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**Individual features in vocalization of the Mashona
mole-rat (*Fukomys darlingi*)**

Master thesis

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Annotation:

The significance of vocal communication in subterranean rodents was confirmed. In this study I tested whether vocalization of the Mashona mole-rats (*Fukomys darlingi*) differs individually and what information about signaller are these mole-rats able to obtain using only acoustic cues.

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V Českých Budějovicích dne 12.12.2013

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Veronika Dvořáková

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Abstract:

Animals can exchange certain information during vocal communication. The clue about the signallers' age, sex, body size, reproductive status, dominance rank or individuality can be incorporated in acoustic calls. In the dark and stuffy burrows of Mashona mole-rats (*Fukomys darlingi*) (Bathyergidae, Rodentia), vocalization is the best means of transferring information over middle distances. Therefore, it would be very useful if their calls did not contain only the communicational meaning but also various useful cues about the signaller and its identity. In this study we tested mole-rat vocalization for presence of diverse individually distinctive features. Using the GMM-UBM-based automatic system for individual recognition we confirmed that calls of these mole-rats differ individually and therefore, have the potential to be the signal that informs about individuality. Moreover, results of simple playback tests demonstrated the ability of Mashona mole-rats (*F. darlingi*) to distinguish individuals of different social ranks. Our findings confirm the prediction that this underground rodent uses vocalization not only for communication but also for obtaining various information about conspecifics.

Introduction:

The use of vocal communication is not an easy task, because of producing sound is energetically demanding and the sound can be distorted and degraded during propagation (Bradbury and Vehrencamp 1998). Animals would not use this type of communication if not benefited by doing so. However, there are situations when different means of communication other than vocal means are not possible or alternatively they are not the best option. How would wolves communicate with temporarily separated pack members to gather for a hunt if not by howling (Nowak et al. 2007)? Can you imagine a quicker way of alerting conspecifics of impending danger than by alarm calls (Schwagmeyer 1980; Seyfarth et al. 1980; Silva et al. 1994; Manser et al. 2002)? Apart from the context, surrounding environment also affects the choice of the means of communication (Bradbury and Vehrencamp 1998). Vocalization is a highly efficient method of communicating at night or in dense vegetation and also in dark environments.

Throughout the animal kingdom vocalization is used for various purposes. For example it can be used to inform about sex, condition and age of the signaller (Rendall et al. 2004; Bouchet et al. 2012). It could also be useful to recognize neighbours, kin or even a particular individual (Beecher et al. 1985; Balcombe 1990; Rendall et al. 1996; Bee and Gerhardt 2002; Min Wei et al. 2011) or to distinguish reproductive or dominance status (Tobias et al. 1998; Semple and McComb 2000; Vannoni and McElligott 2008; Yosida and Okanoya 2009; Hoeschele et al. 2010). Furthermore, vocalization is useful for synchronizing members of a group (Stewart and Harcourt 1994; Boinski and Campbell 1995) or for warning others against danger (Seyfarth et al. 1980; Silva et al. 1994; Manser et al. 2002).

To explain the principles of how different information such as body size, weight, age, sex, reproductive status, dominance rank and individuality can be encoded in mammal vocalization, the so-called source-filter theory was applied (reviewed in Taylor and Reby 2010). The source-filter theory states that vocal signals result from a two-stage production. A glottal wave generated in the larynx (the source) is subsequently filtered in the supralaryngeal vocal tract (the filter) (Fant 1970). The difference in structure of the source and the filter leads to a difference in acoustic parameters which encode individually specific information (Taylor and Reby 2010). Individual recognition (IR) by vocalization occurs when an organism identifies another individual according to these distinctive characteristics. During IR, the signaller is recognized by unique recognition cues, and the receiver learns the cues and uses them to identify the signaller during future mutual interactions (Tibbetts and Dale 2007). IR enables animals to treat conspecifics differently on the basis of their

individuality. Animals can, for example, assess the seriousness of danger by assigning an alarm call to a specific individual, hence, adjusting their response according to the reliability of the caller (Cheney and Seyfarth 1988). Alternatively, they can use vocalization signals to recognize some individuals and then treat them preferentially such as in the case of banded mongooses (*Mungos mungos*), where dependent pups form associations with particular adults and receive the majority of care from these individuals (Müller and Manser 2008).

The dominance rank is often related to the animal's size which is incorporated in the vocalization by the presence and spacing of vocal tract resonances known as formants (Fitch 1997; Riede and Fitch 1999; Reby and McComb 2003; Harris et al. 2006; Sanvito et al. 2007; Vannoni and McElligott 2008; Charlton et al. 2009b; Charlton et al. 2011a). These resonances are especially prominent in atonal sounds because formants are only detectable in tonal calls if a harmonic (multiple of the fundamental frequency) and formant coincide (Lieberman and Blumstein 1988).

Interestingly, there is a strong correlation between vocal communication and sociality. The complexity of calls frequently correlates positively with group size in birds and mammals (Freeberg 2006; Bouchet et al. 2013). For example, McComb and Semple (2005) provided evidence that vocal repertoire size correlates positively with the degree of social bonding in non-human primates. Vocal complexity and repertoire size are not the only parameters of vocalization related to sociality. As suggested by LeRoux et al. (2009), more social species also possess a higher proportion of "friendly" vocalizations compared to solitary species. Friendly vocalizations are described as calls made during fearful or appeasing contexts. Function of such vocalization is to enhance group cohesion (Morton 1977).

