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ORIGINAL ARTICLE

Audible, but not ultrasonic, calls reflect surface-dwelling or subterranean specialization in pup and adult Brandt's and mandarin voles

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Abstract

For human-audible vocalizations (below 20 kHz) of rodents, subterranean lifestyle results in low-frequency calls coupled with low-frequency hearing. For ultrasonic vocalizations (above 20 kHz), the effect of subterranean lifestyle on the acoustics is unknown. This study fills this gap of knowledge, by comparing vocalizations of two closely related species, the surface-dwelling Brandt's vole *Lasiopodomys brandtii* (17 pups, 19 adults) and the subterranean mandarin vole *L. mandarinus* (15 pups, 16 adults). As predicted, the audible calls (AUDs) were substantially higher-frequency in *L. brandtii* than in *L. mandarinus,* in either pups or adults. In contrast to AUDs, the ultrasonic calls (USVs) did not differ in frequency variables between species, in either pups or adults. Interspecies differences were found in duration: AUDs were shorter in adult *L. brandtii* than in adult *L. mandarinus*, USVs were longer in pup *L. brandtii* than in pup *L. mandarinus*, and the low-frequency USVs of adult *L. brandtii* were longer than low-frequency USVs of adult *L. mandarinus*. We advance a hypothesis that shift towards higher-frequency AUDs in *L. brandtii* compared to *L. mandarinus* was triggered by the evolutionary emergence of the high-frequency audible alarm call, which is only present in *L. brandtii* but absent in *L. mandarinus*. We discuss that USVs may be resistant to these selection pressures as close-distant social signals.

Significance statement

Relationship between ecological specialization, such as subterranean or surface-dwelling lifestyle, and the acoustic traits of communicative signals in rodents evoke interest for over than 30 years. So far, the relationship between vocalization and subterranean life (low-frequency calls and low-frequency hearing) was only reported for calls produced by rodents in human-audible range of frequencies. No data was available for ecological adaptations of ultrasonic calls; moreover, even the existence of ultrasonic calls in subterranean rodents was unknown to recent time. Comparative studies of closely related subterranean and surface-dwelling rodent species might highlight the evolution of acoustic traits related to these ecological specializations.

Keywords Acoustic communication · Arvicolinae species · Audible and ultrasonic vocalization · Subterranean rodents

Introduction

Subterranean lifestyle is known in more than 250 rodent species (Nevo 1999; Lacey et al. 2000; Begall et al. 2007a). Life underground under poor ventilation and high humidity leads to many morphological, physiological, and behavioral adaptations (Begall et al. 2007a; Park et al. 2017; Vejmělka et al. 2021) governed by the respective genes (e.g., Jiao et al. 2019; Bondareva et al. 2021; Sahm et al. 2021).

Deprivation from most sensory stimuli due to underground life also affects rodent acoustic communication, which is especially important in the conditions of dark burrow tunnels, where visual communication is obstructed (Begall et al. 2007b; Burda et al. 2007). Rodent human-audible calls (AUDs, below 20 kHz) are more variable in social than in solitary subterranean species (Dvořáková et al. 2016;

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Schleich and Francescoli 2018) and display a convergent evolution of sound-producing and auditory systems (Begall et al. 2007b). This convergent evolution involves the using of low-frequency AUDs for communication (Nevo et al. 1987; Credner et al. 1997; Begall et al. 2007b; Knotková et al. 2009; Pepper et al. 2017; Okanoya et al. 2018; Schleich and Francescoli 2018) and the maximum hearing sensitivity at low frequencies (Müller and Burda 1989; Heffner and Heffner 1992; Kössl et al. 1996; Brückmann and Burda 1997; Dent et al. 2018; Okanoya and Screven 2018). Communication with low-frequency AUDs is effective in burrows, as these calls propagate to a distance of a few meters without weakening and even become more intense due to burrow stethoscope effect (Heth et al. 1986; Lange et al. 2007; Schleich and Antenucci 2009; Okanoya and Screven 2018).

Regarding the underground ultrasonic communication in rodents, data are scarce. The concept of convergent evolution of low-frequency hearing and low-frequency AUDs suggests that ultrasonic calls (USVs, above 20 kHz) might not be used by subterranean rodents (Begall et al. 2007b). However, recent studies show that some subterranean Arvicolinae species, as adult northern mole voles *Ellobius talpinus* (Volodin et al. 2022) and pup mandarin voles *Lasiopodomys mandarinus* (Yu et al. 2011), are capable of producing USVs. Furthermore, one recent study reports the audition in the ultrasonic range of frequencies in the subterranean rodent, the coruro *Spalacopus cyanus* (Caspar et al. 2021). So, a convergent evolution of ultrasonic vocalization and high-frequency hearing is potentially expectable in subterranean rodents.

Comparative studies of AUDs and USVs of subterranean and surface-dwelling Arvicolinae species might highlight the relationship between lifestyle and the acoustic traits of these calls (Rutovskaya 2018). Sister species, the Brandt's vole *L. brandtii* and mandarin vole *L. mandarinus*, represent a promising comparative model for revealing the acoustic adaptations related to surface-dwelling or subterranean lifestyle. Whereas *L. mandarinus* is adapted to subterranean life, *L. brandtii* displays surface-dwelling lifestyle (Tai and Wang 2001; Dong et al. 2018; Sun et al. 2019; Cui et al. 2020). While *L. brandtii* forage on grass aboveground (Cui et al. 2020), *L. mandarinus* primarily forage in tunnels of up to 95 m long with multiple (up to 70) exits and on surface in immediate vicinity to burrow entrance (Dmitriev et al. 1980; Smorkatcheva et al. 1990). Phylogenetic analyses suggest that *L. brandtii* and *L. mandarinus* were the last two species diverged from the common trunk of the genus *Lasiopodomys* approximately 0.5–0.95 million years ago (Abramson et al. 2009; Li et al. 2017; Shi et al. 2021). Lifestyle (surface-dwelling or subterranean) of the common ancestor of *L. brandtii* and *L. mandarinus* is unknown. Both species are steppe-dwellers in China, Mongolia, and Transbaikalia (Russia), with partly overlapping distribution areas between species (Smorkatcheva et al. 1990; Smith and Xie 2008; Alexeeva et al. 2015; Lebedev et al. 2016). Both species live in extended family-based groups (*L. brandtii*: Dmitriev et al. 1980; *L. mandarinus*: Smorkatcheva 1999; Tai and Wang 2001). Both species become mature early: in *L. brandtii*, sexual maturity for males and females is reached at about 35 days of age (Zorenko and Jakobsone 1986). In *L. mandarinus*, males and females are sexually mature at 55–60 and 38–45 days of age, respectively (Zorenko et al. 1994; Smorkatcheva 1999).

As in Arvicolinae rodents, pup age and body size influence the acoustic parameters of both AUDs and USVs (Terleph 2011; Yurlova et al. 2020; Volodin et al. 2021; Warren et al. 2022); correct interspecies comparison of the acoustics is only possible between matched age classes and between species matched in body size. So, careful control of animal body size and age would be necessary for the comparative study of vocalizations in vole species.

Adults of both vole species are active throughout 24-h cycle (*L. brandtii*: Khruscelevsky and Kopylova 1957; *L. mandarinus*: Smorkatcheva et al. 1990). Aboveground activity of adult *L. brandtii* is primarily diurnal (Khruscelevsky and Kopylova 1957; Wan et al. 2006; Cui et al. 2020), but adult *L. mandarinus* emerge to ground surface in dark time (Dmitriev et al. 1980; Smorkatcheva et al. 1990). Newborns of both species are raised at similar conditions of burrow (*L. brandtii*: Khruscelevsky and Kopylova 1957; *L. mandarinus*: Smorkatcheva et al. 1990).

Acoustic structure of adult AUDs differs between *L. brandtii* and *L. mandarinus*. Audible sharp squeaks, occurring in all types of interactions between animals from friendly to aggressive, are twice higher in fundamental frequency (f0) in *L. brandtii* (4.1–7.5 kHz) than in *L. mandarinus* (1.5–1.8 kHz) (Rutovskaya 2011, 2012, 2018). Male courtship songs are substantially higher-frequency in *L. brandtii* (13.7 kHz) than in *L. mandarinus* (1.2 kHz) (Rutovskaya 2018). Only *L. brandtii* produce audible high-frequency (10.2–10.7 kHz) alarm calls, which potentially evolved in this species for defense against avian predators (Rutovskaya 2012, 2018). Pup isolation USVs are only described in 2-–14-day-old *L. mandarinus* (Yu et al. 2011), whereas pup isolation AUDs or adult USVs have yet to be studied in either *L. brandtii* or *L. mandarinus*. Whereas a usual procedure of short-term isolation of pups from the nest is sufficient for eliciting AUDs and USVs in Arvicolinae pup voles (Yu et al. 2011; Yurlova et al. 2020), for adult voles, more elaborated call-eliciting procedures are applied, e.g., touch with a cotton bud, handling, and body measurements (Yurlova et al. 2020; Klenova et al. 2021; Volodin et al. 2021).

The aim of this study was to compare between captive *L. brandtii* and *L. mandarinus* the acoustics of AUDs and USVs, emitted by pups and adults of both species during short-term isolation and handling. For AUDs, we predicted that pup and adult f0s might be higher-frequency in surface-dwelling *L. brandtii* than in subterranean *L. mandarinus*. This prediction was based on published data reporting acoustic differences of AUDs between adult *L. brandtii* and *L. mandarinus* (Rutovskaya 2018) and on published data reporting the low-frequency hearing in subterranean rodents (Heffner and Heffner 1992; Gerhardt et al. 2017; Okanoya et al. 2018). For USVs, we had not any special prediction, in the lack of comparative data.

