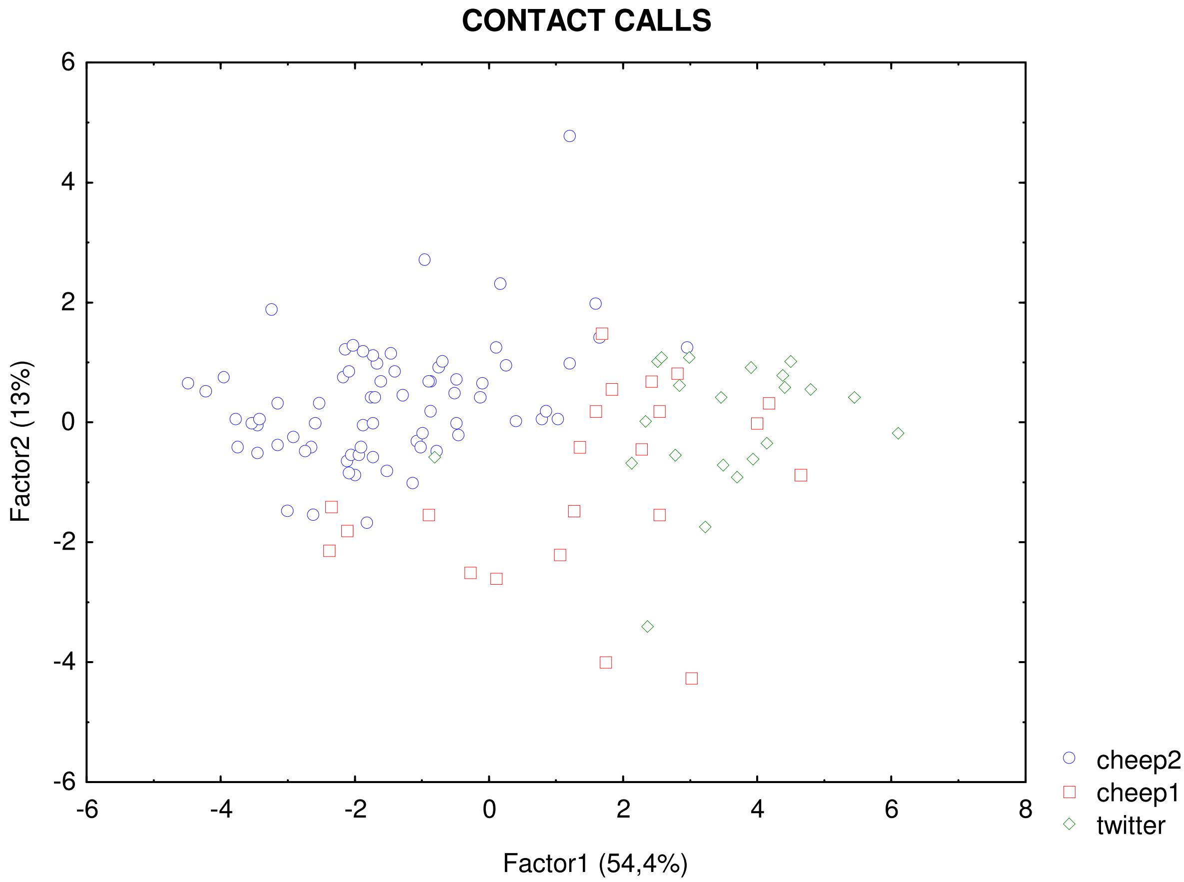


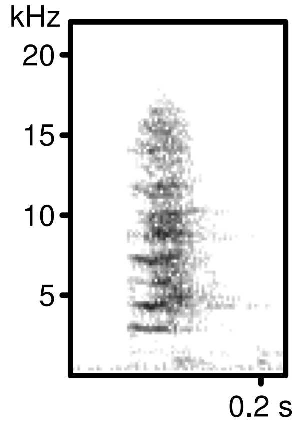
Figure 7.: Separation of contact calls showed by plot of two factors gained in PCA. (N=116)

Table 2.: The Discriminant Functional Analysis (DFA) showing percentage success of separation of contact calls.

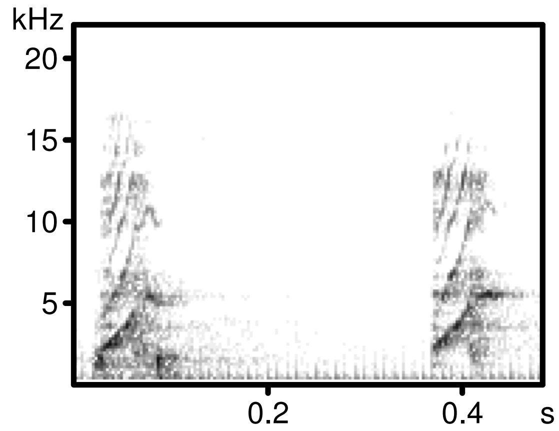
Sound	Percent correct
cheep2	98,61
cheep1	81,82
twitter	81,82
Total	**92,24**

Table 3.: Characteristic physical features of contact calls in adult Mashona mole-rat.

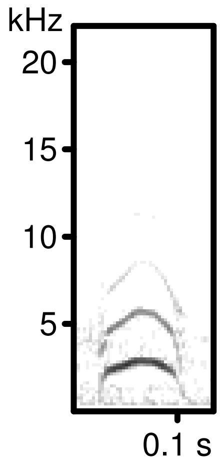
Name of sound	N	Frequency range (kHz)	Fundamental frequency (kHz)	Main frequency (kHz) mean ± SD	Duration of sound (s) mean ± SD
cheep2	72	2,59 – 14,48	3,50 – 5,09	6,43 ± 2,93	0,05 ± 0,01
cheep1	22	1,82 – 13,72	1,91 – 4,69	4,20 ± 2,71	0,07 ± 0,01
twitter	22	1,52 – 7,26	1,53 – 3,65	3,55 ± 2,06	0,06 ± 0,02



a)



b)



c)

Figure 8.: Spectrograph of the sounds: a) cheep2, b) cheep1, c) twitter.