The subterranean ecotope is unique in many aspects and has a great impact on the sensory biology of its inhabitants (reviewed in Burda et al. 1990; Francescoli 2000). Ubiquitous darkness prevents visual communication; reduced air flow limits olfactory sense. Acoustic signals can disperse here over medium distances of a few meters (Heth et al. 1986; Lange et al. 2007). Under such conditions, vocalization becomes a crucial means of communication in mammals living underground.

As vocalization of subterranean rodents has been widely studied, vocal ethograms of several species are available. There is evidence of positive correlation between sociality and vocal repertoire richness and composition (see Pepper et al. 1991; Credner et al. 1997; Francescoli 1999; Veitl et al. 2000; Schleich and Busch 2002; Devries and Sikes 2008; Knotková et al. 2009; Bednářová et al. 2013; Vanden Hole et al. 2013). According to my

opinion, the Mashona mole-rat (*Fukomys darlingi*) mating calls could probably demonstrate the information about identity of the female, to maintain established pair bonds with her mate. Since the females of social mole-rats are probably not capable of raising offspring alone, they are dependent upon the assistance of their partner (or other family members) (Burda 1990). In this case, fidelity of the male is a crucial factor for retaining the function of the family (Bappert et al. 2012). Among subterranean mammals, the ability to recognize the information about social status was found in the naked mole-rat (*Heterocephalus glaber*) (Yosida and Okanoya 2009).

The Mashona mole-rat belongs to the African endemic rodent family of African mole-rats (Bathyergidae, Rodentia). This species was known as *Cryptomys darlingi* (Kock et al. 2006). It is a herbivorous, social subterranean rodent. These mole-rats live in Zimbabwe, Mozambique and southern Malawi in small families up to nine animals (Bennett et al. 1994; Gabathuler et al. 1996). There is strict hierarchy in their families (Gabathuler et al. 1996).

Many studies on subterranean rodents describe their vocal repertoire on the basis of physical characteristics of given calls together with behavioural context in which animals use the calls. Considerably less attention was devoted to the background information encoded in the calls. In this study I concentrate on these background information and address the following questions:

1. Is vocalization of the Mashona mole-rats individually specific?
2. Is this species able to discriminate certain information (body mass, dominance, family membership) about the signaller by using acoustic cues?

Materials and methods:

Studied animals

Vocalizations were recorded in adult individuals of the social Mashona mole-rat (*F. darlingi*). Studied animals were kept in breeding stock at the Faculty of Science in České Budějovice, Czech Republic. Six Mashona mole-rats were trapped in Nsanje, southern Malawi; the rest of the mole-rats were born in captivity. Families or pairs were kept in terrariums with horticultural peat used as substrate and supplemented with plastic tubes as imitations of tunnels and flowerpots to simulate the nest. The room was lighted in 12D/12L (lights on at 0700 h). The temperature was kept at $25\pm 1^\circ\text{C}$. Animals were fed *ad libitum* with carrots, potatoes, apples and dry rodent food.

Data collection and adjustment

For the purpose of this study, I recorded two types of vocalizations of adult individuals based on the vocal repertoire of the Mashona mole-rat described in Dvořáková (2010). Mating calls were used for experiments with individuality. The Snort sound was used for testing what information mole-rats are able to obtain from the signaller. The recordings were taken with the MD 431 II Senheiser dynamic microphone (frequency range 40-16.000 Hz) and recorded with the Marantz card audiorecorder PMD660 (sample frequency 44.1 kHz, resolution 16 bit). The mole-rats were simultaneously recorded using a Panasonic SDR-H60EP-S camera to enable repeated checks of the testing sessions. The audio-recordings were transferred to the computer and analysed using Avisoft-SAS Lab Pro Software, version 5.0.01 (2010), 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%. For playback experiments two loudspeakers were used (Redstar RS-205 and BOSE SoundDock).

This species possess two types of mating calls (Figure 1), both emitted mostly by females during courtship. This call is often produced in a series when one type alternates the other. A cluck is a very short vocalization, with the mean duration of 0.03s. The range of frequency is very low and it usually does not exceed 5 kHz. A shriek is a sound similar to a cluck, but it has a main frequency lower than a cluck and does not show a rising frequency towards the end (Dvořáková 2010). To record the mating calls, opened plastic boxes (55 × 35 × 20cm) with horticultural peat were used. Two individuals of the opposite sex were placed into the box and their sounds were recorded. This type of vocalization was recorded

while founding a new breeding pair or when a female from one pair was added to a male from another pair. Vocalization for one animal was recorded repeatedly during several recording sessions. Later, the recordings were divided into tracks of the same length (20 second tracks in our case). These tracks were then used to detect individuality in mole-rat calls.

To determine whether mole-rats are able to discriminate some information about the signaller, we used an aggressive type of vocalization called a snort (Figure 2). I chose the aggressive snort sound for the experiments because I assumed that since this type of sound is atonal with the evident presence of formant frequencies, it could carry information about the body mass, dominance and about family membership as well. The snort is an atonal sound with very low fundamental frequency (0.14 – 0.94 kHz). Its frequency range is 0.14 – 6.57 kHz and main frequency is also very low: 0.48 ± 0.18 kHz (Dvořáková 2010). This sound is produced by an acute exhalation of air and emitted by a nettled animal that is trying to attack. The snort was recorded in an animal placed in an opened plastic box and irritated by air flow and during handling. Snort vocalization of the particular individual was collected in several recording sessions. Afterward, background noises, long soundless segments and any damaged sounds were removed from the recording using Avisoft-SAS Lab Pro Software. Subsequently, all adjusted recordings from one animal were put together to create one longer audio record. The shortest audio record was at least 80 seconds long. Several audio records had to be placed in a row to produce a soundtrack lasting several minutes. The same procedure was used in each tested individual resulting in a set of soundtracks ready to be used in T-maze experiments.

