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Ultrasound from underground: cryptic communication in subterranean wild-living and captive northern mole voles (*Ellobius talpinus*)

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ABSTRACT

This study provides the first evidence of ultrasonic vocalisations (USVs) in a truly subterranean rodent, the northern mole vole *Ellobius talpinus*. Calls were recorded by attracting callers with a bait to burrow entrances, where they were mostly visible to researchers. USVs recorded from 14 different burrows in southern Russia were verified as belonging to *Ellobius talpinus* by comparison with USVs of two wild-captured young males and by comparison with USVs of four adults from a captive colony. As a first attempt at exploring the function of USV diversity, we defined upward-intense USVs, with a maximum fundamental frequency (f0) of 35.32 ± 5.11 kHz, and variable-faint USVs, with a maximum f0 of 31.40 ± 7.78 kHz. Compared to variable-faint USVs, the upward-intense USVs were longer, had a larger depth of frequency modulation and were produced at high intensity in regular series. The upward-intense USVs were lower in the maximum and peak frequencies in the wild than in captivity, whereas the variable-faint USVs did not differ between recordings from the wild and from captivity. We discuss that similar ranges of acoustic variables found in USVs of *Ellobius talpinus* and surface-dwelling Arvicolinae species do not support the hypothesis that subterranean life has drastically reduced ultrasonic vocalisation in rodents.

Introduction

Like many other mammals, e.g. carnivores, artiodactyls, primates, colugos and lagomorphs (Frey et al. 2016; Hasiniaina et al. 2018; Miard et al. 2019; Sibiryakova et al. 2020; Volodin et al. 2021), rodents use two basic modes of call production: 'phonation' (Titze 1994; Fitch 2016) and air jet-based 'whistle' (Riede 2011, 2013; Mahrt et al. 2016; Pasch et al. 2017; Riede et al. 2017; Hakansson et al. 2021). The phonation mechanism is based on self-sustained oscillations of the vocal folds blowing the air from the lungs through the glottis (Titze 1994; Fitch 2016). With the whistle mechanism, the sound wave is created

Supplemental data for this article can be accessed here

by vorticities arising from blowing air through the narrowings of the vocal tract (Roberts 1975; Brudzynski and Fletcher 2010), as the edge tone at facing/bypassing the obstacles (Riede et al. 2017) or as glottal jet impinging on the thyroid inner wall (Hakansson et al. 2021).

The fundamental frequency (f0) of the calls produced by rodents with the phonation mode commonly lies in the human-audible range (e.g. f0 of the audible calls of laboratory rat *Rattus norvegicus* does not exceed 10 kHz) (Riede et al. 2011). At the same time, the f0 of rodent calls produced with the aerodynamic whistle mode primarily lies in the 'ultrasonic' range of frequencies, above 20 kHz, the upper limit of human hearing ability (Riede 2011) or in the audible through ultrasonic range (Campbell et al. 2014; Riede and Pasch 2020).

The subterranean environment imposes challenges resulting in a set of morphological, physiological, life-history, and molecular adaptations revealed in rodents (Nevo 1979, 1999; Klauer et al. 1997; Lacey et al. 2000; Begall et al. 2007a; Fang et al. 2014; Davies et al. 2015; Du et al. 2015; Sun et al. 2020). Subterranean life affects also the communicative behaviour of rodents (Burda et al. 1990a), probably because of specific environmental demands in the transmission of the communicative signals (Wiley and Richards 1978; Ladich and Winkler 2017; Charlton et al. 2019). Well-developed seismic (Heth et al. 1987; Rado et al. 1987; Mason and Narins 2001; Kimchi et al. 2005), magnetic (Burda et al. 1990b; Kimchi et al. 2004; Moritz et al. 2007; Oliveriusová et al. 2012; Malewski et al. 2018; Caspar et al. 2020), olfactory (Fanjul et al. 2003; Heth and Todrank 2007) and auditory (Schleich et al. 2007; Schleich and Francescoli 2018) perception abilities compensate for vision, which is fully or partially impaired in subterranean rodents (Němec et al. 2007), with some exceptions, as in tuco-tuco *Ctenomys sp.*, which have normal vision (Schleich et al. 2010).

The auditory adaptations of subterranean rodents include the hearing sensitivity shifted to low frequencies compared to the animals of similar size (Heffner and Heffner 1992, 2016; Begall et al. 2004, 2007b; Gerhardt et al. 2017). Correspondingly, the audible calls produced by subterranean rodents in captivity (Nevo 1979, 1990; Burda et al. 1990a; Credner et al. 1997; Francescoli 1999; Veitl et al. 2000; Schleich and Busch 2002) are lower in f0 than in surface-dwelling rodents of similar size (Schleich and Francescoli 2018). The low f0 can represent an adaptation to sound propagation along the burrows, which shows a so-called stethoscope effect of increasing the sound intensity coinciding with resonances of the burrow tunnels which are low-frequency because of the large air volumes of the tunnels (Lange et al. 2007). In addition, high frequencies are less effective at propagating underground, at least over long distances (Lange et al. 2007; Schleich and Antenucci 2009).

Because of the low-frequency hearing and vocalisation in subterranean rodents, there were no predictions of or attempts to find ultrasonic communication (Schleich and Francescoli 2018). However, recent studies with a Gerbillinae rodent (*Pachyuromys duprasi*), which also displays both low-frequency hearing (Lay 1972; Müller et al. 1991; Plassmann and Kadel 1991) and low-frequency audible vocalisation with f0 range of 0.04–3.57 kHz (Zaytseva et al. 2020), showed that this species has nevertheless also a rich repertoire of ultrasonic calls, with f0 ranging of 23.6–120.0 kHz (Zaytseva et al. 2019). Thus, low-frequency hearing and low f0 of audible calls does not exclude the presence of ultrasonic vocalisation in subterranean rodents. Furthermore, blindness may promote

the development of echolocation with ultrasonic calls, as in a bush branch-leaping Vietnamese pygmy dormouse *Typhlomys chapensis* (Panyutina et al. 2017; Volodin et al. 2019; Youlatos et al. 2020; He et al. 2021). Taken together, this evidence encouraged us to search for ultrasonic communication in a subterranean rodent with impaired vision, the northern mole vole *Ellobius talpinus*.