Methods

Study site, animals and dates

Calls (AUDs and USVs) of pup and adult *L. brandtii* and *L. mandarinus* of 1–4 generation in captivity were recorded from the beginning of March 2019 to mid-October 2020 in captive colonies of the Biological Institute of Saint Petersburg University (Russia). To decrease observer bias, blinded methods were mostly used when behavioral data were recorded and/or analyzed: audio recording trials conducted by one researcher (IAV) were primarily analyzed by another researcher (MMD) and vice versa. Colony founders were 7 *L. brandtii* obtained in 2017 from the Chita region, Transbaikalia, Russia, and 20 *L. mandarinus* (7 individuals obtained in 2017 from the Djida region, Buryatia, Russia, and 13 individuals obtained in 2019 from the Selenga region, Buryatia, Russia).

Subject *L. brandtii* were 17 2–5-day-old unsexed pups from 14 litters delivered by 13 parental pairs, 1–2 pups per litter, and 19 adults (10 males, 9 females) aged from 72 to 391 days old. Subject *L. mandarinus* were 15 2–5-day-old unsexed pups from 14 litters delivered by 10 parental pairs, 1–2 pups per litter, and 16 adults (9 males, 7 females) aged from 65 to 867 days old. Day of pup birth was considered zero day of pup life (Supplementary Table S1).

Housing

Animals were kept in pairs with one or a few subsequent litters in glass terraria (25 × 50 × 30 cm or 30 × 60 × 40 cm depending on group size) with wire-mesh roofs, with sawdust layer of 15–20 cm, toilet paper as nest material, and one or two wooden hides. The animals were fed each second day with rabbit chow, oat (grain and sprouts), and willow branches. Carrot, beet, and apples were provided ad libitum as a source of both food and water.

Experimental procedure

Call-eliciting trials were conducted in a separate room where only the focal animal was present. The experimental procedure (following Zaytseva et al. 2019) was the same for pups and adults and for both species. The focal animal was tested singly in only one trial; therefore, all calls could be identified as belonging to the focal individual. Trials were conducted in daytime at room temperature 20–25 °C and natural lighting from the window. All electric equipment (lamps, fridges, computers) were turned off for reducing the audible and ultrasonic background noise. The elicited calls were related to moderate discomfort, experienced by pups due to the cooling out of the nest, and experienced by adults due to short-term social isolation and handling. These calls were not distress-related for pups and for adults, as pup cooling was short term and moderate; whereas for the adults, the short-term isolation from mates and human handling was reminiscent of routine procedure during regular cage cleanings occurring every 5–7 days, to which the animals were habituated.

A focal animal was transferred in a small clean plastic container from a home cage to the experimental room on the same floor within 60 s and subjected to the 4-stage 480-s experimental procedure provoking vocalization. Test trial included four stages: (1) isolation for 120 s in a plastic container 190 × 130 × 70 mm (for pups) or in a plastic cylinder without bottom with diameter 320 mm, height 400 mm (for adults); (2) touch with a cotton bud for 120 s approximately 2 times per second; (3) handling by fixing in human hand and keeping with belly up for 120 s; and (4) body measurements for about 120 s. The start of each trial stage was indicated with voice mark of experimenter (MMD or IAV), and the end of measurements was the end of a trial. After the trial, the focal animal was weighted on the electronic scales G&G TS-100 (G&G GmbH, Neuss, Germany, accurate to 0.01 g), in the same container that served for the animal transfer.

The measurements included successive measuring of body length (from tip of muzzle to anus) and head length (from tip of muzzle to occiput), with electronic calipers (Kraft Tool Co., Lenexa, Kansas, USA) accurate to 0.01 mm. This cycle of measurements was repeated thrice and the average values were calculated. Weighting and measurement data were used for estimating the potential differences in body size between study species.

Focal animal was returned to home cage immediately after the end of a trial and weighting. Before the next test trial, the experimental setup was washed with soapy water and rubbed with cotton with alcohol, to avoid potential odor effects on vocalization.

Call recording

During each 4-stage test trial, a continuous recording of AUDs and USVs of the focal individual was conducted. For recording AUDs at sampling rate 48 kHz and resolution 16 bit, we used a solid-state recorder Marantz PMD 660 (D&M Professional, Kanagawa, Japan) with cardioid microphone Sennheiser K6-ME64 (Sennheiser Electronic, Wedemark, Germany).

For recording USVs at sampling rate 256 kHz and resolution 16 bit, we used a Pettersson D1000X recorder with built-in microphone (Pettersson Electronik AB, Uppsala, Sweden) and an Echo Meter Touch 2 PRO recorder (Wildlife Acoustics, Inc., Maynard, MA USA), which also served for tracking the real-time spectrogram of USVs on compatible smartphone. As parallel recordings with Pettersson and Echo Meter displayed similarly high quality and did not affect the measured acoustic variables, we could use for acoustic analyses calls recorded with either system.

The sonic and ultrasonic microphones were set at 25 cm above the focal animal, providing a good signal-to noise ratio during recording. Acoustic recordings for each test trial were stored as two wave files, one for AUD and one for USV recording.

Call samples

For acoustic analysis, we selected calls (AUDs and USVs) of best quality (not superimposed with strikes or other noises, with a good signal-to noise ratio). To minimize potential pseudoreplication, we avoided taking the calls following each other, because successive calls can be more similar to each other than calls separated with other calls. Calls for analysis were evenly taken from different parts of the trial stages. In addition, contour shape or presence of nonlinear phenomena was not taken into account during selection of calls for analysis. We also limited the number of calls included in analysis per individual.

For analysis of acoustic variables of AUDs, we selected AUDs from 10 individual *L. brandtii* and 10 individual *L. mandarinus* pups (20 AUDs per pup) and selected AUDs from 12 individual *L. brandtii* and 10 individual *L. mandarinus* adults (7–21 AUDs per adult). Pup AUDs were evenly taken from different parts of the 1st (isolation) trial stage. Adult AUDs were primarily taken from the 3rd (handling) and 4th (body measurements) trial stages, because adult voles did not emit AUDs at 1st (isolation) trial stage and only 14 AUDs of *L. brandtii* could be taken from 2nd (touch) stage. In total, we included in analysis 802 AUDs: 200 pup AUDs per species and 201 adult AUDs per species (Supplementary Table S2).

For analysis of acoustic variables of USVs, we selected USVs from 11 individual *L. brandtii* and 11 individual *L. mandarinus* pups (20 USVs per pup, but one individual only provided 14 calls). Pup USVs were primarily taken from the 1st (isolation) trial stage and, in addition, some calls (30 USVs of *L. brandtii* pups and 36 USVs of *L. mandarinus* pups) were taken from the 2nd stage, because the number of calls from the 1st stage was limited.

Adult USVs of each species were split in two non-overlapping categories, the low-frequency USVs (LF USVs) and the high-frequency USVs (HF USVs) (see the "Results" section). Thus, for investigating variation of the full set of acoustic parameters between the two categories of adult USVs and comparing them with pup USVs, we classified all USVs to three categories: (1) pup USVs; (2) adult LF USVs, and (3) adult HF USVs; and called the corresponding nominal variable as "USV category."

Adults rarely produced USVs, so we included in analysis all USVs produced by 15 individual adult *L. brandtii* and 11 individual adult *L. mandarinus*, 6–23 USVs of each category, the low-frequency (LF USVs) and the high-frequency (HF USVs). Adult USVs were taken from all the four trial stages. In total, we included in analysis 1072 USVs: 220 pup USVs of *L. brandtii*, 214 pup USVs of *L. mandarinus*, 211 LF USVs and 139 HF USVs of adult *L. brandtii*, and 105 LF USVs and 183 HF USVs of adult *L. mandarinus* (Supplementary Table S3).

Call analysis

Acoustic variables of AUDs and USVs were measured using Avisoft SASLab Pro (Avisoft Bioacoustics, Berlin, Germany); data of measurements were automatically exported to Microsoft Excel (Microsoft Corp., Redmond, WA, USA). Before measurements, we high-pass filtered all wav-files at 0.2 kHz (for AUDs) or at 10 kHz (for USVs), to remove background noise.

Spectrograms for measurements were created at sampling rate 48 kHz (for AUDs) or 256 kHz (for USVs), Hamming window, fast Fourier transform (FFT) 1024 points, frame 50%, and overlap 93.75% for AUDs and 87.5% for USVs. For each AUD or USV, we manually measured, in the spectrogram window of Avisoft, the duration with the standard marker cursor, and the maximum fundamental frequency (f0max), the minimum fundamental frequency (f0min), the fundamental frequency at the beginning of a call (f0beg), and the fundamental frequency at the end of a call (f0end) with the reticule cursor. For each AUD or USV, we measured the peak frequency (fpeak) in the power spectrum window of Avisoft (Fig. 1).