For DFA purposes, the snort sounds were analysed with Avisoft-SAS Lab Pro Software by using Automatic Parameter Measurements.

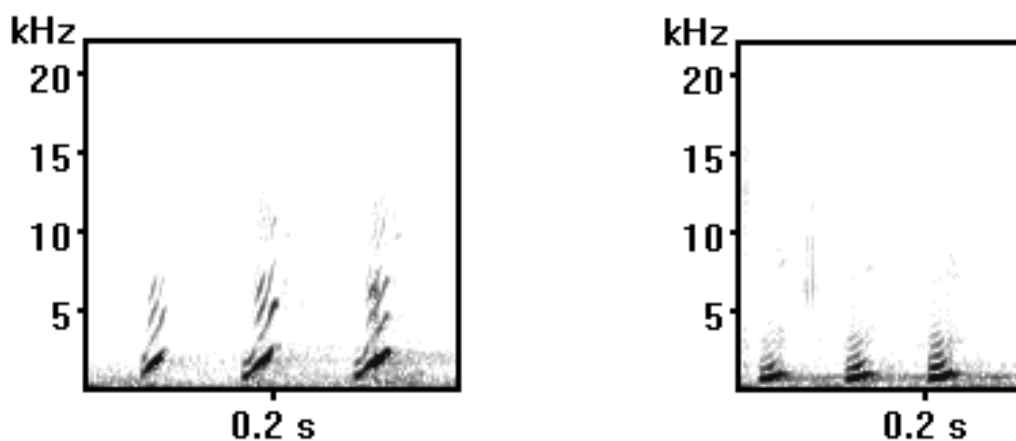


Figure 1 Spectrograms of the mating calls: picture on the left – cluck, picture on the right - shriek

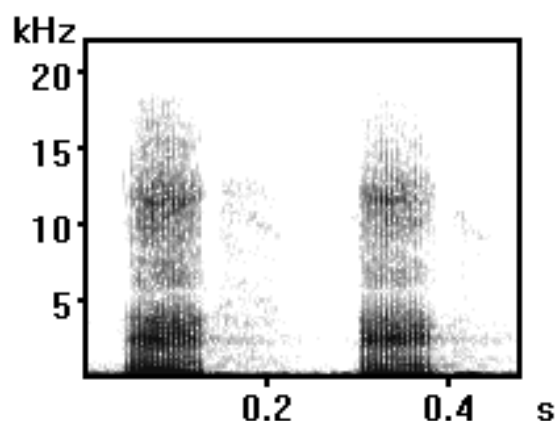


Figure 2 Spectrogram of the snort sound

Individual recognition

The GMM-UBM-based automatic system for individual recognition described by Ptáček (2012) and used for the individual identification of birds (Ptáček et al. submitted) was used. For individual recognition, vocalizations of five dominant (breeding) females were used. As I described earlier, the recordings divided into 20-second tracks were used for individual recognition. I used the verification system to decide whether the recorded sound belonged/not belonged to the target animal. The verification system works on basis of YES or NO decisions (see Figure 1 in the supplementary material). One track belonged to the target animal (the animal whose recognition was tested), the second one to the tested animal. Since the tested animal could be the target or the impostor (all animals except the target animal and animal used for the UBM - explained below in the text), two types of errors could occur. False acceptance, when the tested track did not belong to the target animal, but the method wrongly assigned it to the target animal. False rejection, when the tested track belonged to the target animal, but the method wrongly assigned it to the impostor (not the target) animal. **Correct classifications** were compared with **errors** and the score shows **the success** (in percentage) of recognition of the given animal.

Before starting the individual identification it was necessary to find the correct input parameters. Firstly, I chose input parameters based on characteristics of mole-rat sounds. Then I conducted a series of experiments and changed these parameters in each experiment (see Table 1 in the supplementary material). According to achieved success of recognition I chose the final input parameters which I applied to a particular individual identification experiments.

The method of the individual identification consists of several steps (Figure 3). I applied this method on soundtracks of five Mashona mole-rat females (entitled A – E). First, I extracted multiple relevant characteristics from all recorded tracks of all animals. Then, characteristics from tracks of one animal (e.g. female A) were used to establish the Universal Background Model (UBM). This UBM served to model sounds that do not contain any useful information (background, crackling, noise, etc.) from the recordings. The next step was to divide the remaining four animals into two categories: the target speaker (e.g. female B) and the test speakers (females C, D, E). Only half of the soundtracks of female B served as target. The other half, together with tracks of females C – E, was used for later verification. Then, a GMM (Gaussian Mixture Model) was estimated for a target animal using the target recordings (first half of the female B tracks). A GMM is a model of voice tract of the target female estimated by extracted features of the sound of the target animal and the UBM. The last step was verification. In this phase of the experiment, the pairs of females were compared and the decision whether they are the same individual or not was made. The target individual represented by GMM was compared with the test animals (impostor animals (females C – E) and target animal (the second half of tracks of female B)), each represented by a set of extracted features.