Mole voles (*Ellobius*) are truly subterranean members of the subfamily Arvicolinae distributed in grasslands of Eurasia. These small rodents (40–50 g) display a set of morphological traits associated with a fossorial lifestyle, including cylindrical body, short tail, short soft pelage, small eyes, reduced ears, and a highly modified skull with prominent extrabuccal incisors (Ognev 1950; Shubin 1978).

Mole voles are highly social mammals that live in extended family groups, including a breeding pair and their litters of the current and preceding years (Shubin 1961; Slastenina 1963; Davydov 1988; Evdokimov 2001; Coşkun and Uluturk 2003; Smorkatcheva and Kuprina 2018). Breeding systems with only one breeding female have been reported for most studied species and populations of mole voles (but see Novikov et al. 2007 for the evidence of breeding of a few females). Each mole vole family group occupies an exclusive burrow. The *Ellobius* stand out among all voles in their slow life history with prolonged gestation, delayed sexual maturation and longevity up to 6 years both in nature and in captivity (Evdokimov 2001; Smorkatcheva et al. 2016; Novikov et al. 2017). Unlike most other subterranean rodents, mole voles are relatively easy to keep and breed in captivity (Smorkatcheva et al. 2016), yet their behaviour and communication are poorly understood.

The aim of this study was to classify and describe the previously unknown ultrasonic calls of the northern mole vole. We verify the ultrasonic calls recorded from burrows in the wild with calls recorded in the controlled experimental conditions in captivity. We compare the acoustics of different ultrasonic call types and estimate the usage of the call types according to behavioural contexts in the wild and in captivity.

Methods

USV recording in the wild

Ultrasonic vocalisations (USVs) of wild-living individually unidentified northern mole voles were made in Saratov province, Russia, near Djakovka settlement (50°43′88″N, 46°46′04″E) from 26th July to 11 August 2020. The recordings were made during daylight hours. Animals vocalised when approaching bait (a piece of fresh carrot) placed on the ground near the burrow entrance. For USV recordings (sampling rate 256 kHz, 16-bit resolution) we used an Echo Meter Touch 2 PRO (Wildlife Acoustics, Inc., Maynard, MA USA, https://www.wildlifeacoustics.com/) attached to a smartphone, placed on the ground and directed to an open burrow entrance. The callers were visible in approximately 50% of recording events to the researcher (MMD) sitting near the burrow and recording the calls. The researcher could track the USVs of the callers visualised as spectrograms in real time on a compatible smartphone display. Visualisation of the USVs during the recordings allowed correlating USVs with the behaviour attending the vocalisations. As the lower frequency limit of Echo Meter is 6 kHz, a sonic recorder, Zoom-H1 with built-in microphones

(Zoom Corporation, Tokyo, Japan), was used for recording the researcher's commentary during USV emission. Each audio track (ultrasonic and sonic) was recorded as a wav-file and then uploaded to a PC. During recordings, the distance from microphones to a caller was approximately 10–30 cm. In total in the wild we made 355 min of USV recording from 14 mole vole family groups during 32 recording sessions (from 1 to 6 sessions per family group). Each mole vole family group occupied an exclusive burrow, identified by its aggregation of soil mounds. The burrows of neighbouring family groups were separated by at least 20 m that were free of either old or fresh mounds.

In addition to the recordings from burrows, we recorded, with an Echo Meter Touch 2 PRO, the USVs from two young males, live-trapped in one burrow during a parallel study, which vocalised when placed together for 5 min in a plastic bucket (bottom diameter 25 cm). The distance from microphone to the animals was 30 cm.

USV recording in captivity

Ultrasonic vocalisations of four captive individually identified adult northern mole voles (two males, two females) were recorded in the laboratory of Saint Petersburg University (Russia) from 4th September to 26 October 2020. These recordings were used for verifying the USVs recorded in the wild from burrows as belonging to northern mole voles and for comparing the acoustics and context between captivity and wild conditions. The captive subjects belonged to the same species but originated from a distant natural population from Novosibirsk province, Russia, near Berdsk (54°42′28"N, 83°03′46"E). Two subjects (one male, one female) were unrelated wild-born animals, captured in 2016 from distant burrows; another male and female were the first laboratory-born generation, born in 2018. For the last 4 years, these animals have been housed as two breeding pairs. During audio recordings, they had no offspring.

In the lab, the four subject mole voles were kept in male-female pairs under a 16 h light: 8 h dark cycle at an ambient temperature of 19–22°C in glass terraria (25 cm × 50 cm × 30 cm) half-filled with wood shavings and provided with several wood and/or ceramic shelters. Toilet paper served as nest material. Carrot, apples, beets, pumpkin, oats, and willow twigs were provided *ad libitum*; mashed meat was given in small amounts twice a week.

In captivity, all acoustic recordings were conducted in a separate room where no other animals were present, at a room temperature 22–24°C during daytime, and electric lamps and powered equipment switched off. For USV recordings (sampling rate 256 kHz, 16-bit resolution) we used the same equipment (Echo Meter Touch 2 PRO) as in the wild, so, the recordings from the wild and from captivity were comparable. Additionally, to control the quality of audio recordings, we simultaneously conducted USV recording (sampling rate 384 kHz, 16-bit resolution) using a Pettersson D1000X recorder with built-in microphone (Pettersson Electronik AB, Uppsala, Sweden). The microphones were placed at a distance of 30–40 cm above the tested animals. As with recordings in the wild, we verbally noted USV emissions, as visualised on the screen of the smartphone, to a Pettersson D1000X, thus providing recordings in both ultrasonic and audible ranges of frequencies. Each audio track was recorded as a wav-file and then uploaded to PC. As visual inspection of spectrograms showed that USVs recorded with Echo Meter Touch 2

PRO were as qualitatively similar to those made with Pettersson D1000X, the recordings made with Pettersson were not used further in the acoustic analyses.