AUD and USV contours

By visual inspection of call in the spectrogram window of Avisoft, we classified AUDs and USVs to one of five

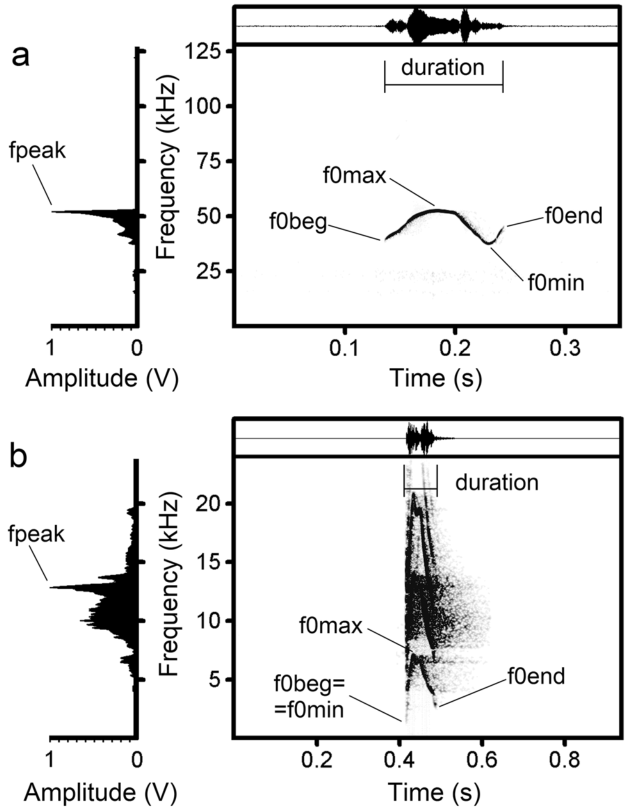


Fig. 1 Measured acoustic variables in: **a** ultrasonic (USV) call of pup *L. mandarinus*; **b** audible (AUD) call of adult *L. brandtii*. Spectrogram (right) and mean power spectrum of the entire call (left). Designations: duration – call duration; f0beg – the fundamental frequency at the onset of a call; f0max – the maximum fundamental frequency; f0end – the fundamental frequency at the end of a call; f0min – the minimum fundamental frequency; fpeak – the frequency of maximum amplitude. Spectrogram was created using sampling frequency 256 kHz (for USVs) or 48 kHz (for AUDs), Hamming window, fast Fourier transform (FFT) 1024 points, frame 50%, overlap 87.5% (for USVs) or 93.75% (for AUDs)

contours (Fig. 2): flat, chevron, upward, downward, and complex (following Yurlova et al. 2020; Kozhevnikova et al. 2021). Flat contour was determined if the difference between f0min and f0max was less than 0.6 kHz (in AUDs) or less than 6 kHz (in USVs). In cases where the difference between f0min and f0max was equal or larger than 0.6 kHz or 6 kHz, respectively, a call contour could be classified as chevron (up and down), upward (ascending from start to end), downward (descending from start to end), or complex (up and down a few times or U-shaped) (Fig. 2).

Nonlinear phenomena and note composition in AUDs and USVs

Each AUD and USV was checked for presence of nonlinear phenomena (Fig. 3): biphonations, subharmonics, deterministic chaos, and frequency jumps (Wilden et al. 1998; Yurlova et al. 2020; Kozhevnikova et al. 2021). Biphonation was noted when two independent fundamental frequencies, the low (f0) and the high (g0), as well as their combinatory frequency bands (g0 minus f0; g0 minus 2f0; etc.) were present in call spectrum. Subharmonics were noted when frequency bands of 1/2 or 1/3 of f0 were present in call spectrum (Fig. 3). Deterministic chaos was noted when a chaotic segment (sometimes with residual fundamental frequency) was present in call spectrum (Fig. 3). We only noted the presence of deterministic chaos and/or subharmonics, if the duration of call fragments containing these nonlinear phenomena comprised at least 10% of the entire call duration (Yurlova et al. 2020; Kozhevnikova et al. 2021).

We noted a presence of frequency jumps, when the f0 increased jump-like up or down for ≥ 1 kHz (for AUDs) or for ≥ 10 kHz (for USVs) (Fig. 3). As frequency jumps break the f0 contour to separate notes, we considered the calls without frequency jumps as one-note calls, the calls with one frequency jump as two-note calls, and calls with two or more frequency jumps as multi-note calls (Fig. 3). For determining the type of f0 contour in the calls containing frequency jumps, we virtually joined the parts of the broken contour of f0, following (Yurlova et al. 2020; Kozhevnikova et al. 2021).

In addition, we classified USVs accordingly to the three possible note compositions (1-note, 2-note, multi-note) based on presence of up or/and down frequency jumps over 10 kHz (Fig. 3). The 1-note USVs lacked frequency jumps; the 2-note USVs had one frequency jump (up or down); and the multi-note USVs had two or more frequency jumps (see, e.g., Zaytseva et al. 2019).

Statistical analyses

Statistical analyses were made with STATISTICA, v. 8.0 (StatSoft, Tulsa, OK, USA) and R 4.1.0 (R Development Core Team 2021). Means were presented as mean ± SD, and all tests were two-tailed and differences were considered significant whenever $p < 0.05$. We used one-way ANOVA for estimating the effect of factors species (separately for pups and for adults) and sex (only for adults, separately for each species) on the morphometric (body size-related) variables.

To analyze the acoustics of AUDs and USVs, we performed linear mixed effect models (LMM) using package *nlme* (Pinheiro et al. 2021) implemented in R. For AUDs, age (pup vs. adult), species, and their interaction were fitted as fixed terms. For USVs, LMMs included the USV category (pup USVs, adult LF USVs and adult HF USVs), species, and their interaction as fixed predictors. Individual identity was fitted as a random term in all models. Post hoc comparisons were performed with Tukey HSD test using *emmeans* package in R (Lenth 2021).

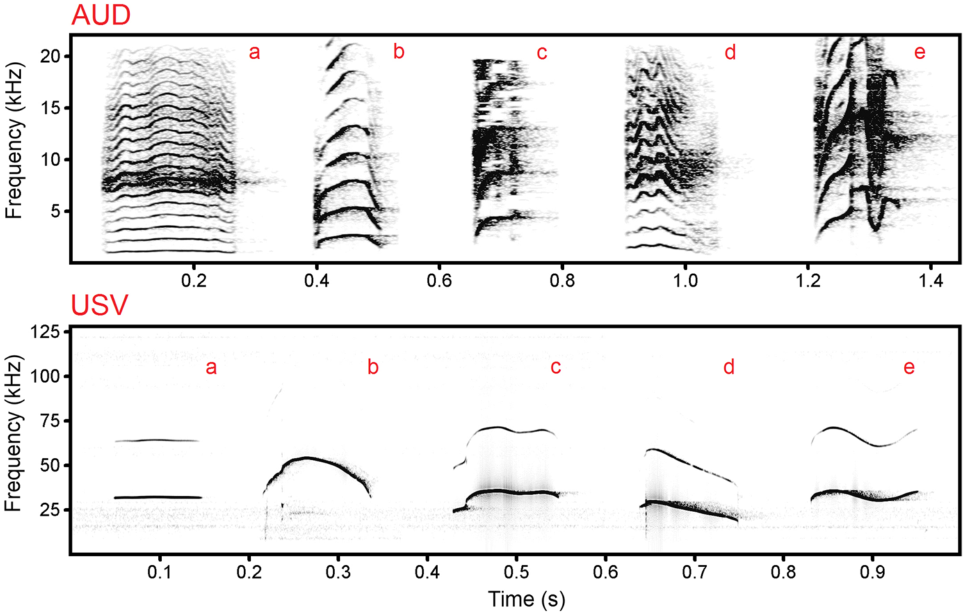


Fig. 2 Five contour shapes in audible (AUDs) and ultrasonic (USVs) vole calls. AUDs: **a** – flat in AUD of adult female *L. mandarinus*; **b** – chevron in AUD of 5-day-old pup *L. mandarinus*; **c** – upward in AUD of 4-day-old pup *L. brandtii*; **d** – downward in AUD of adult male *L. mandarinus*; **e** – complex in AUD of 5-day-old pup *L. brandtii.* USVs: **a** – flat in USV of 5-day-old pup *L. brandtii*; **b** – chevron in USV of 4-day-old pup *L. mandarinus*; **c** – upward in USV of 5-day-old pup *L. brandtii*; **d** – downward in USV of 2-day-old pup *L. brandtii*; **e** – complex in USV of 4-day-old pup *L. brandtii*. Spectrogram was created using sampling frequency 256 kHz (for USVs) or 44.1 kHz (for AUDs), Hamming window, fast Fourier transform (FFT) 1024 points, frame 50%, overlap 87.5% (for USVs) or 96.87% (for AUDs)

We used Fisher's exact test to compare percentages. We used discriminant function analysis (DFA) standard procedure to estimate the differences in values of acoustic variables between two categories of adult USVs (LF USVs and HF USVs). Variables with most contribution to discrimination were determined based on Wilk's lambda values.

Results

Age and body size variables

ANOVA did not reveal any interspecies differences regarding the age, body weight, body length, and head length, either for pups or for adults (Table 1). The comparison of body weight, body length, and head length between adult male and female *L. brandtii* did not reveal any significant differences ($F_{1,17} = 2.02$; $p = 0.17$; $F_{1,17} = 0.11$; $p = 0.75$; $F_{1,17} = 1.29$; $p = 0.27$, respectively). In adult *L. mandarinus*, body weight ($F_{1,14} = 0.42$; $p = 0.53$), and body length ($F_{1,14} = 1.84$; $p = 0.20$) did not differ between sexes as well, whereas head length was larger in males ($F_{1,14} = 5.50$; $p = 0.03$; 32.05 ± 1.38 mm and 30.50 ± 1.22 mm, respectively).

AUD contours and nonlinear phenomena

Pup and adult AUDs of *L. brandtii* and *L. mandarinus* displayed all the five possible contour shapes (Fig. 4). Chevron contour prevailed, being equally frequent in pups of both species ($p = 0.91$, Fisher's exact test). Upward contour was more frequent in pup *L. mandarinus* than in pup *L. brandtii* ($p < 0.001$). Complex contour was more frequent in pup *L. brandtii* than in pup *L. mandarinus* ($p < 0.001$). The remaining two (downward and flat) contours were both rare in pups of either species, without significant differences in the occurrence between them (Fig. 4).

As in pups, chevron contour prevailed in adults of either species; however, it was more frequent in adult *L. brandtii* than in adult *L. mandarinus* ($p < 0.001$, Fisher's exact test) (Fig. 4). In adult *L. brandtii*, flat contour practically lacked and upward contour was rare, whereas in adult *L. mandarinus*, flat and upward contours were similarly frequent ($p < 0.001$ in both cases). Complex contour was more frequent in adult *L. brandtii* than in adult *L. mandarinus* ($p < 0.001$). Downward contour was infrequent compared to other contours in adults of either species ($p = 0.06$) (Fig. 4).