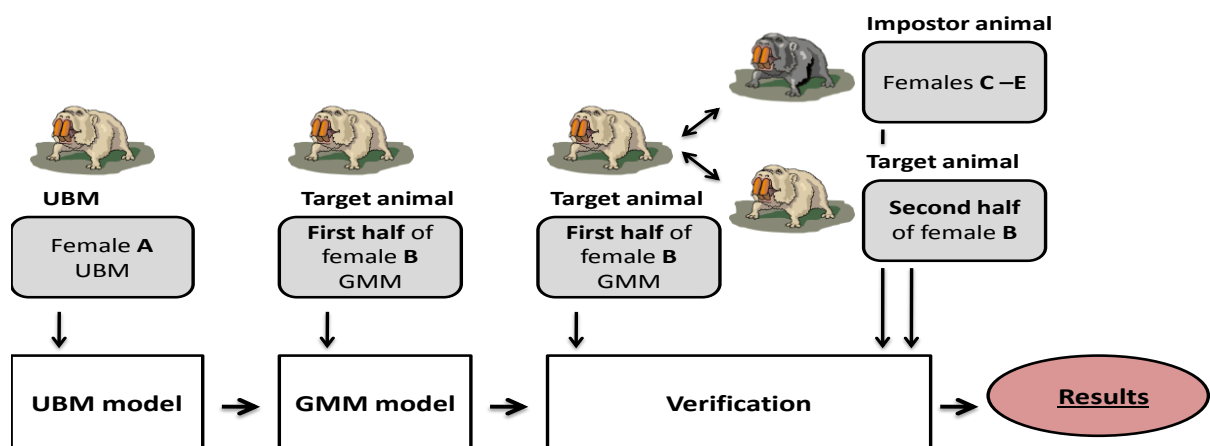


Figure 3 Steps of individual identification process – modified according Ptáček et al. submitted
 UBM = Universal Background Model, GMM = Gaussian Mixture Model

This procedure is repeated for every female used as a target animal. To ensure the objectivity of testing, two rounds which differed in the animal used for the UBM were performed for every target animal (Table 1).

Table 1 Classification of females (A, B, C, D, E) into categories as it was used in experiments on individual recognition. UBM = Universal Background Model, GMM = Gaussian Mixture Model. A $_{1/2}$ = first half of the tracks of female A, A $_{2/2}$ = second half of the tracks of female A, the same applies to females B, C, D, E.

Target female	Experiment round	UBM	GMM	Test animals
A	round 1	C	A $_{1/2}$	B, D, E, A $_{2/2}$
	round 2	D	A $_{1/2}$	B, C, E, A $_{2/2}$
B	round 1	E	B $_{1/2}$	A, C, D, B $_{2/2}$
	round 2	A	B $_{1/2}$	C, D, E, B $_{2/2}$
C	round 1	B	C $_{1/2}$	A, D, E, C $_{2/2}$
	round 2	A	C $_{1/2}$	B, D, E, C $_{2/2}$
D	round 1	B	D $_{1/2}$	A, C, E, D $_{2/2}$
	round 2	E	D $_{1/2}$	A, B, C, D $_{2/2}$
E	round 1	B	E $_{1/2}$	A, C, D, E $_{2/2}$
	round 1	C	E $_{1/2}$	A, B, D, E $_{2/2}$

In the case of the Mashona mole-rat recordings, I used four older recordings from female B (recorded in 2010). These four recordings were of poor quality as they were recorded by a different type of audiorecorder (Sony Digital Audio Tape-corder TCD-D100) and probably negatively affected the results when used for estimating GMM of female B. On the other hand, these recordings did not have any impact when used for estimating UBM and in the verification phase. Hence, I removed these recordings from experiments when female B was used as the target animal, but used them when other females were used as target animals.

Experiments on individuality

I tried to use the habituation-discrimination paradigm as described elsewhere (see Cheney and Seyfarth 1988; Rendall et al. 1996; Hare 1998; Reby et al. 2001; Charlton et al. 2007; Hauser 2007; Charlton et al. 2009a; Charlton et al. 2011b), but tested mole-rat species did not respond to this method. Therefore, I conducted preference tests in order to determine whether the Mashona mole-rat males are able to discriminate between the mating call of their own female partner and the mating call of an unknown dominant female. As far as I know, this method (T-maze experiments) has never been used for testing the ability of

animals to discriminate information about the signaller by using acoustic cues. Four dominant males were used in these tests. The transparent Perspex T-maze (8 cm in diameter, a 50 cm long preparatory section of the T-maze with a chamber and each arm of 50 cm) was used. The preparatory section was divided in the middle by wire mesh so the animal could not enter further into the maze before the trial started. Two loudspeakers were placed at the end of each arm (Figure 4).