In total, we conducted eight experimental trials with the two male and two female captive individuals: four trials with nonfamiliar partners (all possible pairwise combinations of members of the different pairs, i.e. two male–female trials, one female–female trial and one male–male trial), and four trials with familiar pair mates (two trials per mated pair). Three different experimental protocols were applied. The time interval between experiments involving the same individuals was at least 1 day.

For the four trials with nonfamiliar individuals, immediately before an experimental trial, one animal was placed in a clean big plastic container 66 cm × 46 cm × 38 cm without a roof. At the same time, a second animal was placed in a clean small glass container 22 cm × 14 cm × 20.5 cm without roof, which was placed inside the big plastic container. The small container had two narrow gaps 1.4 cm wide and 15 cm length, as two side walls did not reach the container bottom. These gaps allowed the animals to contact but prevented them from aggression. The recording started when the second animal was placed in the experimental setup. Five minutes after the start of a trial the animals were swapped. The trial lasted 10 min. After the end of a trial, the animals were returned to their home cages. The experimental setup was washed with soapy water and then rubbed with a napkin wetted with alcohol after each experimental trial, to avoid effect of smell on USVs of subsequent focal animals (Lemasson et al. 2005; Sirotin et al. 2014).

The two trials with familiar pair mates were started in the same experimental setup, however, after the first 5 min of a trial, when the animals could only contact each other through the glass container gaps, the animals were unrestricted in the large plastic container, where they could contact each other freely for the following 5 min, and then were placed for 2 min together in a plastic bucket (bottom diameter 25 cm) to simulate the recording in the bucket in the wild. The total duration of the trials with familiar animals in captivity was therefore 12 min. After the end of a trial, the animals were returned to their home cages.

The other two trials with familiar pair mates were conducted in animal home cages in response to mild disturbance by humans. Immediately before a trial, the home cage with the pair mates was transferred to a separate room where no other animals were present. The animals were disturbed by the removal of some shelters out of the cage and moving the remaining shelters from place to place within the cage. These manipulations imitated the routine cage cleaning and forced the animals to move around the cage following the replaced shelters and to contact each other. The USV recording started when the first shelter was removed from the home cage. The duration of each trial was 22 min; after the trial all shelters were returned to a cage and the cage was returned to the colony room.

Thus, by applying the four possible combinations of two nonfamiliar animals in the four experimental trials, we obtained 40 min of USV recordings. In addition, by applying the two possible combinations of the familiar partners of mating pairs in the four experimental trials, we obtained 68 min of USV recordings. In total, we obtained in captivity 108 min of USV recordings.

Acoustic analysis

Visual inspection of spectrograms of the wav-files was conducted with Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany). Two researchers (MMD and IAV) independently inspected all the files (recorded in the wild and in captivity) in the spectrogram window of Avisoft. All the acoustic files recorded during the eight experimental trials in captivity contained USVs. However, among the acoustic files recorded in the wild, the USVs were only found in 16 recording sessions from 10 family groups, which in total comprised 120 min of acoustic recordings.

Following Zaytseva et al. (2019), we defined ultrasonic calls according to whether their frequency contour was continuous without breaks or had breaks shorter than 10 ms. If the separation break exceeded 10 ms, we considered that the contours belonged to two different calls. If the duration of sound emission was less than 5 ms, we did not register it as a separate USV. We labelled all USVs where the f0 was visible and where we could measure all six acoustic variables. In total, we labelled 532 USVs for acoustic measurements.

Measurements of acoustic variables of USVs were conducted with Avisoft and automatically exported to Microsoft Excel (Microsoft Corp., Redmond, WA, USA). As the minimum f0 of ultrasonic calls always exceeded 10 kHz (based on visual inspection of spectrograms), all wav-files were subjected to 10 kHz high-pass filtering before measurements to remove low-frequency noise. For each USV, we measured in the spectrogram window of Avisoft (sampling frequency 256 kHz, Hamming window, FFT 1024 points, frame 50%, overlap 93.75%, providing frequency resolution 250 Hz and time resolution 0.25 ms) the duration with the standard marker cursor, the maximum f0 (f0max), the minimum f0 (f0min), the f0 at the onset of a call (f0beg), and the f0 at the end of a call
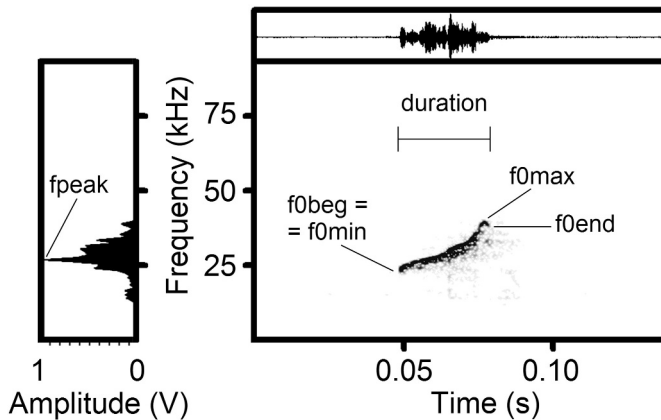
Figure 1. Measured variables for the northern mole vole ultrasonic calls exemplified by a call with upward contour. Spectrogram (right) and mean power spectrum of the entire call (left). Designations: duration – call duration; f0beg – the fundamental frequency at the onset of a call; f0end – the fundamental frequency at the end of a call; f0max – the maximum fundamental frequency; f0min – the minimum fundamental frequency; fpeak – the frequency of maximum amplitude. The spectrogram was created using a sampling frequency of 256 kHz, Hamming window, FFT 1024 points, frame 50% and overlap 93.75%.