Overall, chevron contour prevailed in pup and adult AUDs of either species, whereas all other contours were substantially less frequent. Complex contour was a few

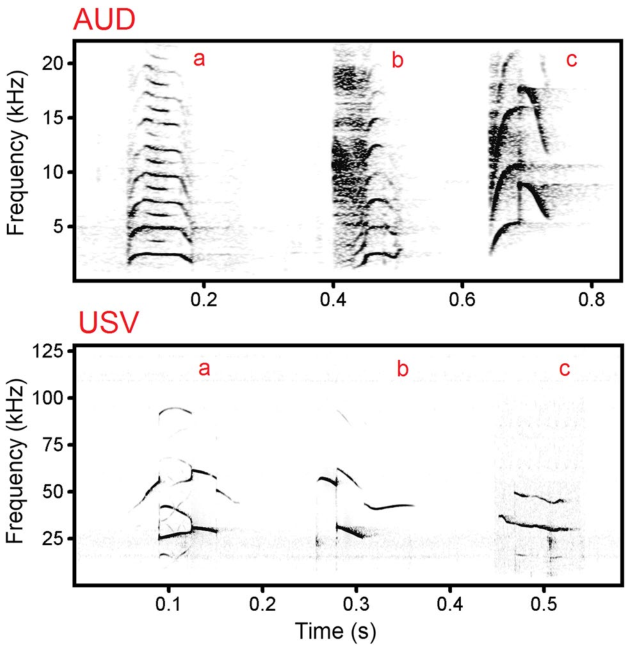


Fig. 3 Nonlinear phenomena in audible (AUDs) and ultrasonic (USVs) vole calls. AUDs: **a** – subharmonics in AUD of 5-day-old pup *L. mandarinus*; **b** – deterministic chaos in AUD of 5-day-old pup *L. mandarinus*; **c** – frequency jump up in AUD of 2-day-old pup *L. brandtii*. USVs: **a** – biphonation in USV of 4-day-old pup *L. mandarinus*; **b** – frequency jump down-up in USV of 2-day-old pup *L. mandarinus*; **c** – subharmonics in USV of an adult male *L. brandtii*. Spectrogram was created using sampling frequency 256 kHz (for USVs) or 44.1 kHz (for AUDs), Hamming window, fast Fourier transform (FFT) 1024 points, frame 50%, overlap 87.5% (for USVs) or 96.87% (for AUDs)

Table 1 Values (mean ± SD) for age and body size variables of pup and adult *L. brandtii* and *L. mandarinus*, and the results of interspecies comparison. *n* – number of individuals

Variable	*L. brandtii*	*L. mandarinus*	ANOVA
Pups	$n=17$	$n=15$	
Age (days)	3.11 ± 1.18	3.53 ± 1.13	$F_{1,30}=0.99$; $p=0.33$
Body weight (g)	3.67 ± 0.83	4.13 ± 1.12	$F_{1,30}=1.75$; $p=0.20$
Body length (mm)	33.80 ± 3.05	34.12 ± 4.60	$F_{1,30}=0.05$; $p=0.82$
Head length (mm)	16.53 ± 1.18	17.39 ± 1.33	$F_{1,30}=3.71$; $p=0.06$
Adults	$n=19$	$n=16$	
Age (days)	201.0 ± 87.2	302.9 ± 229.9	$F_{1,31}=3.04$; $p=0.09$
Body weight (g)	35.80 ± 7.51	35.92 ± 5.02	$F_{1,33}=1.71$; $p=0.20$
Body length (mm)	93.9 ± 7.56	94.10 ± 5.56	$F_{1,33}=0.01$; $p=0.93$
Head length (mm)	31.60 ± 1.61	31.38 ± 1.50	$F_{1,33}=0.18$; $p=0.67$

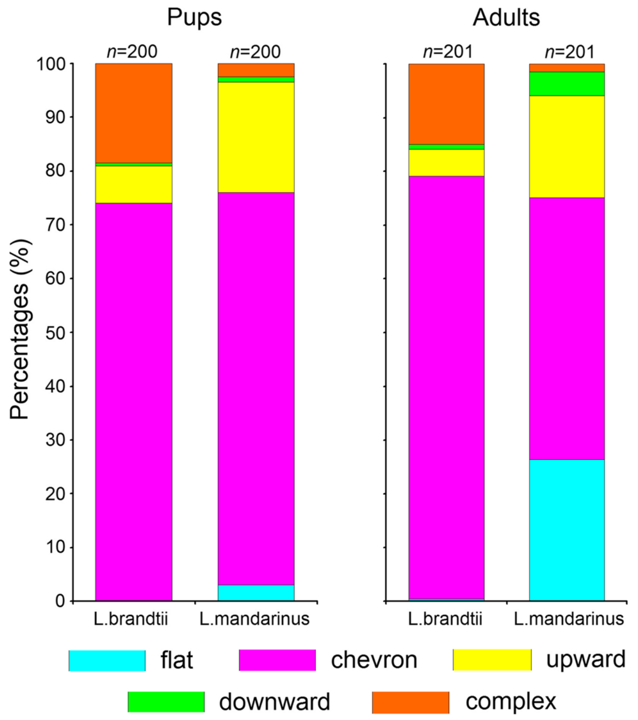


Fig. 4 Percentages of five different contour shapes in pup and adult audible calls (AUDs) of *L. brandtii* and *L. mandarinus*. Contour names are provided on the Fig. *n* – number of calls

times more frequent in *L. brandtii*, whereas the upward and flat contours were a few times more frequent in *L. mandarinus*.

In both pup and adult *L. brandtii* and *L. mandarinus*, AUDs could contain three kinds of nonlinear phenomena: frequency jumps, subharmonics and deterministic chaos (Fig. 5). Nonlinear phenomena were found in 68.0% of AUDs in pup *L. brandtii*, but in only 35.5% of AUDs in pup *L. mandarinus* ($p < 0.001$, Fisher's exact test). In pup *L. brandtii*, most frequent nonlinear phenomena were subharmonics and deterministic chaos. Frequency jump was the least frequent in pup *L. brandtii* and lacked entirely in pup *L. mandarinus*. In pup *L. brandtii*, percentage of AUDs with deterministic chaos was comparable with those in pup *L. mandarinus* ($p=0.59$), whereas subharmonics were less frequent in pup AUDs of *L. mandarinus* ($p < 0.001$) (Fig. 5).

In adult AUDs of both species, percentage of calls with nonlinear phenomena was small: 7.0% in adult *L. brandtii* and 17.9% in adult *L. mandarinus* (differences are significant, $p=0.001$) (Fig. 5). In adult AUDs of *L. brandtii*, subharmonics practically lacked, whereas in adult AUDs of *L. mandarinus*, subharmonics were most widespread among nonlinear phenomena (differences are significant, $p < 0.001$). Deterministic chaos was present at the same level in adults of either species ($p=0.39$). Frequency jumps occurred rarely and only in adults (Fig. 5).

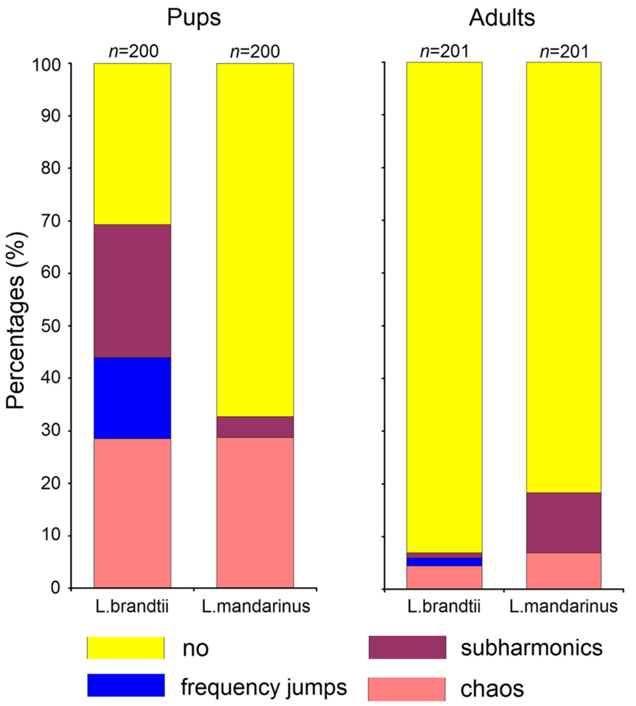


Fig. 5 Percentages of three kinds of nonlinear phenomena in pup and adult AUDs of *L. brandtii* and *L. mandarinus*. Nonlinear phenomena names are provided on the Fig. *n* – number of calls

AUD acoustics

For AUDs, LMM showed that the effect of factor species was significant for the duration and all f0 variables, but not for fpeak (Table 2). Factor age affected significantly the duration, f0end, f0min, and fpeak. Interaction of factors species and age was significant only for duration and f0end (Table 2), reflecting the differences in age-related dynamics between species for these acoustic variables. Specifically, the duration markedly decreased with age in *L. brandtii* and increased in *L. mandarinus*.

Between species, pup AUDs did not differ by duration and fpeak (Table 2). All f0 variables of AUDs were higher in pup *L. brandtii* than in pup *L. mandarinus*. In adults, AUDs were shorter in *L. brandtii* than in *L. mandarinus*. As in pups, in adults, the values of all f0 variables of AUDs were higher in *L. brandtii* than in *L. mandarinus*, whereas fpeak did not differ between species (Table 2).

Comparison between ages within species showed, that in *L. brandtii*, adult AUDs were shorter and lower in f0end and fpeak than pup AUDs, whereas f0beg, f0max, and f0min did not differ between pups and adults (Table 2). In *L. mandarinus*, adult AUDs did not differ from pup AUDs in duration and fpeak, whereas the values of all f0 variables were lower in adults than in pups (Table 2).