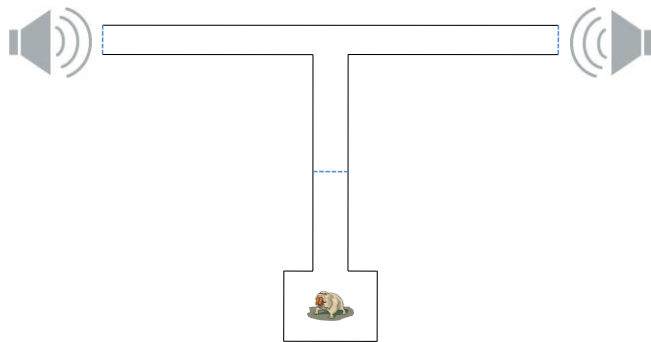


Figure 4 T-maze composition for testing preferences

The loudspeakers were used to play back recorded calls within natural occurring amplitudes estimated by my hearing. Before the beginning of each trial, the mole-rat was placed into a preparatory chamber and left for ten minutes to habituate. After the habituation, the playback recordings were turned on and the wire mesh was removed. Each male was provided with the series of calls belonging to his mate coming from one side and the series of calls of an unfamiliar dominant female coming from the other. Since two different loudspeakers were used, the loudspeaker used to play back sounds of the female partner/unfamiliar female was changed after each trial. The trial ended when the tested male reached the end of one arm. Since (Heffner and Heffner 1992; Heffner and Heffner 1993) provided evidence that the threshold for sound localization in the naked mole-rats (*H. glaber*) is 63° and in the blind mole rat (*Spalax ehrenbergi*) 180° , we used an 180° angle of separation to ensure that Mashona mole-rats are able to localize it.

Experiments on dominance, body mass and family membership

The experiment set-up was the same as for the individuality trials (see above). For these T-maze experiments, we used playbacks of snort sounds from seven individuals from five different families. All recorded snort sounds belonged to adult males, two of them were dominant (breeding mole-rats) and the five subordinate (nonbreeders). Only subordinate mole-rats were used for testing the preference of different sounds. The testing apparatus was turned to a different position after each trial to ensure that no other factor besides the sounds affected the tested individuals. I also conducted side trial to be certain that no side preference occurred. As in the case of experiments on individuality, the loudspeaker used to play back the sound of the given male (dominant/subordinate, bigger/smaller, familiar/unfamiliar) was changed after each trial. Only one playback experiment per subject was done per day and a minimum of three weeks of separation was used between experiments with playbacks to avoid habituation. The side trial took place one week after completion of all other T-maze experiments.

I conducted the following trials:

Dominance trial

The sound of the dominant mole-rat male was played from one loudspeaker and the sound of the subordinate mole-rat male from the second one. Both dominant and subordinate males belong to the same family. Given the fact that the mole-rats live in families where only the dominant pair reproduces and the rest of family are nonbreeders, the dominance status was assigned on the basis of reproductive status. Every tested animal was provided with soundtracks of males that did not belong to his or her family.

Body mass trial

In this experiment, the tested mole-rat was provided with the sound of two subordinate males of different body masses from different families. The smaller male was always the same individual since it was the only adult male small enough to make sufficient difference in body mass when paired with other males. This male weighed 109 grams (the weight measured at the time of recording the soundtrack). The bigger males used in trials weighed 165, 167 and 168 grams.

Family membership trial

In this experiment, I tested whether mole-rats are able to distinguish between the snort sound of own family member and the snort sound of member of different family. One of the playback sounds belonged to the male from the same family as the tested animal, the other to

the male from a different family, both were nonbreeders. The males whose sounds were used have very similar body mass (151, 165, 167 and 168 grams).

Side trial

In this experiment, I tested if animals prefer one side more than the other. Animals were habituated in a preparatory chamber and then released without being provided with any sound.

Statistical analysis

To test whether there is any preference between two types of played sounds (T-maze experiments), I used the chi-square test. The duration of the experiments is given as mean \pm SD. I used the Discriminant Functional Analysis (DFA) to find which parameters of the snort sound causes the difference between dominant and subordinate males. For the DFA, I used 428 snort calls in total from four males (107 calls each), two of them were dominant, two subordinate. The results for each of the significant parameters are given as mean \pm SD. All of the tests were performed in STATISTICA 10 (StatSoft, Inc.).

Results:

Individual recognition

Table 2 shows the overall success rate of individual identification. The number of obtained recordings (20s soundtracks) varied from 10 to 40 (Table 2).

Table 2 Success rates of the individual recognition method. The “overall success rate” was computed as the mean value of success rates obtained in individual rounds. The number of errors is the sum of false acceptances and false rejections. The overall success rate given in the last line of the table was computed as the ratio of the overall number of errors and overall number of tests.

Target female	N of recordings	Experiment round	N of tests	N of errors	Success rate (%)	Overall success rate (%)
A	33	round 1	1394	332	76.2	82.3
		round 2	1904	253	86.7	
B	26	round 1	1067	223	79.1	79.3
		round 2	1012	207	79.5	
C	40	round 1	1860	391	79.0	79.0
		round 2	1700	358	78.9	
D	10	round 1	540	202	62.6	59.2
		round 2	1386	584	57.9	
E	29	round 1	1190	192	83.9	83.5
		round 2	1260	212	83.2	
OVERAL			13313	2954		77.8

The success rate of correct identification of particular individual varied between 59.2% and 83.5% (Table 2). The lowest number of correct identification was obtained in female D which died at the time of recordings. I obtained only 10 soundtracks from this female, which is significantly less compared to any other female (26, 29, 33, 40). When results of recognition of female D are excluded, the overall success rate increases to 80.9%.

Testing individuality

Mean duration of the trials was 202.5 ± 82.6 s (120 – 300s). Three males chose to approach their own female, and one male visited an unfamiliar female (Table 3).

Table 3 Males preferences for own or foreign female based on individuality in vocalization.