(f0end) with the reticule cursor (Figure 1). We calculated the depth of frequency modulation (df0) as the difference between f0max and f0min.

For each USV, we measured in the power spectrum window of Avisoft the frequency of maximum amplitude (fpeak) from the call's mean power spectrum (Figure 1). We did not measure the power quartiles, as many calls were produced during the loud background noise arising from animal digging and movements. Additionally, for USVs in regular series, we measured the time interval between the calls (from the end of the preceding call to the start of the next call) and calculated the number of calls within series.

USV contour shapes and nonlinear vocal phenomena

In the spectrogram window of Avisoft, we classified the ultrasonic calls manually according to four f0 contour shapes: flat, chevron, upward and downward (Figure 2). This classification was based (with modifications) on classifications developed for domestic mice *Mus musculus* (Scattoni et al. 2008; Grimsley et al. 2011; Arriaga and Jarvis 2013), yellow steppe lemmings *Eolagurus luteus* (Yurlova et al. 2020) and gerbils (Zaytseva et al. 2019; Kozhevnikova et al. 2021). The flat contour was denoted when the difference between f0min and f0max was less than 6 kHz. When the difference between f0min and f0max exceeded 6 kHz, the denoted contours could be the chevron (up-down one time), upward (ascending from start to end) or downward (descending from start to end). We did not encounter USVs with complex contours (up-down many times or U-shaped with difference between f0min and f0max more than 6 kHz).

For each USV, we noted the presence of nonlinear vocal phenomena (Figure 2): frequency jumps and subharmonics (Wilden et al. 1998; Zaytseva et al. 2019; Yurlova et al. 2020; Kozhevnikova et al. 2021). A frequency jump was noted when f0 suddenly changed for ≥ 10 kHz up or down (Figure 2) following Scattoni et al. (2008); Grimsley et al. (2011); Arriaga and Jarvis (2013); Yurlova et al. (2020) and Kozhevnikova et al. (2021). Subharmonics were denoted when the intermediate frequency bands of 1/2 of f0 were present between harmonics (Figure 2) following (Yurlova et al. 2020). We considered that subharmonics were present in call spectrum, if they occupied 10% or more of the entire call duration. For calls with frequency jumps, we identified the contour shape by virtually smoothing the contour, as if frequency jumps were lacking and the fundamental frequency contour were continuous (Yurlova et al. 2020; Kozhevnikova et al. 2021).

Call samples

Based on the acoustic structure, we subdivided USVs to the two call types: the upward-intense USVs and the variable-faint USVs (see the descriptions in the Results). The numbers of the two call types were strongly unequal in the acoustic recordings both in the wild (8 upward-intense USVs and 58 variable-faint USVs) and in captivity (358 upward-intense USVs and 108 variable-faint USVs). Thus, we used two different call samples for the statistical analyses of call acoustics.

A reduced call sample of 180 USVs was used for estimating the effects of call type and wild *vs* captivity recording on USV acoustic variables. For obtaining more balanced call samples, we shortened the number of USVs from captivity, by including in analysis 60
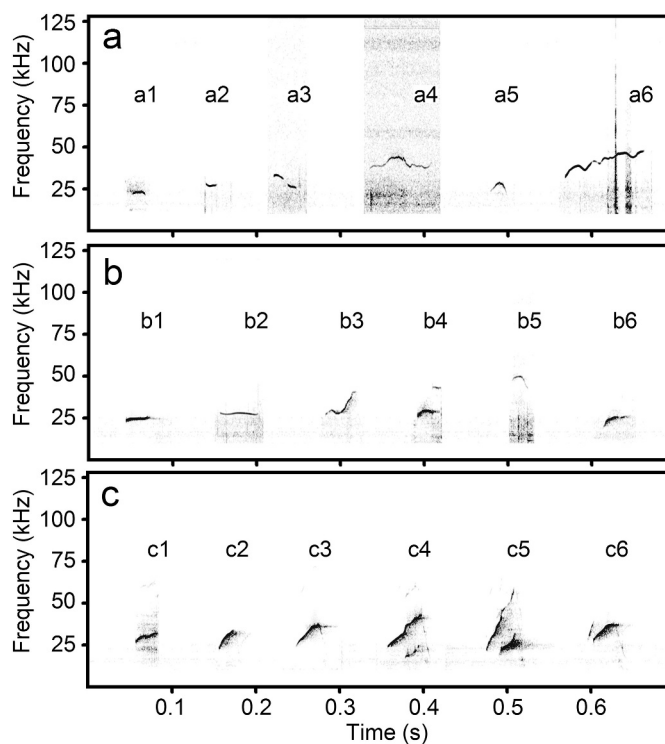
Figure 2. Spectrogram illustrating the four contour shapes and the two nonlinear phenomena (frequency jumps and subharmonics) occurring in two types of USVs in wild and captive northern mole voles. a: the variable-faint USVs recorded in the wild; b: the variable-faint USVs recorded in captivity; c: the upward-intense USVs recorded in captivity. a1: flat contour; a2: flat contour; a3: downward contour with break of fundamental frequency band; a4: chevron contour; a5: chevron contour; a6: upward contour; b1: flat contour; b2: flat contour; b3: upward contour; b4: flat contour with frequency jump up; b5: downward contour; b6: upward contour; c1: flat contour; c2: upward contour; c3: upward contour; c4: upward contour with subharmonics; c5: upward contour with frequency jump down; c6: upward contour with frequency jump down. c4 and c6 also display an additional weak-intense descending contour part. Spectrogram was created using a sampling frequency of 256 kHz, Hamming window, FFT 1024 points, frame 50% and overlap 87%. Wav-file of these calls is available in Supplementary Audio 1.

upward-intense USVs (each sixth measured call in order) and 54 variable-faint USVs (each second measured call in order).