Cheep2

Cheep2 is the only atonal contact call. This sound has broad frequency range 2,59 – 14,48 kHz and relatively high main frequency 6,43 kHz ± 2,93. Cheep2 was produced by female in nest or plastic tube when male came to her. It was also recorded when two familiar animals were placed into the perspex tunnel divided in the middle by perforated partition. The subordinate animal vocalized to alpha member of his family.

Cheep1

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

Twitter

The last type of contact calls is twitter, this sound has markedly lower frequency range than remaining two sounds 1,52 – 7,26 kHz, while cheep2 and cheep1 reach near to 14 kHz. This sound was recorded in a family kept in the perspex system. The sound was produced when animals passed each other in a tunnel.

Aggressive and distress calls

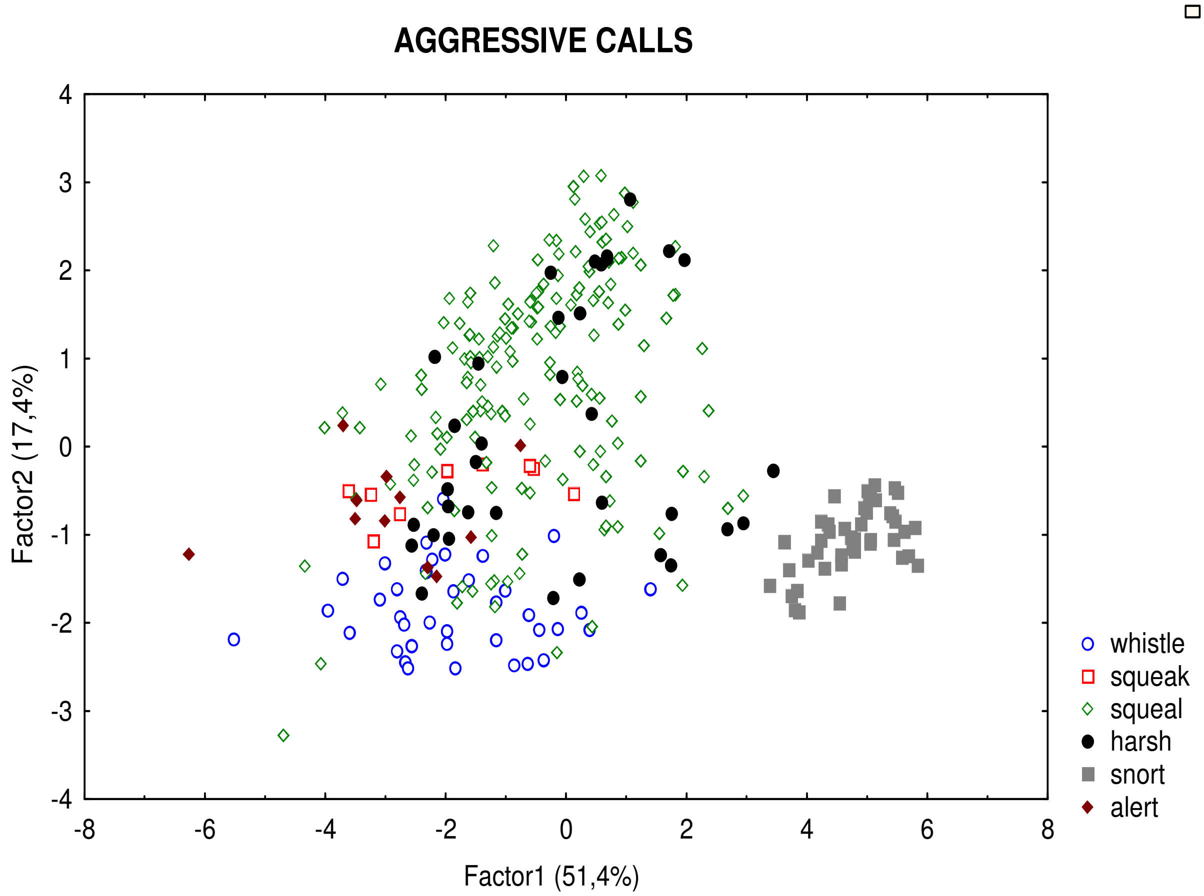


Figure 9.: Separation of aggressive calls showed by plot of two factors gained in PCA. (N=306)

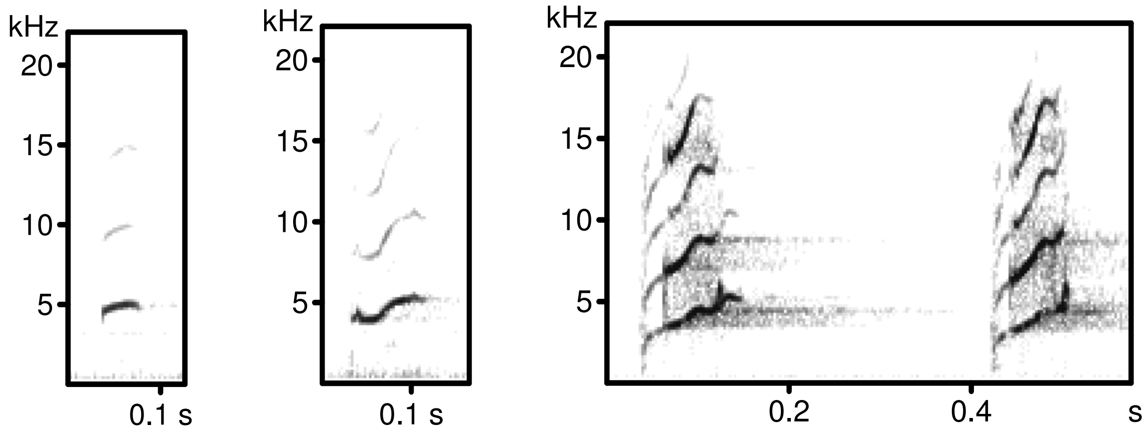
Table 4.: The Discriminant Functional Analysis (DFA) showing percentage success of

separation of aggressive calls.