Two categories (LF and HF) of adult USVs

While pups only produced one type of USVs, distributions of fpeak and f0max values of adult USVs were two-humped, thus indicating a presence of two non-overlapping call categories, the low-frequency USVs (LF USVs) and the high-frequency USVs (HF USVs) (Fig. 6). So, based on values of fpeak and f0max, each USV was assigned to one of these call categories (Fig. 6). For *L. brandtii*, LF

Table 2 Values (mean ± SD) of acoustic variables of audible calls (AUDs) of pup and adult *L. brandtii* and *L. mandarinus*, and LMM results for the effects of species and age on the acoustics. The *B* ± SE correspond to parameter estimates and standard errors in LMM. Individual identity was introduced as a random term in all LMMs. *duration* – call duration, *f0beg* – the fundamental frequency at the beginning 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 peak frequency, *n* – number of calls. The same superscripts indicate the values, which are non-significantly different from other values by the given acoustic parameter (post hoc Tukey HSD test, $p < 0.05$)

Variable	Pups		Adults		LMM		
	L. brandtii, $n = 200$	*L. mandarinus*, $n = 200$	*L. brandtii*, $n = 201$	*L. mandarinus*, $n = 201$	Species	Age	Species × Age interaction
Duration (s)	0.103 ± 0.027^{a}	0.101 ± 0.026^{a}	0.071 ± 0.040^{b}	0.128 ± 0.047^{a}	$B = 1.4 \pm 0.3$, $\mathbf{p < 0.001}$	$B = 1.0 \pm 0.3$, $\mathbf{p < 0.001}$	$B = -1.5 \pm 0.4$, $\mathbf{p < 0.001}$
f0beg (kHz)	2.63 ± 1.42^{a}	1.34 ± 0.24^{b}	2.14 ± 1.20^{a}	0.96 ± 0.20^{c}	$B = -1.5 \pm 0.3$, $\mathbf{p < 0.001}$	$B = 0.4 \pm 0.3$, $p = 0.16$	$B = 0.3 \pm 0.4$, $p = 0.34$
f0max (kHz)	7.30 ± 1.35^{a}	2.43 ± 0.29^{b}	6.49 ± 2.69^{a}	1.67 ± 0.34^{c}	$B = -2.0 \pm 0.1$, $\mathbf{p < 0.001}$	$B = 0.3 \pm 0.1$, $p = 0.07$	$B = 0.3 \pm 0.2$, $p = 0.13$
f0end (kHz)	4.88 ± 1.42^{a}	1.62 ± 0.43^{b}	2.46 ± 1.10^{c}	1.10 ± 0.28^{d}	$B = -1.2 \pm 0.2$, $\mathbf{p < 0.001}$	$B = 1.1 \pm 0.2$, $\mathbf{p < 0.001}$	$B = -0.5 \pm 0.2$, $\mathbf{p = 0.04}$
f0min (kHz)	2.57 ± 1.37^{a}	1.28 ± 0.23^{b}	1.88 ± 0.88^{a}	0.92 ± 0.19^{c}	$B = -1.4 \pm 0.3$, $\mathbf{p < 0.001}$	$B = 0.5 \pm 0.3$, $\mathbf{p = 0.04}$	$B = 0.2 \pm 0.4$, $p = 0.65$
fpeak (kHz)	11.62 ± 3.44^{a}	8.90 ± 4.53^{a,b}	8.83 ± 2.20^{b}	7.48 ± 1.51^{b}	$B = -0.3 \pm 0.3$, $p = 0.24$	$B = 0.9 \pm 0.3$, $\mathbf{p = 0.005}$	$B = -0.4 \pm 0.4$, $p = 0.29$

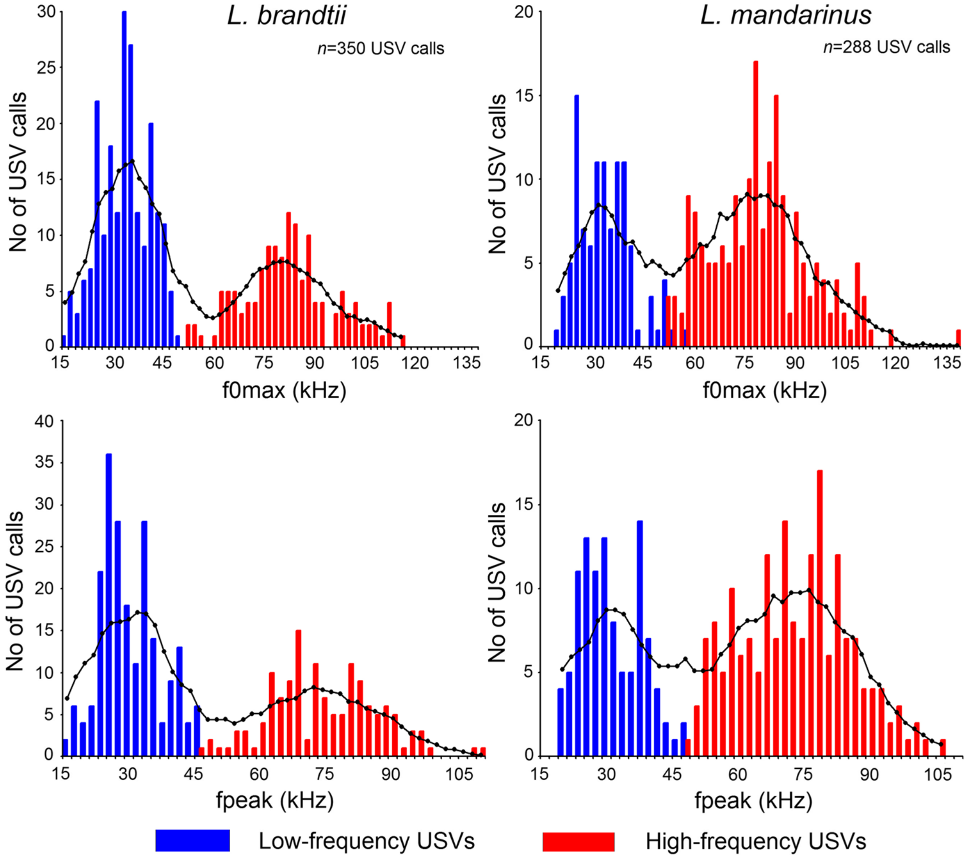


Fig. 6 Distribution of ultrasonic calls (USVs) of adult *L. brandtii* and *L. mandarinus* according to the maximum fundamental frequency (f0max) and peak frequency (fpeak), $n = 350$ USVs for *L. brandtii* and $n = 288$ USVs for *L. mandarinus*. The averaged over 11 points smoothing lines are shown

USVs had f0max values ≤ 48 kHz, whereas HF USVs had f0max values ≥ 50 kHz. For *L. mandarinus*, LF USVs had f0max values ≤ 53 kHz, whereas HF USVs had f0max values ≥ 53 kHz, although one LF USV had a value of 56 kHz and one HF USV had a value of 50 kHz (Fig. 6). For *L. brandtii*, LF USVs had fpeak values ≤ 44 kHz, whereas HF USVs had fpeak values ≥ 44 kHz. For *L. mandarinus*, LF USVs had fpeak values ≤ 46 kHz, whereas HF USVs had fpeak values ≥ 47 kHz (Fig. 6).

In adults of either species, LF USVs were more frequent at stages 1 (isolation) and 2 (touch) of test trials: 210 of 211 (99.5%) LF USVs in *L. brandtii* and 67 of 105 (64%) LF USVs in *L. mandarinus*. In adults of either species, HF USVs occurred nearly exclusively at stages 3 (handling) and 4 (body measurements) of test trials: 139 of 139 (100%) HF USVs in *L. brandtii* and 172 of 183 (94%) HF USVs in *L. mandarinus*.

DFA based on six acoustic variables (duration, f0beg, f0max, f0end, f0min, fpeak) confirmed subdivision of adult USVs to the two categories, LF USVs and HF USVs (Table 3). Parameters most contributing to discrimination, in the order of decreasing importance, were the duration, f0max and fpeak in *L. brandtii* and fpeak, f0max and f0beg in *L. mandarinus*.

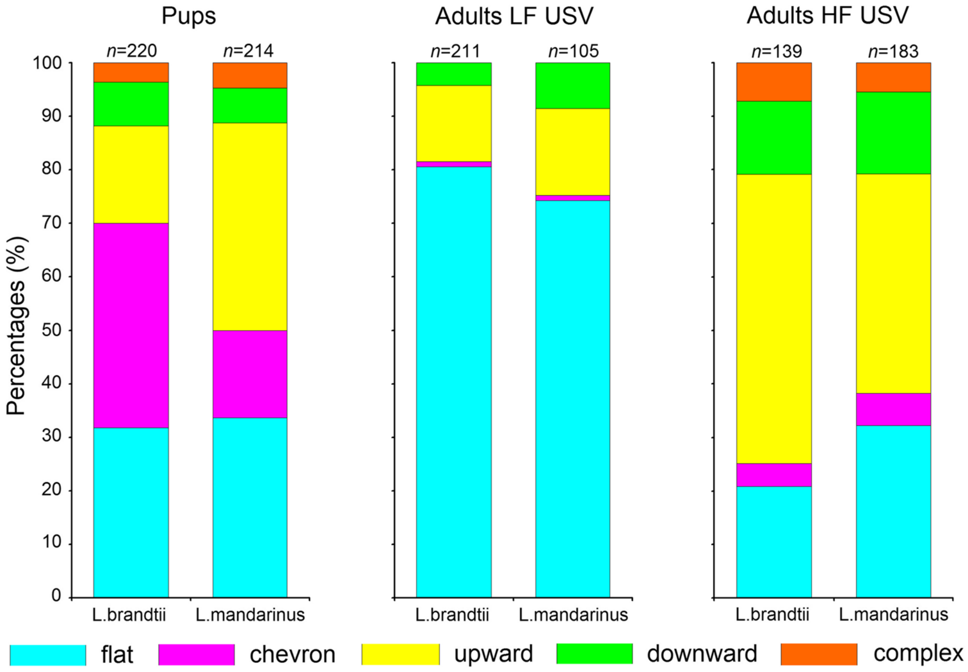
Table 3 Percent of correct classifying of ultrasonic calls of adult *L. brandtii* and *L. mandarinus* to the two USV categories, low-frequency USVs (LF USVs) and high-frequency USVs (HF USVs), based on discriminant function analysis (DFA) standard procedure

USV category	Classifying to a predicted category		Total	Correct classifying (%)
	LF USV	HF USV		
L. brandtii				
LF USV	211	0	211	100.0
HF USV	5	134	139	96.4
Total	216	134	350	98.6
L. mandarinus				
LF USV	105	0	105	100.0
HF USV	2	181	183	98.9
Total	107	181	288	99.3

USV contours, note compositions, and nonlinear phenomena

Pups and adults of both species produced USVs with all the five contour shapes (Fig. 7). In pup *L. brandtii*, chevron contour was more frequent than in pup *L. mandarinus*, whereas pup *L. mandarinus* produced more frequently USVs with upward contour ($p < 0.001$ in both cases, Fisher's exact test).