Type of experiment	N of tested animals	Own female (n)	Foreign female (n)	χ^2	p
individuality	4	3	1	1.000	0.317

Testing of dominance, body mass and family membership

Mean duration of the dominance trials was $118.2 \pm 145.6s$ (10 – 540s.) Tested animals preferred the side with sounds of the subordinate compared to the side with the sound of the dominant male (Table 4). Mean duration of the body mass trials was $23.6 \pm 16.2s$ (8 – 95s). Mole-rats did not prefer the snort sound of the small or snort sound of the large male (Table 4). Mean duration of the family membership trials was $76 \pm 77.9s$ (10 – 385s). Tested individuals did not discriminate between the snort sounds of the familiar subordinate males versus non-familiar subordinate males (Table 4). In the side trials, tested animals reached the end of one arm in an average of $22 \pm 15.2s$ (8 – 90s). There was no preference for any side of the T-maze (Table 4).

Table 4 The preferences for vocal characteristics of dominance, body mass, family membership and side apparatuses in the Mashona mole-rats.

Type of experiment	N of tested animals	Dominant (n)	Subordinate (n)	χ^2	p
Dominance	37	8	29	11.919	0.001
		Large (n)	Small (n)		
Body mass	35	19	16	0.257	0.612
		Familiar (n)	Non-familiar (n)		
Family membership	31	16	15	0.032	0.857
		Left (n)	Right (n)		
Side	35	15	20	0.714	0.398

The dominance rank

I used 428 snort calls from two dominant and two subordinate males (107 calls each), to test if there is physical difference between dominant and subordinate males in this type of sound. Total classification success of given dominance ranks was 71.7% (Table 5).

Table 5 The success rates of a classification of the dominance rank according to DFA.

N of tested calls	Dominance rank	Success rates (%)	Total classification success (%)	Wilk's Lambda
428	dominant	79.4	71.7	0.782
	subordinate	64		

The main parameters that cause the difference between dominant versus subordinate males are shown in Table 6. The sounds of dominant males were longer $83 \pm 22\text{ms}$ ($0.040 - 0.171\text{ms}$) than the sounds of subordinate males $78 \pm 19\text{ms}$ ($0.034 - 0.150\text{ms}$). Snorts of dominant males possess a lower level of entropy (0.280 ± 0.085) than those of subordinate ones (0.303 ± 0.093). Entropy demonstrates the level of linearity of a given sound, where white noise has an entropy value of 1, and a pure tone has an entropy value of 0. Quartiles showed that energy distribution differs between sounds of dominant and subordinate animals with dominant males having most of the energy in lower frequencies of the sound compared to subordinate ones: mean for dominant was 447.80 ± 377.92 , mean for subordinate was 490.23 ± 632.74 for quartile 25 (max): and 1532.29 ± 1009.17 , 2324.90 ± 1294.95 for quartile 50 (max) respectively.

Table 6 The main parameters that cause the difference between the snort calls of dominant and subordinate males according to DFA.

N of tested calls	Parameters	Wilk's Lambda	p
428	duration	0.796	0.008
	quartile 25 (max)	0.799	0.003
	quartile 50 (max)	0.830	<0.001
	entropy (max)	0.808	<0.001

Discussion:

In this study I tried to determine how informative the vocalization of the Mashona mole-rats in intraspecific communication context can be. Due to its social lifestyle and life in very specific environment with lack of the most traditional cues used for communication, I expected that vocal communication may play a very important role in the social life of this species. My results indicate that the vocalization of Mashona mole-rats possesses the ability to carry information about the individuality of the signaller. Whether these animals are really able to perceive this information could not be confirmed due to the low number of tested animals. As for other information encoded in vocalization, the dominance status seems to be the characteristic important enough to be discriminated in these mole-rats. Nevertheless, tested animals did not discriminate between males of different body mass and between males from the own and a foreign family.

The GMM-UBM-based automatic system used for individual recognition was able to match the soundtrack to the particular female with an overall success rate of 77.8% (even more 80.9% if the female that died, i.e. with the lowest number of the sounds recorded is excluded). The overall percentage is thus high enough to show that the mating calls of the Mashona mole-rat can carry information about mole-rat individuality. Of course, the analysis of overall success rate is only the first step to determine the ability of mole-rats to use vocal communication for individual recognition; therefore, I conducted T-maze experiments to show whether there is any preference of mole-rat males to approach own or foreign female. Three of the four males followed the sound of their own mate rather than the sound of an unfamiliar dominant (breeding) female. Unfortunately, the number of tested animals is too low to provide any conclusive results. I was able to obtain a sufficient amount of recordings only from five females and one of them died, which excluded her male partner from T-maze testing. If Mashona mole-rats have preferences for their own mate, it could correspond to the suggestion of Bappert et al. (2012) that the maintenance of mole-rat families (in case of their study, the Ansell's mole-rat was analysed) depends on the fidelity of the reproductive males and monogamy of mole-rat families. In this context, it is important to mole-rats to know their sexual partners well and vocal communication could be important way how to maintain strong pair bonds. More experiments carried on a larger sample size needs to be done to determine whether mole-rats really perceive the individuality encoded in their voices.