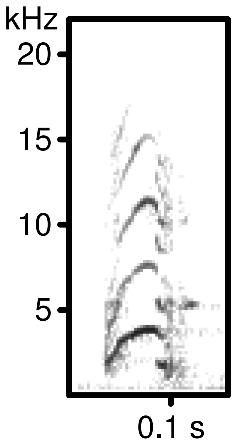
Sound	Percent correct
whistle	87,18
squeak	33,33
squeal	80,02
harsh	31,43
snort	100,00
alert	63,64
Total	**80,72**

Table 5.: Characteristic physical features of aggressive calls in adult Mashona mole-rat.

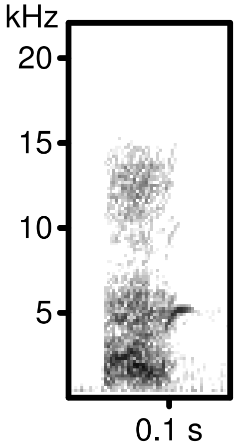
Name of sound	N	Frequency range (kHz)	Fundamental frequency (kHz)	Main frequency (kHz) mean ± SD	Duration of sound (s) mean ± SD
whistle	39	3,50 – 10,41	3,60 – 4,81	4,58 ± 1,46	0,04 ± 0,01
squeak	9	3,28 – 11,00	3,29 – 5,68	4,57 ± 0,81	0,06 ± 0,01
squeal	167	1,96 – 12,45	2,03 – 5,33	3,80 ± 1,57	0,07 ± 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
alert	11	2,85 – 16,06	3,73 – 5,48	5,21 ± 1,76	0,07 ± 0,02



a) b) c)



d)



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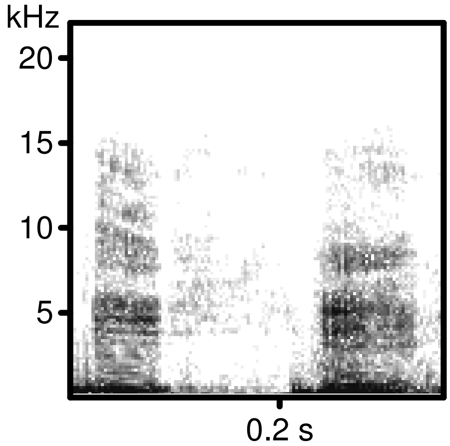

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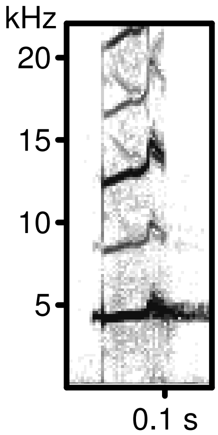


g)

Figure 10.: Spectrograph of sounds: a) whistle, b) squeak, c, d) squeal, e) harsh, f) snort, g) alert.

Whistle

Whistle is the shortest sound of all aggressive calls 0,04 ± 0,01 kHz. This tonal sound has the most intensive frequency around 4,58 kHz. This sound was recorded when two unfamiliar animals were placed into the perspex tunnel divided in the middle by perforated partition and was emitted probably by dominant animal.

Squeak

Squeak is tonal sound similar to whistle, but possess quite longer duration 0,06 ± 0,01 kHz and also differ in inclination of the curve when maximal fundamental frequency reach quite higher around 5,68 kHz, than in case of whistle. This sound was also probably emitted by dominant animal.

Squeal

Squeal is often produced sound during aggressive encounters. This sound has together with harsh quite low minimal frequency. The frequency range of squeal 1,96 – 12,45 kHz is higher than the frequency range of remaining aggressive calls except alert. 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 subordinate animal.

Harsh

Harsh is atonal sound with low minimal frequency around 1,51 kHz. This is probably distress call emitted by subordinate animal.

Snort

Snort is atonal sound with fundamental frequency orientated very low 0,14 – 0,94 kHz. This sound also has noticeably lower frequency range 0,14 – 6,57 kHz than other aggressive calls and main frequency is very low too 0,48 ± 0,18 kHz. This sound is produced by an acute exhalation. Animals produced this sound while being handled. In this situation animals used to be nettled and try to attack anything nearby (e.g. approaching hand).

Alert

Alert is very loud and high tonal sound with frequency range 2,85 – 16,06 kHz. The main frequency of alert is located much higher 5,21 ± 1,76 kHz than in case of other aggressive calls. The alert is produced by animals as a reaction to pain or when one animal restricts the movement of the other.