The total sample of 532 measured USVs was used for comparison of percentages of different USV contour shapes in the two call types, of percentages of different nonlinear phenomena in the two call types, and for comparison of percentages of different call types between behavioural contexts. We identified three behavioural contexts, in which USVs were produced: 'from burrow' (51 USVs recorded from free-ranging individuals in the wild); 'between familiars' (15 USVs recorded during the single recording session in the bucket in the wild and 65 USVs recorded during the 4 experimental trials in captivity) and 'between nonfamiliars' (401 USVs recorded during the 4 experimental trials in captivity). Contexts 'familiars' and 'nonfamiliars' were selected because, for social

underground rodents, the primary factor affecting social behaviour is familiarity (Spinks et al. 1998).

Statistical analyses

Statistical analyses were conducted using STATISTICA, v. 8.0 (StatSoft, Tulsa, OK, USA). All means are given as mean ± SD. Significance levels were set at 0.05, and two-tailed probability values are reported. Distributions of 25 measured parameter values of 28 distributions did not depart from normality (Kolmogorov–Smirnov test, $p > 0.05$). As ANOVA is relatively robust to departures from normality (Dillon and Goldstein 1984), this was not an obstacle to the application of the parametric tests.

We used a Generalised Linear Mixed Model (GLMM) with Tukey's HSD (Honest Significant Difference) test to estimate the effects of call type and wild/captive factors on the acoustic variables of USVs with call type and wild/captive as fixed factors. To take into account animal identities, we also included in model the animal combination ID as random factor nested in wild/captive factor. The animal combination ID corresponded to all animals from the same family groups in the wild (IDs from 1 to 10) or to one of the six possible combinations of two individuals in the experimental trial in captivity (IDs from 11 to 16).

We used a GLMM to estimate the effects of call number per series on the value of inter-call interval between USVs in a series, with call number per series as fixed factor and animal combination ID as a random factor. We used a two-tailed Fisher exact test to compare percentages of different USV contour shapes in the two call types, percentages of different nonlinear phenomena in the two call types, and percentages of call types present in different contexts.

Results

Description of USVs

We identified two types of USVs which occurred in the northern mole voles both in the wild and in captivity. This distinction was the one we could objectively achieve with available data, so finer distinctions might be potentially possible with more call samples in the future.

The <u>upward-intense USV</u> (Table 1, Figures. 2, 3) was the call type with f0beg coinciding with the f0min and the f0end coinciding with the f0max. The duration ranged from 6 to 49 ms. The f0 contour was upward in the most USVs (87.7% calls) or flat (12.3% calls) if the f0 increase was less 6 kHz or if the caller interrupted the call (Figure 4). The depth of frequency modulation could reach 29 kHz. The peak frequency always coincided with the fundamental frequency band. Nonlinear phenomena were present in 18.3% of upward-intense USVs: 1.1% USVs contained subharmonics and 17.2% USVs contained frequency jumps, primarily jump-down (14.8%) (Figure 4).

The upward-intense USVs were produced, as a rule, at high intensity and in regular series (Figure 3). Only 33 (9.0%) of the 366 upward-intense USVs were produced alone, whereas the remaining 333 were emitted in series of 2–32 calls (mean 3.98 ± 5.10 calls, $n = 92$ series) with inter-call intervals from 36 ms to 493 ms (mean 146 ± 80 ms, $n = 273$

Table 1. Values (mean ± SD) of the acoustic variables of USVs of northern mole voles and GLMM results for comparisons between upward-intense and variable-faint call types and between calls of wild and captive animals on a reduced balanced sample of 180 USVs.

Acoustic variable	Upward-intense USV			Variable-faint USV			GLMM results		
	All, $N = 68$	Wild, $N = 8$	Captive, $N = 60$	All, $N = 112$	Wild, $N = 58$	Captive, $N = 54$	Upward-intense USV and variable-faint USV	Wild and captive	Interaction effect
Duration (ms)	26.8 ± 7.0	32.3 ± 5.7 [a]	25.6 ± 6.8 [a]	17.7 ± 13.6	18.4 ± 16.9 [b]	17.0 ± 9.0 [b]	$F_{1,162} = 13.37$; ***p < 0.001***	$F_{1,162} = 0.10$; $p = 0.76$	$F_{1,162} = 0.42$; $p = 0.52$
f0max (kHz)	35.32 ± 5.11	29.48 ± 2.86 [a]	36.10 ± 4.84 [b]	31.40 ± 7.78	31.13 ± 8.70 [a]	31.69 ± 6.73 [a]	$F_{1,162} = 0.01$; $p = 0.99$	$F_{1,162} = 4.77$ ***p = 0.03***	$F_{1,162} = 11.05$; ***p = 0.001***
f0min (kHz)	24.29 ± 3.01	20.63 ± 0.97 [a]	24.77 ± 2.96 [a]	27.02 ± 7.43	26.73 ± 8.07 [b]	27.34 ± 6.73 [b]	$F_{1,162} = 20.53$; ***p < 0.001***	$F_{1,162} = 4.60$; ***p = 0.03***	$F_{1,162} = 10.78$; ***p = 0.001***
f0beg (kHz)	24.50 ± 3.30	20.73 ± 1.12 [a]	25.01 ± 3.17 [a]	27.95 ± 7.42	28.23 ± 8.03 [b]	27.66 ± 6.77 [b]	$F_{1,162} = 25.55$; ***p < 0.001***	$F_{1,162} = 4.20$; ***p = 0.04***	$F_{1,162} = 13.68$; ***p < 0.001***
f0end (kHz)	34.44 ± 4.76	29.47 ± 2.86 [a,b]	35.10 ± 4.58 [b]	29.78 ± 8.15	28.78 ± 9.05 [a]	30.84 ± 7.00 [a]	$F_{1,162} = 0.39$; $p = 0.53$	$F_{1,162} = 5.16$; ***p = 0.02***	$F_{1,162} = 7.82$; ***p = 0.006***
fpeak (kHz)	30.43 ± 4.83	24.66 ± 1.87 [a]	31.20 ± 4.58 [b]	29.14 ± 7.52	28.99 ± 8.33 [a,b]	29.29 ± 6.17 [a,b]	$F_{1,162} = 3.01$; $p = 0.08$	$F_{1,162} = 5.19$; ***p = 0.02***	$F_{1,162} = 12.82$; ***p < 0.001***
df0 (kHz)	11.03 ± 4.80	8.85 ± 3.12 [a]	11.32 ± 4.93 [a]	4.38 ± 3.97	4.40 ± 4.11 [b]	4.35 ± 3.84 [b]	$F_{1,162} = 31.74$; ***p < 0.001***	$F_{1,162} = 0.32$; $p = 0.57$	$F_{1,162} = 0.70$; $p = 0.40$