To determine what further information about the signaller might be encoded in Mashona mole-rats vocalization, I conducted a series of preference tests. In the first trial the sounds of unknown dominant and unknown subordinate males were presented. My results

convincingly demonstrated that mole-rats chose to follow the sound of the subordinate male. Since the snort sound was described as an aggressive type of call produced by a nettled animal in this species (Dvořáková 2010), it is not surprising that tested mole-rats preferred subordinate, probably less dangerous individuals. Gabathuler et al. (1996) reported that, in the mature family of Mashona mole-rats, the dominant (breeding) pair was among the least popular individuals in terms of number of interactions received subtracted from the number of interactions initiated. This could mean that avoiding dominant males reflects the experiences from one's own family where the dominant male is not the one with which to interact.

Mashona mole-rats thus demonstrated the ability to distinguish between two conspecifics differing in dominance status. This recognition was also found in another social mole-rat species, the naked mole-rat (*H. glaber*). After presenting a synthesized soft chirp sound (SC) to these mole-rats, they responded more frequently to stimuli resembling SCs from larger animals (Yosida and Okanoya 2009). It is known that larger naked mole-rat individuals have SCs lower in the overall frequencies and higher in the onset frequency (Yosida et al. 2007). In this species, body weight is highly correlated with social rank (Yosida et al. 2007); therefore, a frequent response to larger individuals could mean more frequent responses to the dominant individual. Inspired by this result, I conducted a second series of preference trials to test whether Mashona mole-rats respond differently to sounds of animals of different body mass. In these experiments, tested subordinate mole-rats did not show a preference for sounds of subordinate individuals differing in body mass. This could mean either that the mole-rats do not recognize different size of conspecifics based on vocalization or they simply do not display any preference for each of them. Lack of preference in the receivers may reflect a lack of motivation rather than an inability to discriminate between individuals of different body mass. I could speculate that since the breeding pairs are most dominant individuals in mole-rat families, the tested animals did not need to differentiate between subordinates in spite of their different body mass. Interestingly, a lack of motivation was proposed as general explanation for the absence of response to different acoustical stimuli in some other mammals as well (Fischer et al. 2001; Jansen et al. 2013). Adult banded mongooses (*M. mungos*) did not use an individual signature in close calls for discrimination between individuals (Jansen et al. 2013), although there is evidence that pups can discriminate between close calls of their escorts (long-lasting and exclusive associations) versus other escorting individuals and also escorting mongooses show an increased responsiveness towards signals of their escorted pup (Müller and Manser 2008).

Similarly, infant chacma baboons (*Papio ursinus*) discriminated between two variations of the barks; the intermediate alarm barks and the clear contact barks (Fischer et al. 2000). Nevertheless, adult chacma baboons failed to show a difference in response to these two call variations (Fischer et al. 2001).

The possibility, that Mashona mole-rats do not recognize different body size of conspecifics based on vocal communication, even though they recognize the dominance status, could indicate that these two characteristics of the signaller do not correlate and, thus, the dominance rank is characterized by different acoustic features than body mass. Interestingly, our captive mole-rats do not show the body mass pattern observed in free living Mashona mole-rats (Bennett et al. 1994), because dominant males in our animal facility are not always the biggest ones in the family; hence, the dominance status does not correlate positively with the body mass. This is probably due to the impossibility of dispersal of adult nonbreeder in our captive breed. Nevertheless, it could be useful to vocally demonstrate one's dominant status regardless of the body mass. This was exactly described in fallow deer (*Dama dama*) (Vannoni and McElligott 2008). In groans of fallow deer males the information about social dominance was displayed mostly by fundamental frequency. However, the body size was not related to the fundamental frequency parameters of groans, but rather to the minimum formant dispersion (Vannoni and McElligott 2008). There is also possibility that the body mass trial in my study was biased, because only one male was used as the smaller individual in tests. That is because this mole-rat was the only one considerably smaller than the other subordinate adult males.

The last playback trial was conducted to determine whether the snort sound of the Mashona mole-rats carry the information about the membership to a particular family. Tested individuals were provided with the snort sound of two subordinate males, one of them belonged to the same family as the tested animal (brother), and the other one was from an unfamiliar family. Mole-rats did not respond differently to the sound of familiar versus non-familiar which indicates that the snort sound probably does not carry information about familiarity. This finding is not surprising because the sound used for discriminating family members should be some of the "friendly" contact calls commonly used for communication within the family, as described in other mammals (Rendall et al. 1996), rather than an aggressive one that I used. Another explanation could be that Mashona mole-rats do not use vocalization for this recognition because they use odour cues as in the case of the naked mole-rat which uses the common colony odour to discriminate between a colony member and an unfamiliar mole-rat (O'Riain and Jarvis 1997).

The results of the Discriminant Functional Analysis (DFA) demonstrate that duration, entropy (max) and two quartiles (25 max, 50 max) are the parameters making the most of the differences between the sounds of dominant and subordinate males. The sounds of dominant males are longer and possess a lower level of entropy than those of subordinate ones. Similarly, quartiles showed that the dominant males have most of the energy in lower frequencies of the sound than the subordinates have. It would be useful to also use the DFA on the sounds of small versus large individuals to see whether the parameters that explain the difference are others than those in dominant versus subordinate sounds. This was not feasible since only one male was used as smaller one.