Mating calls

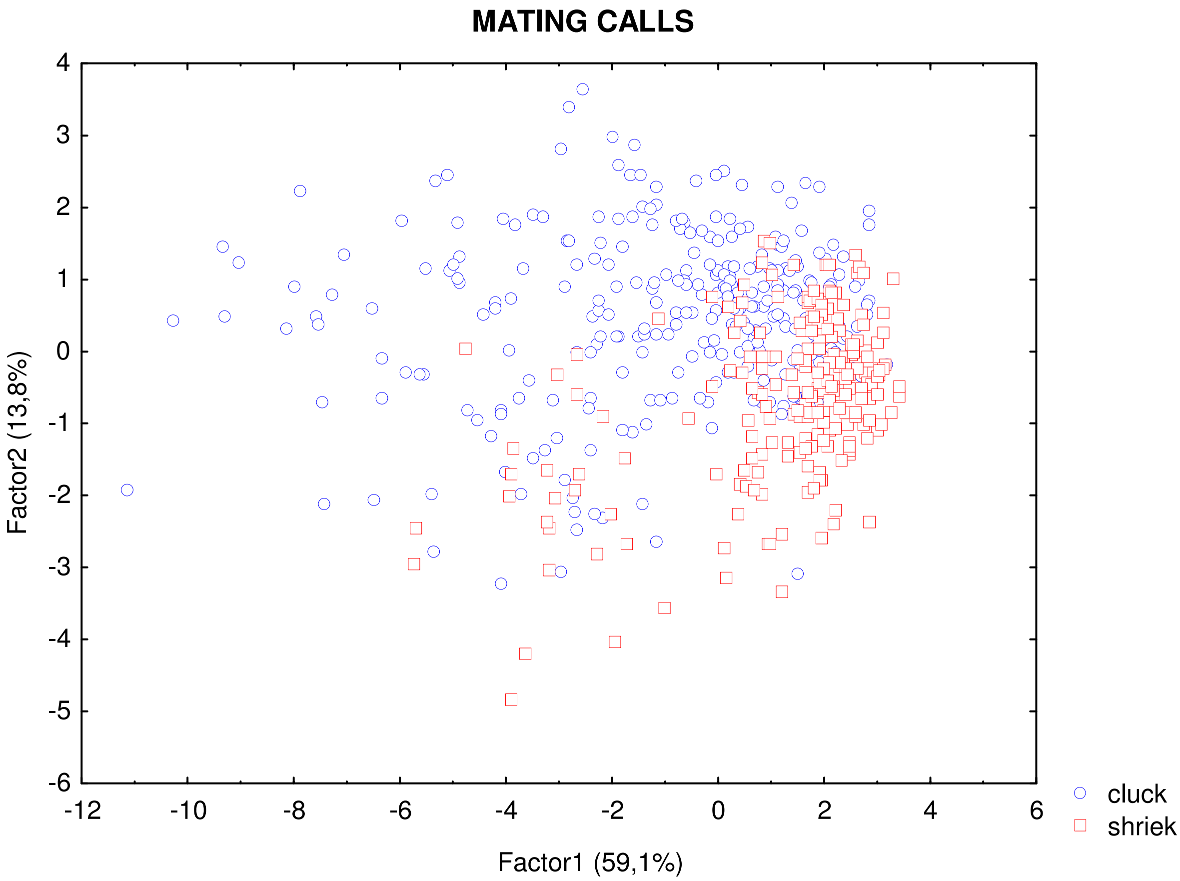


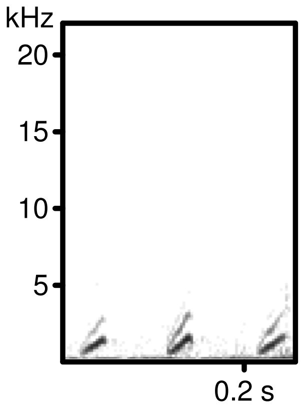
Figure 11.: Separation of mating calls showed by plot of two factors gained in PCA. (N=510)

Table 6.: The Discriminant Functional Analysis (DFA) showing percentage success of separation of mating calls.

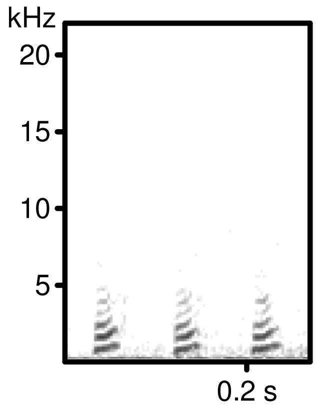
Sound	Percent correct
cluck	82,47
shriek	84,47
Total	**83,33**

Table 7.: Characteristic physical features of aggressive calls in adult Mashona mole-rat.

Name of sound	N	Frequency range (kHz)	Fundamental frequency (kHz)	Main frequency (kHz) mean ± SD	Duration of sound (s) mean ± SD
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



a)



b)