Fig. 7 Percentages of five different USV contours in pup and adult *L. brandtii* and *L. mandarinus*. Contour names are provided on the figure. LF USV – low-frequency USV, HF USV – high-frequency USV, *n* – number of calls



Flat, downward, and complex contours occurred at the same levels in pups of either species (Fig. 7).

In adults, we did not find any significant interspecies difference in the occurrence of different contours of LF USVs (Fig. 7). In either species, flat contour was most widespread (present in 74% LF USVs of *L. brandtii* and in 80% LF USVs of *L. mandarinus*); the upward and downward contours were less frequent. In either species, chevron was the rarest contour, occurring in only 0.95% LF USVs, and complex contour was not found at all (Fig. 7).

In HF USVs of adults of both species, the most widespread contour was upward, which was more frequent in *L. brandtii* than in *L. mandarinus* ($p = 0.024$) (Fig. 7). Flat contour, second in order by the occurrence, was more frequent in adult *L. mandarinus* than in adult *L. brandtii* ($p = 0.024$); remaining three contours were equally present in both species (Fig. 7).

Nonlinear phenomena detected in pup and adult USVs of both species were frequency jumps, subharmonics, and biphonations (Fig. 8). Deterministic chaos, which was usual nonlinear phenomenon in AUDs, lacked in USVs. In pups, nonlinear phenomena were present in about half of USVs (in 43.2% USVs of pup *L. brandtii* and in 53.8% USVs of pup *L. mandarinus*, differences are marginally significant, Fisher's exact test, $p = 0.055$) (Fig. 8). In pup USVs, the most widespread nonlinear phenomenon was frequency jump (42.3% USVs of *L. brandtii* and 50.9% USVs of *L. mandarinus*) and biphonations were rare (in 5.0% and 7.0% USVs, respectively); subharmonics were the rarest nonlinear phenomena (0.5% USVs, only in pup *L. brandtii*, all differences between species were non-significant (Fig. 8).

In LF USVs and HF USVs of adults of both species, nonlinear phenomena (from 13 to 20% USVs) occurred rarer than in pup USVs (Fig. 8). Frequency jumps were most frequent, subharmonics occurred rarer, and biphonations lacked (Fig. 8). All differences between species were non-significant.

Overall, pup USVs contained more nonlinear phenomena than adult USVs. Most widespread nonlinear phenomenon in both pups and adults and in both species was frequency jump. Pup USVs often contained biphonations, lacking in adults, however, adult USVs often contained subharmonics, practically lacking in pups.

In pups of both species, 1-note USVs prevailed (interspecies differences are non-significant, $p = 0.08$, Fisher's exact test) (Fig. 9). Two-note pup USVs were rarer than 1-note USVs, but more often in *L. mandarinus* than in *L. brandtii* ($p = 0.016$, Fisher's exact test). Multi-note pup USVs were rare in either species (interspecies differences are non-significant, $p = 0.51$, Fisher's exact test) (Fig. 9).

In adults of both species, most LF USVs and HF USVs were 1-note calls; 2-note calls occurred rarer and multi-note USVs were scarce (Fig. 9). All interspecies differences were non-significant.

USV acoustics

We observed a significant variation between species on duration but not on fpeak or f0 variables for USVs (LMM, Table 4). The USV category significantly affected all measured acoustic variables of USVs. Significant interaction of

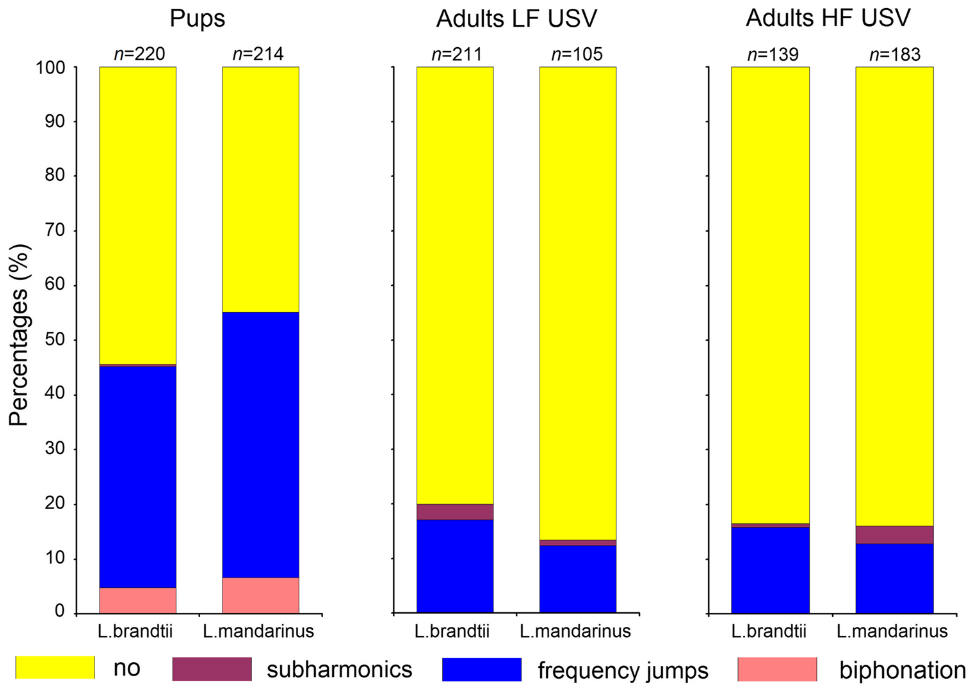


Fig. 8 Percentages of different nonlinear phenomena in different USV categories: pup USVs, adult LF USVs and adult HF USVs for *L. brandtii* and *L. mandarinus.* Nonlinear phenomena names are provided on the figure LF USV – low-frequency USV, HF USV – high-frequency USV, *n* – number of calls

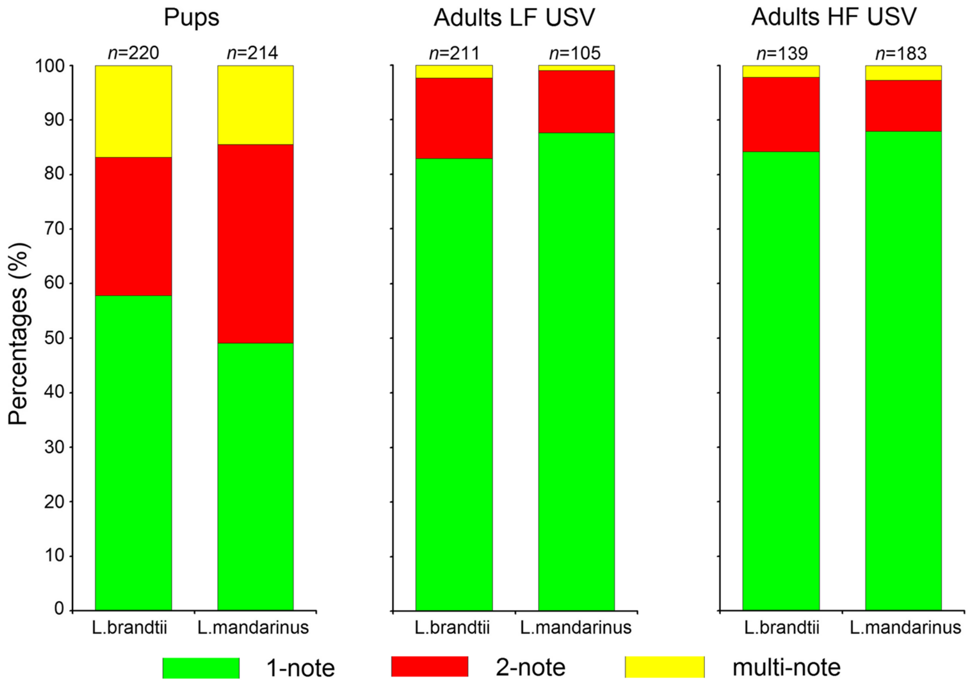


Fig. 9 Percentages of three possible note compositions (1-note, 2-note, multi-note) in pup and adult USVs of *L. brandtii* and *L. mandarinus*. Note compositions are provided on the figure. LF USV – low-frequency USV, HF USV – high-frequency USV, *n* – number of calls

species and USV category was observed only in a model with the duration of USVs as a response (Table 4).

Between species, pup USVs only differed by duration: *L. brandtii* pup USVs were longer than *L. mandarinus* pup USVs (Tukey post hoc test, $p < 0.05$; Table 4). Values of fpeak and all f0 variables of pup USVs did not differ between species. In LF USVs of adults, the duration of AUDs was significantly longer in *L. brandtii* than in *L. mandarinus* (Tukey post hoc test, $p < 0.05$). As in pups of these species, all other variables of adult LF USVs did not differ between species (Table 4). In HF USVs of adults, the duration, fpeak, and all f0 variables did not differ between species (Table 4).