Designations: N – number of ultrasonic calls; duration – call duration; f0max – the maximum fundamental frequency; f0min – the minimum fundamental frequency; f0beg – the fundamental frequency at the onset of a call; f0end – the fundamental frequency at the end of a call; fpeak – the frequency of maximum amplitude; df0 – depth of frequency modulation. The same letters next to values indicate the lack of significant differences between them (for interaction effect between call type and wild *vs* captive animals, $p > 0.05$, Tukey post hoc)
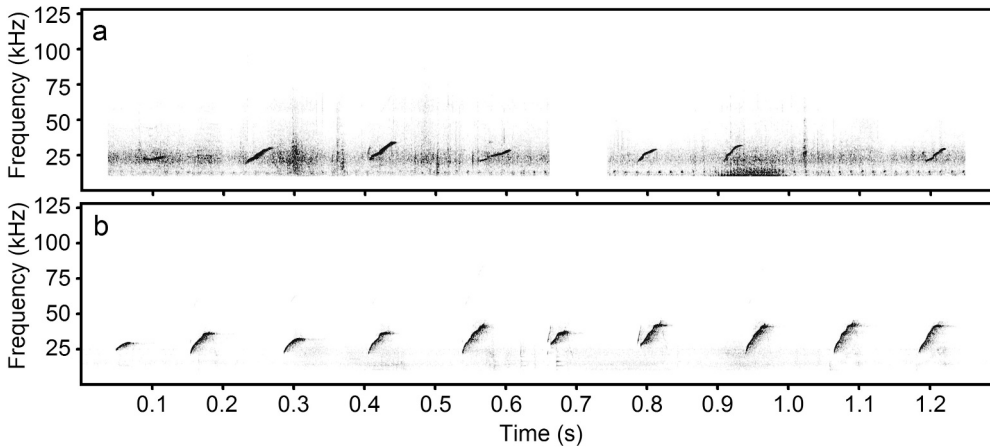
Figure 3. Spectrogram illustrating the series of upward-intense USVs in wild and captive northern mole voles. a: two natural series of 4 and 3 upward-intense USVs produced by two familiar males in the wild; b: a natural series of 10 upward-intense USVs produced by two nonfamiliar males in captivity. Spectrogram was created using a sampling frequency of 256 kHz, Hamming window, FFT 1024 points, frame 50% and overlap 87%. Wav-file of these calls is available in Supplementary Audio 2.
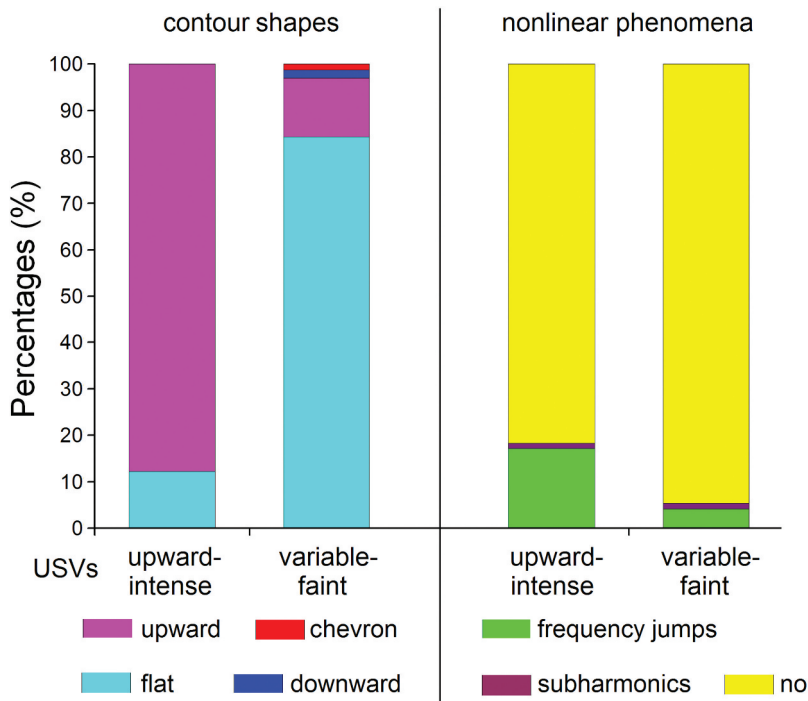

Figure 4. Percentages of four different USV contour shapes and percentages of two different nonlinear phenomena in the total sample of 366 upward-intense and 166 variable-faint USVs. Contour and nonlinear phenomena names are provided on the figure.

intervals). The value of the inter-call interval within a series did not depend on the number of calls within series ($F_{13,252} = 1.21$; $p = 0.27$).

In 46 of the 366 upward-intense USVs (all the 46 were recorded in captivity) we noticed an additional weak-intense contour part, descending from the point of the f0max (Figure 2). We ignored this weak-intense call part during our acoustic measurements, as it could only be recorded at closest distance and was only attributable to some very intense calls. In the wild, the upward-intense USVs did not occur in the recordings made from burrows and were only recorded from the two familiar males in the bucket. At the same time, in captivity, the upward-intense USV was the most widespread call type.