Figure 12.: Spectrograph of the sounds: a) cluck, b) shriek

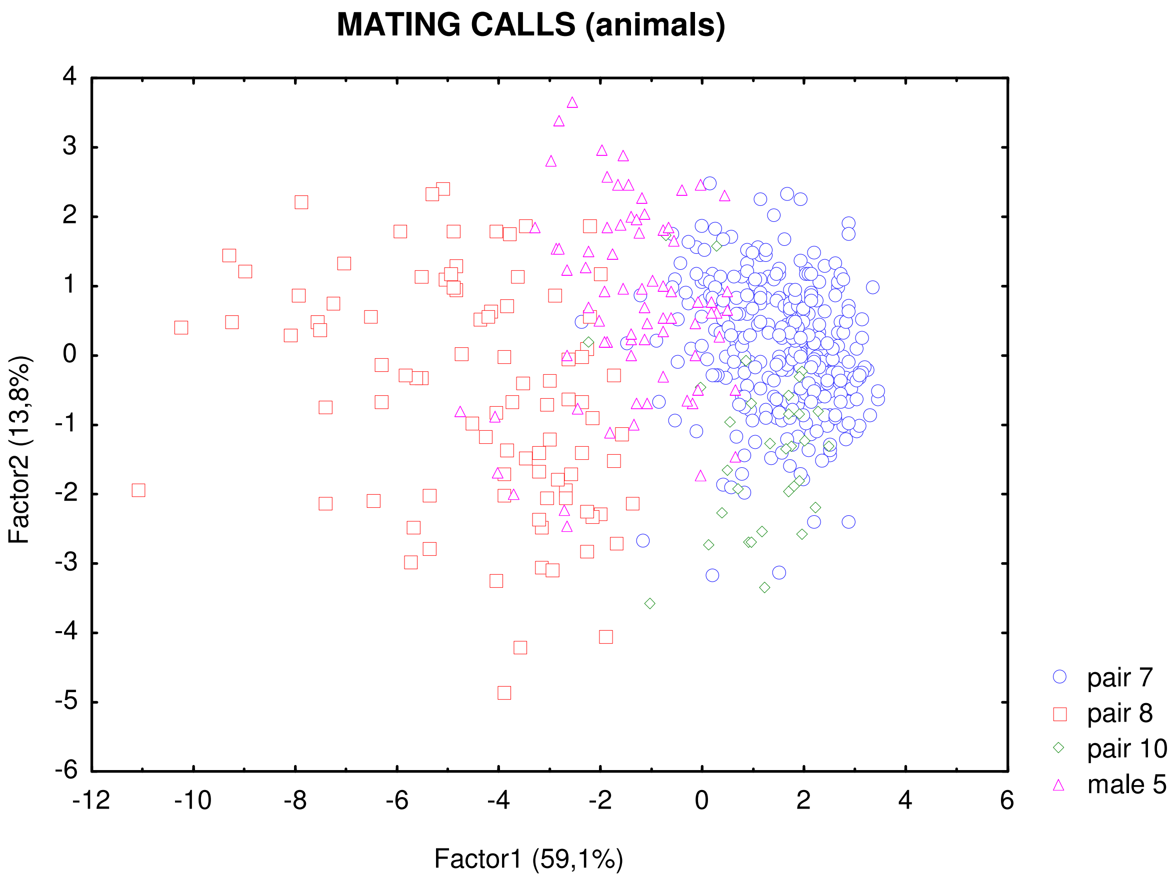


Figure 13.: Separation of mating calls by single pairs showed by plot of two factors gained in PCA. (N=510)

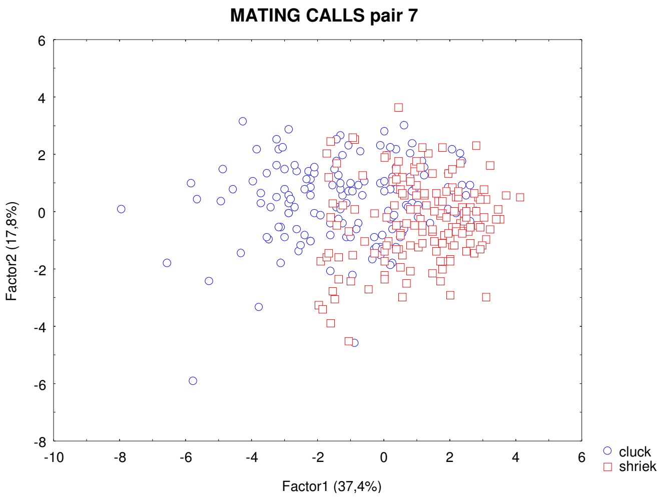


Figure 14.: Separation of mating calls in a case of pair 7, showed by plot of two factors gained in PCA. (N=311)

Table 8.: The Discriminant Functional Analysis (DFA) showing percentage success of separation of mating calls in a case of pair 7.

Sound	Percent correct
cluck	80,92
shriek	87,97
Total	**84,52**

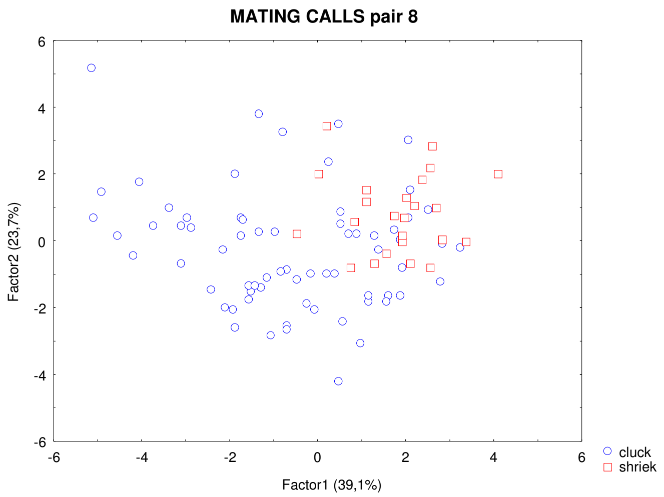


Figure 15.: Separation of mating calls in a case of pair 8, showed by plot of two factors gained in PCA. (N=92)

Table 9.: The Discriminant Functional Analysis (DFA) showing percentage success of separation of mating calls in a case of pair 8.

Sound	**Percent correct**
cluck	88,24
shriek	58,33
Total	**80,43**

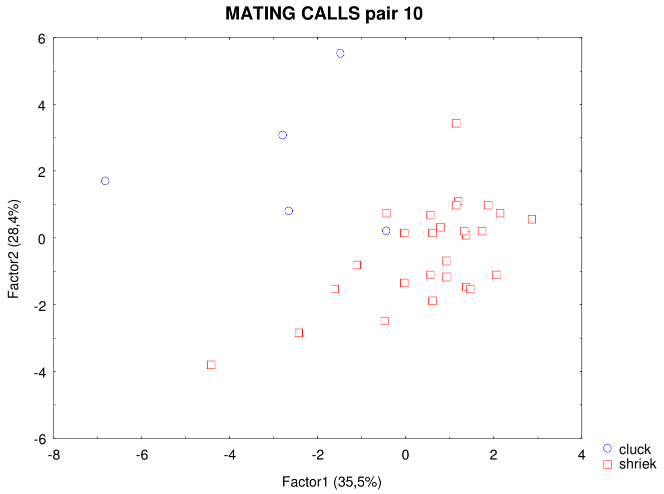


Figure 16.: Separation of mating calls in a case of pair 10, showed by plot of two factors gained in PCA. (N=32)

Table 10.: The Discriminant Functional Analysis (DFA) showing percentage success of separation of mating calls in a case of pair 10.