In *L. brandtii*, pup USVs were longer than adult LF USVs, whereas all f0 variables and fpeak did not differ from adult LF USVs and were significantly and substantially (twice) lower compared to adult HF USVs (Tukey post hoc test, $p < 0.05$; Table 4).

Table 4 Values (mean ± SD) of USV acoustic variables of pup and adult *L. brandtii* and *L. mandarinus*, and LMM results for the effects of species and USV category (pup USV/Adult LF USV/Adult HF USV) on the acoustics. The B ± SE correspond to parameter estimates and standard errors in LMM. Individual identity was introduced as a random term in all LMMs. *duration* – call duration, *f0beg* – the fundamental frequency at the beginning 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 peak frequency, *n* – number of calls. The same superscripts indicate the values, which are non-significantly different from other values by the given acoustic parameter (post hoc Tukey HSD test, $p < 0.05$)

Variable	Pup USV		Adult LF USV		Adult HF USV		LMM		
	L. brandtii, $n=220$	*L. mandarinus*, $n=214$	*L. brandtii*, $n=211$	*L. mandarinus*, $n=105$	*L. brandtii*, $n=139$	*L. mandarinus*, $n=183$	Species	USV category	Species × USV category interaction
Duration (s)	0.082 ± 0.039^{a}	0.055 ± 0.037^{b}	0.043 ± 0.020^{b}	0.019 ± 0.019^{c}	0.015 ± 0.012^{c}	0.017 ± 0.016^{c}	$B=0.4 \pm 0.2$, **$p=0.05$**	$B=1.5 \pm 0.1$, **$p<0.001$** $B=2.2 \pm 0.2$, **$p<0.001$**	$B=-1.4 \pm 0.1$, **$p<0.001$** $B=1.0 \pm 0.3$, **$p=0.001$**
f0beg (kHz)	$31.66 \pm 7.39^{a,b}$	36.37 ± 7.79^{b}	30.43 ± 7.33^{a}	30.11 ± 7.62^{a}	71.89 ± 13.75^{c}	68.33 ± 12.34^{c}	$B=-0.1 \pm 0.2$, $p=0.7$	$B=-1.9 \pm 0.1$, **$p<0.001$** $B=-1.9 \pm 0.1$, **$p<0.001$**	$B=-0.1 \pm 0.1$, $p=0.34$ $B=0.4 \pm 0.2$, $p=0.06$
f0max (kHz)	$39.66 \pm 9.80^{a,b}$	44.77 ± 9.11^{b}	33.26 ± 7.48^{a}	33.40 ± 7.90^{a}	81.25 ± 13.83^{c}	78.50 ± 15.19^{c}	$B=-0.1 \pm 0.1$, $p=0.6$	$B=-2.0 \pm 0.1$, **$p<0.001$** $B=-1.8 \pm 0.1$, **$p<0.001$**	$B=-0.1 \pm 0.1$, $p=0.33$ $B=0.3 \pm 0.2$, $p=0.10$
f0end (kHz)	29.63 ± 7.09^{a}	33.41 ± 7.98^{a}	30.14 ± 7.27^{a}	29.86 ± 7.66^{a}	76.03 ± 13.04^{b}	73.44 ± 15.60^{b}	$B=-0.02 \pm 0.1$, $p=0.9$	$B=-1.9 \pm 0.1$, **$p<0.001$** $B=-1.9 \pm 0.1$, **$p<0.001$**	$B=-0.04 \pm 0.1$, $p=0.69$ $B=0.3 \pm 0.2$, $p=0.14$
f0min (kHz)	25.24 ± 5.25^{a}	28.80 ± 7.00^{a}	27.35 ± 6.43^{a}	27.74 ± 7.21^{a}	67.23 ± 11.71^{b}	64.42 ± 11.51^{b}	$B=-0.05 \pm 0.1$, $p=0.7$	$B=-1.9 \pm 0.1$, **$p<0.001$** $B=-2.1 \pm 0.1$, **$p<0.001$**	$B=-0.1 \pm 0.1$, $p=0.39$ $B=0.3 \pm 0.2$, $p=0.09$
fpeak (kHz)	30.33 ± 5.30^{a}	34.11 ± 8.22^{a}	29.58 ± 6.73^{a}	30.56 ± 6.80^{a}	72.99 ± 12.25^{b}	71.46 ± 12.59^{b}	$B=-0.01 \pm 0.1$, $p=1.0$	$B=-2.0 \pm 0.1$, **$p<0.001$** $B=-1.9 \pm 0.1$, **$p<0.001$**	$B=-0.01 \pm 0.1$, $p=0.98$ $B=0.2 \pm 0.2$, $p=0.15$

In *L. mandarinus*, pup USVs were longer than adult LF USVs, and their f0beg and f0max were higher than in adult LF USVs (Tukey post hoc test, $p < 0.05$). Values of f0end and f0min and of fpeak did not differ between USVs of pups and LF USVs of adults. Compared to HF USVs of adults, pup *L. mandarinus* USVs were longer and had twice lower values of all f0 variables and of fpeak (Table 4).

Discussion

The most remarkable novelty of the results of this study was that, in contrast to AUDs, USVs were surprisingly similar between species in frequency parameters: the values of f0 and fpeak did not differ between species in either pups or adults. So, our data suggest that ultrasonic vocalization is unaffected with way of living, subterranean or surface-dwelling. These results indicate that selection pressure for frequency parameters of USVs is evidently lacking at any lifestyle. At the same time, the audible vocalization was strongly affected with lifestyle in both adults and in pups (in spite of pup living in the same acoustic environment in both species).

This study confirmed the results by Rutovskaya (2018) that AUDs are much higher in f0 in adult surface-dwelling *L. brandtii* (mean f0max 6.5 kHz) than in adult subterranean *L. mandarinus* (mean f0max 1.7 kHz). In addition, our study revealed that this trend of interspecies differences can be expanded on AUDs of pups (mean f0max 7.3 kHz in *L. brandtii* vs 2.4 kHz in *L. mandarinus*). We can therefore conclude that, at least in the two *Lasiopodomys* vole species, frequency parameters of USVs remain resistant to the shifts from surface-dwelling to subterranean lifestyle or vice versa. We can also conclude that lifestyle of these species is only reflected in frequency parameters of AUDs, but not USVs. Consistently, selection on ultrasonic call rate in neonatal laboratory rats *Rattus norvegicus* affects low-frequency, but not ultrasonic, vocalizations in adult rats (Lesch et al. 2020). Thus, our study provides additional evidence that rodent AUDs may be more reactive to selection pressures for behavior than rodent USVs.

Our results on the lower-frequency AUDs in the subterranean species, *L. mandarinus*, compared to the surface-dwelling *L. brandtii*, and on similar-frequency USVs in both species, can be explained by acoustic adaptation hypothesis (Ey and Fisher 2009). Better sound transmission in burrows is only applicable to low-frequency AUDs, as these calls propagate to a distance of a few meters (Heth et al. 1986) being even increased by burrow stethoscope effect (Lange et al. 2007; Schleich and Antenucci 2009; Okanoya and Screven 2018. In contrast, USVs rapidly attenuate, greater scatter, have poorer localizability compared to the low-frequency AUDs (Musolf and Penn 2012) and propagate to a shorter distance irrespectively on surface or in burrow, thus being indifferent to selection pressure for propagation ability. Compared to the low-frequency calls, the high-frequency calls can only be heard at close range and can therefore be only used for communication in the immediate vicinity with conspecifics, as suggested for other rodents (Wilson and Hare 2006) and for canids (Sibiryakova et al. 2021).

A question remains, whether the transit to subterranean lifestyle provoked the shift towards lower-frequency AUDs in *L. mandarinus* or, alternately, the transit to surface-dwelling lifestyle provoked the shift towards higher-frequency AUDs in *L. brandtii*. For other vole species, related studies indicate that f0max of their audible sharp squeaks commonly does not exceed 2–3 kHz (Rutovskaya 2018, 2019a, b, c). Exclusions are the Harting's vole (*Microtus hartingi*) (10.2–17.6 kHz: Pandourski 2011; Rutovskaya 2019a) and the narrow-headed vole (*Lasiopodomys gregalis*) (3.6–5.6 kHz: Rutovskaya 2018). In surface-dwelling *L. brandtii* and *L. gregalis*, AUDs are high-frequency, whereas in subterranean *L. mandarinus* they are low-frequency. At the same time, f0max of AUDs (sharp squeaks) of *L. mandarinus* (up to 2 kHz) overlaps with those of other vole species, whereas AUDs of *L. brandtii* are distinctively high-frequency (f0 up to 6 kHz) compared to AUDs of other vole species (Rutovskaya 2018). Thus, *Lasiopodomys* species display a relatively large range of f0max values. We can therefore advance a hypothesis that shift of AUDs towards higher frequencies in *L. brandtii* outcomes from surface-dwelling lifestyle and the respective emergence of the high-frequency (10.2–10.7 kHz, Rutovskaya 2012) audible alarm call in this species. This hypothesis is alternative to the hypothesis suggesting that shift of AUDs towards lower frequencies in *L. mandarinus* outcomes from the subterranean lifestyle of this species.

This study provides new results that f0 of AUDs displays an ontogenetic shift towards lower frequencies with maturation in both species. The ontogenetic lowering of f0 in AUDs is typical for mammals, because of age-related increase of the vocal fold length and mass, resulting in the lower vibration rate at phonation (Fitch and Hauser 2002). The ontogenetic lowering of f0 in AUDs was reported, e.g., in giant panda (*Ailuropoda melanoleuca*) (Charlton et al. 2009), steppe marmot (*Marmota bobak*), and great gerbil (*Rhombomys opimus*) (Nikolskii 2007). Exclusions from this common rule (i.e., mammals with non-lowering f0 with age) are found, e.g., in a few species of ground squirrels (Matrosova et al. 2007, 2011; Swan and Hare 2008; Schneiderová et al. 2015) and in two shrew species (Schneiderová 2014; Volodin et al. 2015).