The variable-faint USV (Table 1, Figure 2) was the call type with more variable f0 contour and only slight f0 modulation. Duration was not long, although reaching up to 96 ms in one call. The f0 contour was flat in most USVs (84.3%), the upward contour occurred less frequently (12.7% USVs), we also registered USVs with downward (1.8%) and chevron (1.2%) contours (Figure 4). The peak frequency always coincided with the fundamental frequency band. Only 5.4% calls among the variable-faint USVs had non-linear phenomena: subharmonics (1.2% USVs) and frequency jumps (4.2% USVs), primarily jump up (2.4%) (Figure 4). The variable-faint USVs were produced at low intensity compared to the upward-intense USVs, and were not organised in the regular series. The variable-faint USVs were recorded both in the wild and in captivity.

Acoustic comparison of call types

GLMM showed that upward-intense USVs had a longer duration and a larger depth of frequency modulation compared to variable-faint USVs (Table 1). At the same time, the upward-intense USVs had a lower f0min and f0beg than the variable-faint USVs, whereas the f0max and f0end and fpeak values did not differ between call types (Table 1).

The upward-intense USVs from the wild had a lower f0max and fpeak values compared to the upward-intense USVs from captivity ($p = 0.03$ and $p = 0.02$ respectively, Tukey post hoc); the remaining acoustic variables did not differ between call types (Table 1). We did not find any differences in values of acoustic variables between variable-faint USVs from the wild and from captivity (Table 1).

Contextual use of call types

The use of the two call types differed among the three behavioural contexts (Figure 5). In the context 'from burrow' only the variable-faint USVs were present. In the context 'between nonfamiliars', 79.8% registered calls were the upward-intense USVs and 20.2% calls were variable-faint USVs. In the context 'between familiars', 57.5% registered calls were the upward-intense USVs and 42.5% calls were variable-faint USVs (Figure 5). All differences between contexts were significant (Fisher exact test, $p < 0.001$ for all comparisons). No differences (Fisher exact test, $p = 0.78$) was found for the contextual comparisons between familiars in nature (53.3% upward-intense USVs and 46.7% variable-faint USVs) and in captivity (58.5% upward-intense USVs and 41.5% variable-faint USVs) (Figure 5).

Observations of behaviour during emission of USVs showed that northern mole voles produced the upward-intense USVs at olfactory and tactile contacts with each other
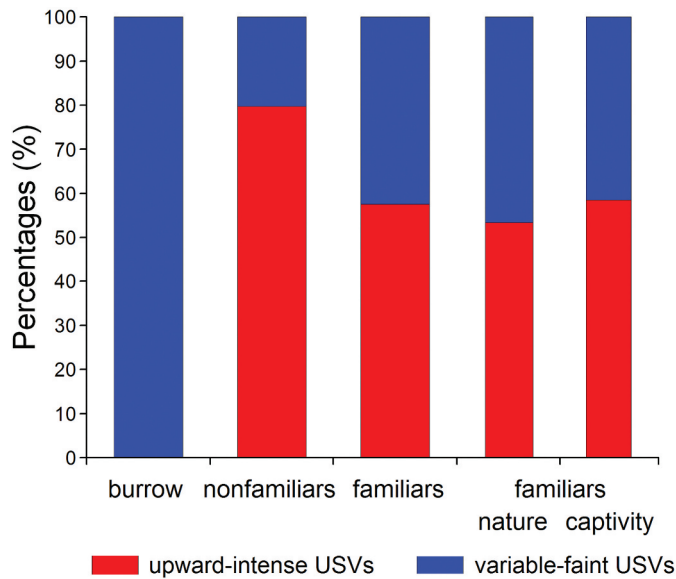
Figure 5. Percentages of upward-intense USVs and variable-faint USVs in three different contexts: from burrow, between nonfamiliars and between familiars in the total sample of 532 ultrasonic calls from northern mole voles. The context 'between familiars' was additionally subdivided to between familiars in nature and between familiars in captivity.

(primarily naso-nasal contacts) but only very rarely produced the upward-intense USVs when moving without interaction with conspecific. Contact between animals commonly resulted in eliciting a few upward-intense USVs organised in a series rather than one single USV. Sometimes, two contacting animals vocalised simultaneously; in such cases, their upward-intense USVs superimposed each other so that, on spectrogram, a researcher could see the overlapping contours of the calls from the two different individuals.

In the experimental trials with nonfamiliar animals, emission of the upward-intense USVs attended nearly all contacts, both peaceful and aggressive. In the three experimental trials with nonfamiliar animals (two trials female-male and trial male–male) we only observed the peaceful contacts, in the remaining female–female trial, the contacts were attended with weak aggression. Probably in this trial, the upward-intense USVs were produced by the aggression recipient, because the aggressive individual produced a series of audible calls. In the experimental trials with familiar animals, the emission of upward-intense USVs attended only some contacts of animals, whereas in most cases the familiars contacted without emission of upward-intense USVs.

Variable-faint USVs were the only call type produced from burrows by wild northern mole voles, when a caller moved towards the burrow entrance to plug it. The animals also produced the variable-faint USVs when moving in the experimental setup or in the own cage without immediate contact with conspecifics. We did not register the emission of variable-faint USVs during contacts between animals. The animals did not produce the variable-faint USVs simultaneously as we did not find any single overlap of the variable-

faint USVs on each other. We also did not find any single overlap of variable-faint USVs with upward-intense USVs.