Sound	**Percent correct**
cluck	80,00
shriek	100,00
Total	**96,88**

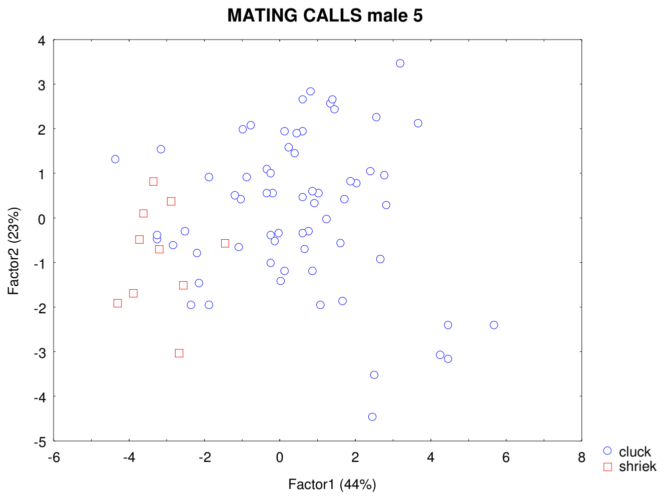


Figure 17.: Separation of mating calls in a case of male 5, showed by plot of two factors gained in PCA. (N=75)

Table 11.: The Discriminant Functional Analysis (DFA) showing percentage success of separation of mating calls in a case of male 5.

Sound	Percent correct
cluck	95,38
shriek	80,00
Total	**93,33**

Classification of mating call types was easier for each animal separately, because variability of the whole data set could be better explained by the individuality of the animal (90,18%) than call type (83,3%) (also see Fig. 14,15,16,17). This finding suggests that mating calls might be used for individual recognition.

Cluck

Cluck is very short vocalization, with the mean duration of 0,03s. 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 rituals, when animals were sniffing each other anogenital area. Cluck was also produced by one male during aggressive encounter with unfamiliar male (Fig. 17).

Shriek

Shriek is sound similar to cluck. There exist many interstages between shriek and cluck. Shriek has main frequency placed lower than cluck and is not raising in frequency towards the end.

5. Discussion

Vocalization appears to play an important role in communication of subterranean rodents. The Mashona mole-rat (*F. darlingi*) possess 12 different types of acoustic communication, 11 sounds of true vocalization and one mechanically produced sound. This amount of calls corresponds to acoustic repertoire of other social subterranean rodents. *F. anselli* possess amount of 14 different calls (Credner *et al*. 1997) and *S. cyanus* emit 12 acoustics calls (Veitl *et al*. 2000). The remaining two social species, which vocalization has been studied, possess larger amount of sound, eusocial *H. glaber* emit 17 different calls (Pepper *et al*. 1991), and the largest vocal repertoire had been described in *F. mechowii* with total amount of 18 calls (Bednářová 2008).

Teeth grinding is a mechanical sound described in all studied subterranean rodents and even in all rodents. This sound is not a true vocalization but it could have communicative purpose (Schleich and Busch 2002). Teeth grinding is characterized by a broad frequency range 0,43 – 13,98 kHz. Mashona mole-rat emitted this sound when relaxed and also during aggressive encounters. The similar behavioral context was observed in *F. mechowii* (Bednářová 2008) and *F. anselli* (Credner *et al*. 1997). In a case of *C. talarum* or *H. argenteocinereus* this sound was accompanied by fighting behaviour (Schleich and Busch 2002, Knotková *et al.* 2009).

Vocalizations of subterranean rodents differ in behavioral contexts. Normally, sounds are divided into five groups according to behavioral context (see Materials and Methods).

Contact calls are non-aggressive signals used during encounters between familiar animals and may serve to identificate animals, to greet or to coordinate activities of the group (Bradbury and Vehrencamp 1998). *F. darlingi* emits three diffrent types of contact calls, two tonal and one atonal sound with broad frequency range 1,52 - 14,48 kHz, when only twitter possess markedly lower maximal frequency 7,26 kHz. *F. anselli* (Credner *et al*. 1997) and *H. glaber* (Pepper *et al*. 1991) possess two types of conatct calls each; this amount is similar as in case of *F. darlingi*. Remaining studied social subterranean rodents exhibit larger quantity of contact calls, *S. cyanus* emits four types of contact vocalization (Veitl *et al*. 2000), and *F. mechowii* possess five different types of contact calls, which is the most of all subterranean rodents (Bednářová 2008). *S. cyanus* and *F. mechowii* contact calls represent the richest group of the true vocalization.

Mating calls are a type of vocalization emitted during courtship and mating interactions (Bradbury and Vehrencamp 1998). Some type of mating call has been described in every studied species of subterranean rodents. *F. darlingi* emit two types of mating calls.

Cluck and shriek were both recorded in initiative and advanced phases of soliciting and they loosely turn one to another. The same situation occur in *F. anselli* and also in *F. mechowii,* when clucks are produced by a male in initial phases of soliciting and shrieks emitts female during advanced soliciting (Credner *et al*. 1997, Bednářová 2008). *F. anselli* and *F. mechowii* both possess also the third type of vocalization conected with courtship and mating. This sound is called "cry" and it accompany copulation (Credner *et al*. 1997, Bednářová 2008), unlike these two species *F. darlingi* does not emit any vocalization during copulation. Only one type of mating vocalization has been described in *H. glaber*, the "V-trill"was produced by breeding females while soliciting copulation (Pepper *et al*. 1991). Mating calls were usually produced by *F. darlingi* in context of initiative mating but this sound was also recorded in a different context. One male produced both type of mating calls during aggresive encounters with male from other family. This male used clucks and shrieks probably as a demonstration of dominance over other male. The mating calls in *F. darlingi* are easily recognizable since this type of vocalization possesses narrower range and thus lower maximal frequency than any other type of Mashona mole-rats calls.