Life in families of mole-rats in the dark of the underground burrows probably made social mole-rats highly dependent on vocal communication. A richness of vocal repertoires of many social subterranean rodents (Pepper et al. 1991; Credner et al. 1997; Veitl et al. 2000; Dvořáková 2010; Bednářová et al. 2013; Vanden Hole et al. 2013), together with a larger amount of so-called contact calls (from two in case of the *Fukomys anelli* and the *Heterocephalus glaber* up to five in the *Fukomys mechowii*), indicate the need for these rodents to communicate acoustically. Since the vocalization is of high importance to these mammals, it would be advantageous to manifest different information about the signaller by using sounds. Such ability of the Mashona mole-rat calls to carry information about social rank and even individuality was described in this paper.

To conclude, my results showed that studied vocal signals in the Mashona mole-rat are individually specific. It indicates the possibility of individual vocal recognition in this species. For future studies, it will be very interesting to test whether mole-rats really use such information about individuality for discrimination of particular individuals. My results also suggest that this species can use vocalization to obtain information about counterpart's dominance status. Surprisingly, this vocalization was not correlated with the body mass of the signaller. Similarly, I did not find the ability of Mashona mole-rats to discriminate between the vocalizations of the family member compared to an unfamiliar individual. It would be useful to test this ability with some other vocalization for example a friendly vocalization. Alternatively, to test the abovementioned parameters of vocalization in social bathyergids, we could use species with richer vocal repertoire such as giant mole-rat (*F. mechowii*), which is the species with the richest vocal repertoire (Bednářová et al. 2013).

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Supplementary material:

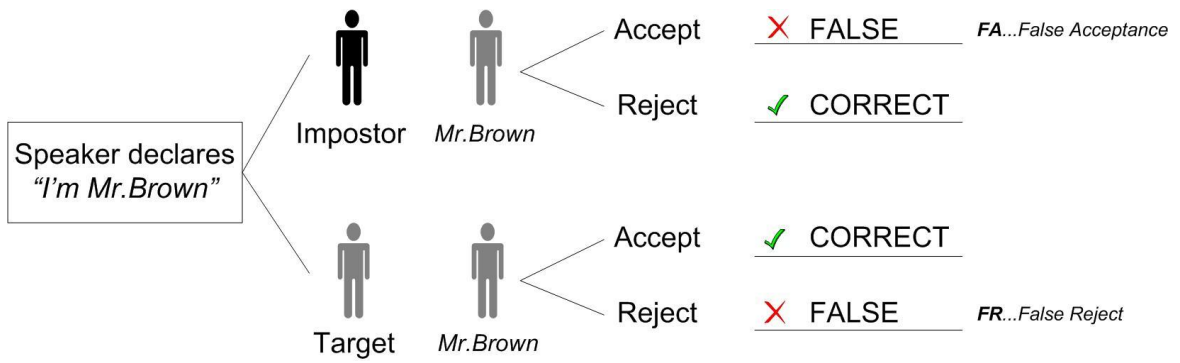


Figure 1 Types of errors occurring in verification task (Ptáček 2012)

Table 1 Settings of the input parameters. Parameters in line 16 were chosen as input parameters for the method of individual recognition

#	Window length [ms]	Window Shift [ms]	N of filters	Low frequency filter [Hz]	High frequency filter [Hz]	VAD (On/Off)	Mel Filters (On/Off)	Threshold	Success rate of identification (%)
1	30	20	5	2500	20000	off	off	5,20	75
2	30	20	5	200	10000	off	off	3,30	49
3	30	20	5	100	20000	off	off	4,50	61
4	20	10	5	100	20000	off	off	4,10	56
5	20	10	5	2000	20000	off	off	3,90	71
6	20	10	5	1000	20000	off	off	3,65	60
7	40	20	5	1000	20000	off	off	4,40	63
8	40	20	5	2000	10000	off	off	2,67	65
9	20	10	25	500	19000	off	off	0,19	62
10	20	10	25	500	19000	on	off	0,09	65
11	20	10	25	500	19000	on	off	1,38	64
12	20	10	25	500	19000	on	on	0,28	79
13	20	10	25	100	19000	on	off	0,45	66
14	20	10	25	500	20000	on	off	0,36	76
15	20	10	25	100	20000	on	on	0,24	75
16	20	10	25	250	20000	on	on	0,28	80
17	20	10	25	50	20000	on	on	0,19	77
18	30	15	25	500	20000	on	on	1,64	78

The first column has a non-informative value; it only represents the number assigned to the given experiment. *Window length*: The sliding window is used to sample the record. The recording is divided into several windows of given length and characteristics of the sound are taken in each window. The length of the window gives the resolution fineness: the shorter the window, the finer the temporal resolution. The window cannot be too short because of the risk of losing some characteristics. Since the sound elements of the Mashona mole-rats are approximately 50 to 60 ms, the length of the window should be the same or shorter. *Window Shift*: Set up the overlapping of the window. *Number of filters*: Number of filters applied to the sound. The higher the number means the finer the resolution. It is necessary to balance the finest resolution and processor load. *Low Frequency filter / High frequency filter*: The low and high frequency filters provide the range of frequencies in which the sound is analyzed. *VAD, Automatic segmentation of sound (On/Off)*: The function of the VAD is to select the sound in the track. When the VAD is on then the silent section between separate calls is not analyzed. The VAD has to correctly detect the silences. It may lead to a higher error level if wrong detection occurs. *Mel Filters (On/Off)*: Mel filters adjust the signal to distribution near to the human hearing. It makes the sound well-perceived by the human ear. These filters are commonly used for human speech. *Threshold*: Result values which are positioned below the threshold are identified as belonging to the target animal; values above threshold are identified as not belonging to the target animal.