Discussion

In this study, we revealed for the first time the ultrasonic vocalisations in a rodent strongly specialised for subterranean life. We recorded the subterranean northern mole voles *Ellobius talpinus* in nature from their burrows and then verified the recorded ultrasonic calls as belonging to this species during experiments conducted in captivity. We were able to distinguish two types of ultrasonic calls, the upward-intense USVs and the variable-faint USVs, differing in the shape of fundamental frequency contour and in the values of acoustic variables. In nature from the burrows, only the variable-faint USVs were produced, whereas wild-captured and captive animals produced both call types. We did not find any differences in the acoustic variables of the variable-faint USVs from the wild and from captivity. At the same time, some acoustic variables of the upward-intense USVs differed between the calls recorded in the wild and in captivity, which could be due to a small sample of calls of this type available from the wild.

The presence of ultrasonic calls in a subterranean rodent argues against the hypothesis of convergent evolution of the vocal and auditory systems in subterranean rodents, involving low-frequency hearing and low-frequency vocalisations within the audible range of frequencies (Begall et al. 2007b; Schleich and Francescoli 2018). Instead, our study supports previous findings that rodents can produce ultrasonic vocalisations, even when they have very low-frequency audible calls (Zaytseva et al. 2019, 2020) and hear in a very low frequency range (Lay 1972).

Overall, the acoustics of ultrasonic calls of northern mole voles (17.0–32.3 ms in duration, 20.63–36.10 kHz in fundamental frequency) were similar to those reported in adults of other Arvicolinae species, which primarily range in fundamental frequency from about 25 to 45 kHz (reviews in: Sales 2010; Rutovskaya 2018; Yurlova et al. 2020). Most USVs of adult surface-dwelling vole species were recorded in captivity, either in the aggressive context (encounters of same-sex and different-sex animals during experiments) or in a sexual context (matings, copulations), including the hormonal stimulation of sexual behaviour.

During aggressive behaviour, bank voles *Cletrhrionomys* (*Myodes*) *glareolus* produce 61–71 ms USVs with f0 of 25–33 kHz (Kapusta et al. 2007; Kapusta and Sales 2009; Kapusta and Pochroń 2011; Kapusta 2012); root voles *Microtus oeconomus* produce 15–20 ms USVs with f0 of about 31–35 kHz (Kapusta et al. 1999); common voles *Microtus arvalis* produce 66–68 ms USVs with f0 of about 28–35 kHz (Kapusta et al. 2007; Kapusta and Sales 2009) and field voles *Microtus agrestis* produce 63–68 ms USVs with f0 of about 42–45 kHz (Kapusta et al. 2007; Kapusta and Sales 2009).

During sexual interactions, male bank voles produce three types of USVs differing in the shape of fundamental frequency contour, of overall duration 61–70 ms and f0 of 22–37 kHz (Kapusta and Kruczek 2016). During sexual and friendly social interactions, male and female prairie voles *Microtus ochrogaster* produce USV types ranging in duration from 30 to 150 ms and with f0 of 30–45 kHz, varying in contour shape and in the number of frequency jumps (Ma et al. 2014). In other surface-dwelling voles, the reported during sexual behaviour f0 ranges of USVs were 35–40 kHz in the field vole (Mandelli and Sales 1997), 25–50 kHz in the

pine vole *Microtus pinetorum* (Geyer 1979) and about 31 kHz in the montane vole *Microtus montanus* (Pierce et al. 1989). We can therefore conclude that calls of surface-dwelling vole species were acoustically similar with USVs of northern mole voles.

Among lemmings, USVs produced by the steppe lemmings *Lagurus lagurus* in a sexual context, were up to 60 ms in duration and had f0 from 50 to 75 kHz (Sales 1972). In the northern collared lemming *Dicrostnyx groenlandicus* in a sexual context, both males and females produced ultrasonic twitters with rapid and deep modulation of fundamental frequency between 15 and 35 kHz (Brooks and Banks 1973). In the yellow steppe lemmings, USVs produced under discomfort had duration of about 30 ms, f0 ranging of about 25–39 kHz and often contained frequency jumps, similar with northern mole voles (Yurlova et al. 2020; Klenova et al. 2021).

Our data suggest that USVs of subterranean northern mole voles do not display any prominent differences in contour shapes and the values of fundamental frequency and duration from the USVs of the surface-dwelling Arvicolinae species. We can therefore conclude that transit of a vole species to subterranean life seems did not affect the acoustic communication in the ultrasonic range of frequencies. The explaining hypothesis for the lack of substantial changes in the acoustic characteristics of USVs in the subterranean rodents compared to those of surface-dwelling species can be that the northern mole voles communicate with USVs primarily at close range during friendly interactions (as in this study) and probably also during sexual and aggressive contacts. For such close-distance communication, sound propagation through the environment seems unimportant. Our findings of USV-based communication in a subterranean rodent suggest that USVs attending animal interactions at close distance can probably also be found in other species of subterranean rodents, especially during observations of animal groups in captivity.

However, whereas the prominent differences in USVs are lacking between adults of the subterranean mole vole and surface-dwelling Arvicolinae species, some important differences between USVs are possible between USVs of the infants. Whereas studies of USVs of infant Arvicolinae species are available (Brooks and Banks 1973; Mandelli and Sales 2004; Szentgyörgyi et al. 2008; Terleph 2011; Blake 2012; Yurlova et al. 2020), similar studies of infant USVs of subterranean rodents have yet to be conducted.

Furthermore, in many subterranean rodents, rich vocal repertoires of human-audible calls are reported (Pepper et al. 1991; Credner et al. 1997; Veitl et al. 2000; Bednářová et al. 2013; Dvořáková et al. 2016). Overall, the number of call types is larger in the subterranean than in surface-dwelling rodents and the number of call types is larger in the social species than in the solitary species (Schleich et al. 2007; Schleich and Francescoli 2018). The northern mole vole is a subterranean social species, whose repertoire of the audible calls has yet to be studied. It is expected that mole voles have a more diverse repertoire of audible calls compared to the relative surface-dwelling species.

Ethics

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Disclosure statement

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