Aggressive calls accompanied aggressive encounters between unfamiliar and also familiar animals and are emitted by dominant animal. This type of vocalization is emitted by animal to show ownership of territory, mate or commodity (Bradbury and Vehrencamp 1998). All studied subterranean rodents had been described to possess aggressive calls (Pepper *et al*. 1991, Credner *et al*. 1997, Francescoli 1999, Veitl *et al*. 2000, Schleich and Busch 2002, Bednářová 2008, Devries and Sikes 2008, Knotková *et al*. 2009). Aggressive calls of *F. darlingi* are whistle and squeak. Both are emitted by dominant animal when encountered unfamiliar animal. Main frequency of these sound is quite high around 4,58 kHz, but squek possess markedly longer duration than whistle. One more aggressive call has been observed in *F. darlingi,* 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 2008), and "grunt" sound in *H. glaber* (Pepper *et al*. 1991) and *H. argenteocinereus* (Knotková *et al*. 2009) was accompanied by the same behavior. The richest amount of aggressive sound has been described in social *F. anselli* who possess six different aggressive vocalizations.

Distress calls are emitted by subordinate animal while being attacked by predator or dominant animal (Bradbury and Vehrencamp 1998). 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, Bednářová 2008, Knotková *et al*. 2009). 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. The similar sound, also called squeal, has been described in *F. mechowii* (Bednářová 2008), this sound was classified as aggressive call, but since it was emitted by subordinate animal during the fight, as in case of *F. darling,* I would rather categorize it as a distress call. Another type of distress call observed in *F. darlingi* is harsh, this is atonal sound with quite low minimal frequecy around 1,51 kHz. This sound was emitted by subordinate and/or attacked animal during agression. "Grunt", the sound similar to harsh has been described in solitary *C. talarum* (Schleich and Busch 2002). The last type of distress vocalization in *F. darlingi* is alert. Alert is very loud sound (frequency range: 2,85 – 16,06 kHz) with high main frequncy around 5,21 kHz and is emitted by both sexes as a reaction to pain or when one animal restricts the movement of the other. Similar sound has been described in many others subterranean rodents. *F. mechowii* emits alert during the food competition and also when one aminal restricts the movement of the other (Bednářová 2008), "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).

The last group of vocalization are alarm calls. This vocalization is used when colony is disturbed, as a warning against predator or other threats (Bradbury and Vehrencamp 1998). Most of the social species emit at least one type of alarm call, as in the case of *S. cyanus* or *F. mechowii* (Veitl *et al*. 2000, Bednářová 2008), *H. glaber* possess even three different types of alarm calls (Pepper *et al*. 1991). In a case of *F. darlingi* none alarm sound has been observed and the same situation occur in *F. anselli* (Credner *et al*. 1997). However, these species could posses this type of vocalization, but we were not able to record it thanks to unsuitable experimental setting in artifficial contidions.

As described in introduction, several subterranean rodents use besides the vocal communication also seismic signals. In case of *F. darlingi* beating with chest against the burrow floor has been observed. This behavior was suggested as a seismic communication in *F. mechowiii* (Bednářová 2008). We were not able to record audiable part of this signal, because *F. darlingi* is much smaller than *F. mechowii*, therefore the sound is much more silent. We did not attempt to record seismic part of the signal due to technical constraints.

5.1. Vocalization in dependence on social system

Vocalizations of solitary and social species differ in richness of calls and also in behavioral context in which they emit these sounds. Solitary subterranean rodents possess markedly lower amount of vocalizations, since they does not usually come in contact with conspecifics otherwise than during mating. Every studied solitary species emit lower amount of calls than any social subterranean rodent. The widest vocal repertoire of all studied solitary species possess *H. argenteocinereus* with amount of eight types of calls (Knotková *et al*. 2009. The vocal repertoire of *F. darlingi* and *S. cyanus* (Veitl *et al*. 2000) includes only 12 call types, which make it the smallest among social subterranean rodents, but it is still large enough to overtop considerably the solitary species.

Since the contact calls are emitted during friendly encounters within known animals, and were described often as a greeting sounds, these calls are usually missing in solitary living species. *C. pearsoni,* or *C. talarum, G. breviceps* and *H. Argenteocinereus* all have been described to lack any contact calls (Francescoli 1999, Schleich and Busch 2002, Devries and Sikes 2008, Knotková et al. 2009). However, there is suggestion that purring sound of *G. breviceps*, which is a mating call, might serve also as a contact call (Devries and Sikes 2008). On the other hand, contact calls are widely developed in social species, and in *S. cyanus* or *F. mechowii* represent the richest group of all the sounds (Veitl *et al*. 2000, Bednářová 2008). In *F. darlingi* and remaining two studied social species *H. glaber* and *F. anselli* (Pepper *et al*. 1991, Credner *et al*. 1997) contact calls are represented but not as plentifully as in case of *S. cyanus* or *F. mechowii.*

Mating calls are considered as primary type of vocalization in solitary species because they find each other only during the mating season and so their vocalization serve mainly to lower agresivity or to sexually stimulate the mate (Francescoli 1999, Schleich and Busch 2002, Knotková *et al*. 2009). The amount of mating calls correspond to this suggestion. For solitary *C. talarum* and *H. argenteocinereus* mating calls present the most extensive group of vocalizations (Schleich and Busch 2002, Knotková *et al*. 2009). Also social subterranean rodents emit sveral different types of mating calls, the amount of this sounds vary from two as in case of *S. cyanus* (Veitl *et al*. 2000) or *F. darlingi* to three, as described in *F. anselli* and *F. mechowii* (Credner *et al*. 1997, Bednářová 2008). But in none of social species mating calls represent the most extended group of sound and in case of *H. glaber* only one type of this call has been described (Pepper *et al*. 1991).

Aggressive and distress calls are emitted by both social and solitary species. Social species possess more types of agressive calls, three in case of *F. darlingi*, four in the case of

H. glaber (Pepper *et al*. 1991). *F. anselli* emit even six different agressive calls (Credner *et al*. 1997). As the richness of vocal repertoire of solitary species is lower they also possess fewer types of agressive calls than social living species. *H. argenteocinereus* has been described to emit two different types of agressive calls (Knotková *et al*. 2009), *C. pearsoni* and *C. talarum* both emit one type of aggressive call (Francescoli 1999, Schleich and Busch 2002). Since aggressive calls accompany both unfamiliar and familiar encounters, the aggressive behaviour could be more often provoked and should include different types of aggression (accompanied by different type of aggressive vocalization) in larger groups. Social species would use different type of aggresive call when facing unfamiliar intruder or predator, than when encountering the member of colony. Opposite to this, there should be only slight difference in aggressive encounters of solitary living species. The amount of distress calls appear to be similar in social and solitary species. As this type of call could serve to appease aggressor, it should be of the same importance for social and solitary species.

Since alarm calls serves to alert colony members, it is not surprising that solitary species lack these calls, as described in *C. pearsoni, C. talarum, H. argenteocinereus* (Francescoli 1999, Schleich and Busch 2002, Knotková *et al*. 2009). Contrariwise, most of the social species emit some type of alarm call, with exeption of *F. anselli* and also *F. darlingi.*

Among African mole-rats *F. anselli* and *F. darlingi* possess similar size of vocal repertoire. This could indicate the similar group size . Since the relationship between quantity of the vocal repertoire and size of the group has been described at least in case of non-human primates (McComb and Semple 2005). According to this contention, the species with the largest size of group (*H. glaber*) should possess the the biggest vocal repertoire. But as described by Bednářová (2008) *F. mechowii* emits more types of calls than *H. glaber.* This indicates, that vocal repertoire of subterranean rodents could depend on more factors than just on the group size.

Table12.: Comparison of the richness of the adult vocal repertoires of several studied species.

	C. talarum	*H. argenteocinereus*	*S. cyanus*	*F. anselli*	*H. glaber*	*F. mechowii*	*F. darlingi*
Contact calls			Cooing Twitter I TwitterII Squeak	Grunt Twitter	Soft chirp Toilet call	Twitter Gabbling Squeak Grunt Harsh	Cheep1 Cheep2 Twitter
Aggressive (territorial) calls	Tuc-tuc	Low cluck Hissing	Cluck I Cluck II	Whistle Trill I Trill II Hiss Grunt I Grunt II	Hiss Grunt Upsweep trill Loud chirp	High trill Swing trill Scream Squeal	Whistle Squeak Snort
Distress calls	Grunt	Squeaking Scream	Cluck III Squeal	Loud Scream	Scream	Squeal Alert	Squeal Harsh Alert
Mating calls	Female mating call Male mating call	Female mating call High cluck Gabbling	Creaking Scream	Cluck Shriek Cry	V-trill	Cluck Shriek Cry	Cluck Shriek
Alarm calls			Trill		Tap Sneeze Low-pitched Chirp	Trill	
Mechanical sounds	Tooth grinding	Teeth grinding	Teeth chattering	Tooth grinding	Tooth grinding	Teeth grinding Seismic Hiss Snorting	Teeth grinding
Total	5	8	12	14	12	18	12
Reference	Schleich and Busch 2002	Knotková *et al*. 2008	Veitl *et al*. 2000	Credner *et al*. 1997	Pepper *et al*. 1991	Bednářová *et al*. 2008	Present study

5.2. Individual vocal recognition

We suppose that since social subterranean rodents possess quite extensive amount of vocal communication, this could also serve to individual recognition. It was described that *H. glaber* is able to vocaly distinguish the social rank (Yosida *et al*. 2007, Yosida and Okanoya 2009).

Individual vocal recognition of subterranean rodents has never been studied. However, in some mole-rat species individual odour recognition has been described as in case of *F. anselli* (Burda 1995) and *F. damarensis* (Jacobs and Kuiper 2000).

We assume, that vocalization applied for individual recognition would be one of frequently used contact calls. As in case of distinguishing the dominance rank using the soft chirp sound in *H. glaber* (Yosida *et al*. 2007, Yosida and Okanoya 2009). However *F. darlingi* possesses rather smaller amount of contact calls and they are used seldom. Also the reason why the amount of recorded contact calls was so small could be, that contact vocalization was primary recorded in families composed of two animals (a pair) where none juveniles were present to ensure that adult vocal communication was recorded. Also vocal repertoire of *F. darlingi* and *F. anselli* are quite similar and since *F. anselli* uses odour for individual recognition (Burda 1995), it could be the same for *F. darlingi.* With odour individual recognition, vocal individual recognition could be of lesser importance.

On the contrary, the mating calls of *F. darlingi* display extensive individual differences (Fig. 8). And since vocalization used for individual recognition has to show a strong individual stereotypy, this type of sound should be used for such purpose.

6. Conclusions

Vocal repertoire of social Mashona mole-rat (*F. darlingi*) consists of twelve different types of calls, one of it is mechanically produced sound. Frequency range of sounds fit in interval between 0,14 and 16,06 kHz and such frequency range corresponds to findings in other subterranean rodents. The size of vocal repertoire is consistent with social system of *F. darligi* and markedly differ from amount and complexity of vocalization of solitary species. The group of mating calls has been selected as a vocalization suitable for individual recognition, since it shows high individual variability.

In master thesis we would like to focus on vocal individual recognition of *F. darligi*. First task would be to confirm their ability to recognize each other by acoustics signals. Second, to find the precise physical features of the calls, which are individually variable.

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