We found, for the first time for Arvicolinae species, that, with maturation, f0 values of USVs split to two categories: the low-frequency USVs (LF USVs of 27–33 kHz), indistinguishable in f0 from pup USVs, and the high-frequency USVs (HF USVs of 65–81 kHz) lacking in pups. In pups, we only analyzed USVs emitted at the 1st (isolation) and 2nd (touch) trial stages, but in adults of both *L. brandtii* and *L. mandarinus*, LF USVs were more frequent at 1st and 2nd (isolation and touch) trial stages, whereas HF USVs were more frequent at 3rd and 4th (handling and body measurements) trial stages. In adult rodents, the isolation and touch procedures are potentially related to a weaker negative emotional arousal than handling and body measurements, during which the animals try to escape or bite a human hand (Klenova et al. 2021). We can propose that, in *Lasiopodomys* voles, emission of LF USVs and HF USVs may be related to different levels of caller' negative emotional arousal. This is reminiscent of the situation in laboratory rat, the species in which initially broad range of pup USV frequencies (30–65 kHz) split in ontogeny to two call categories, of 22-kHz and 50-kHz USVs, related in adults to negative and positive emotional arousal, respectively (Brudzynski et al. 1999; Brudzynski 2005; Riede 2011; Riede et al. 2015). Thus, the ontogenetic split of pup USVs to the two different categories with maturation is not to be unique for laboratory rat.

Interspecies differences in USVs were only found in duration. The USVs were longer in pup *L. brandtii* than in pup *L. mandarinus*, and LF USVs of adult *L. brandtii* were longer than LF USVs of adult *L. mandarinus*. Age-related changes of USV duration from pups to adults may represent a common trend for rodents. Aside *L. brandtii* and *L. mandarinus* (this study), the shortening of USVs from pups to adults was reported for yellow steppe lemming (Yurlova et al. 2020) and for five Gerbillinae species (Zaytseva et al. 2019; Kozhevnikova 2021). At the same time, the age-related changes of duration from pups to adults in AUDs seem to be not a common trend in mammals. For example, in speckled ground squirrels *Spermophilus suslicus*, the alarm call duration increases with maturation (Volodina et al. 2010); whereas in some other species of ground squirrels, it remains unchanged (Swan and Hare 2008; Volodina et al. 2010). Duration of audible squeaks decreases with maturation in fat-tailed gerbil *Pachyuromys duprasi* (Zaytseva et al. 2020) and in yellow steppe lemming *Eolagurus luteus* (Volodin et al. 2021).

In our study, body size and age of pups and adults did not differ between species, so these factors could not be responsible for the detected acoustic differences. This is an additional argument that the two closely related species, *L. brandtii* and *L. mandarinus*, represent a most convenient model for comparative studies of the effects of surface-dwelling and subterranean lifestyle on the acoustics (this study) as well as on other biological aspects, as physiology, genetics and behavior (e.g., Dong et al. 2018; Sun et al. 2020).

Predation could be one of the key factors affecting the transit to underground or surface-dwelling lifestyle in *L. brandtii* and *L. mandarinus*. Potentially, predation of raptors (e.g., Zhong et al. 2022) could promote the emergence of the high-frequency audible alarm call (10.2–10.7 kHz, Rutovskaya 2012, 2018) in *L. brandtii*. The alarm call of *L. brandtii* might not be well audible for raptors, who hear well the audible frequencies below 6–8 kHz (Yamazaki et al. 2004; McGee et al. 2019).

Distinctive to raptors, which primarily rely on their vision for capturing small mammalian prey (Potier et al. 2020), the nocturnal avian predators (owls) may primarily rely on their hearing (de Koning et al. 2020). Although the potential effect of owl predation on transit of *L. brandtii* to diurnal lifestyle was not yet considered by any study, this hypothesis seems to be reasonable for habitats with a high press of owl hunting on the voles.

Pup isolation calls and adult discomfort-related calls analyzed in both vole species in this study are not directly related to predation, being either addressed to parents (pup calls) or expressing the internal state of discomfort of a caller (adult calls). However, potentially, terrestrial predators (foxes and mustelids) can rely on hearing these calls (AUDs and USVs) when hunting by digging out the animals from burrows, as foxes, or coming into the burrow, as mustelids. Mustelids and foxes can hear all the range of both audible and ultrasonic calls of voles, up to 51 kHz in the least weasel *Mustela nivalis* (Heffner and Heffner 1985) and up to 48–51 kHz in red fox *Vulpes vulpes* (Malkemper et al. 2015). Red foxes hear substantially better the audible calls around 2 kHz than ultrasonic frequencies (Peterson et al. 1969; Malkemper et al. 2015) and therefore can rely on rustling sounds of voles rather than their audible or ultrasonic calls (Frey et al. 2016). In addition, pup voles can be potentially predated in burrows by infanticidal conspecifics or other species of rodents, e.g., by Daurian ground squirrels *Spermophilus dauricus*, which can be captured in burrows at the same colonies as voles (own observations by the authors). Previously, the potential effect of infanticide on the acoustics of alarm calls was considered for ground squirrels (Matrosova et al. 2007).

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Author contribution IAV, AVS, and EVV designed the study. MMD, IAV, AVS, and EVV collected the data. MMD and IAV performed acoustic analyses. NAV and IAV performed statistical analyses. All authors wrote the first draft of the manuscript, commented on and approved the final manuscript before submission.

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Data availability The datasets used in this study are available from the supplementary information files.

Declarations

Ethics approval The authors adhered to the “Guidelines for the treatment of animals in behavioural research and teaching” (Anim Behav (2020) 159:I-XI) and the legal requirements of Russia pertaining to the protection of animal welfare. The experimental procedure was approved by the Committee of Bio-ethics of Lomonosov Moscow State University, research protocol # 2011–36.

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References

Abramson NI, Lebedev VS, Tesakov AS, Bannikova AA (2009) Supraspecies relationships in the subfamily Arvicolinae (Rodentia, Cricetidae): an unexpected result of nuclear gene analysis. Mol Biol 43:834. https://doi.org/10.1134/S0026893309050148

Alexeeva N, Erbajeva M, Khenzykhenova F (2015) *Lasiopodomys brandti* in Pleistocene of Transbaiklia and adjacent territories: distribution area, evolutionary development in context of global and regional events. Quatern Int 355:11–17. https://doi.org/10.1016/j.quaint.2014.08.017

Begall S, Burda H, Schleich CE (eds) (2007a) Subterranean rodents. News from Underground. Springer, Berlin

Begall S, Lange S, Schleich C, Burda H (2007b) Acoustics, audition and auditory system. In: Begall S, Burda H, Schleich CE (eds) Subterranean rodents: News from underground. Springer, Berlin, pp 97–111

Bondareva OV, Potapova NA, Konovalov KA, Petrova TV, Abramson NI (2021) Searching for signatures of positive selection in cytochrome b gene associated with subterranean lifestyle in fast-evolving arvicolines (Arvicolinae, Cricetidae, Rodentia). BMC Ecol Evol 21:92. https://doi.org/10.1186/s12862-021-01819-4

Brückmann G, Burda H (1997) Hearing in blind subterranean Zambian mole-rats (*Cryptomys* sp.): collective behavioural audiogram in a highly social rodent. J Comp Physiol A 181:83–88. https://doi.org/10.1007/s003590050095

Brudzynski SM (2005) Principles of rat communication: quantitative parameters of ultrasonic calls in rats. Behav Genet 35:85–92. https://doi.org/10.1007/s10519-004-0858-3

Brudzynski SM, Kehoe P, Callahan M (1999) Sonographic structure of isolation-induced ultrasonic calls of rat pups. Devel Psychobiol 34:195–204. https://doi.org/10.1002/(sici)1098-2302(199904)34:3%3c195::aid-dev4%3e3.0.co;2-s

Burda H, Šumbera R, Begall S (2007) Microclimate in burrows of subterranean rodents - revisited. In: Begall S, Burda H, Schleich CE (eds) Subterranean rodents: News from underground. Springer, Berlin, pp 21–33

Caspar KR, Heinrich A, Mellinghaus L, Gerhardt P, Begall S (2021) Evoked auditory potentials from African mole-rats and coruros reveal disparity in subterranean rodent hearing. J Exp Biol 224:243371. https://doi.org/10.1242/jeb.243371

Charlton BD, Keating JL, Rengui L, Huang Y, Swaisgood RR (2009) Female giant panda (*Ailuropoda melanoleuca*) chirps advertise the caller's fertile phase. Proc R Soc Lond B 277:1101–1106. https://doi.org/10.1098/rspb.2009.1431

Credner S, Burda H, Ludescher F (1997) Acoustic communication underground: vocalization characteristics in subterranean social mole-rats (*Cryptomys* sp., Bathyergidae). J Comp Physiol A 180:245–255. https://doi.org/10.1007/s003590050045

Cui C, Xie Y, Hua Y, Yang S, Yin B, Wei W (2020) Brandt's vole (*Lasiopodomys brandtii*) affects its habitat quality by altering plant community composition. Biologia 75:1097–1104. https://doi.org/10.2478/s11756-020-00469-z

de Koning M, Beatini JR, Proudfoot GA, Gall MD (2020) Hearing in 3D: directional auditory sensitivity of northern saw-whet owls (*Aegolius acadicus*). Integr Comp Biol 60:1058–1067. https://doi.org/10.1093/icb/icaa024

Dent ML, Screven LA, Kobrina A (2018) Hearing in rodents. In: Dent ML, Fay RR, Popper AN (eds) Rodent Bioacoustics. Springer, Cham, pp 71–105

Dmitriev PP, Tamir Z, Davaa N (1980) Characteristics of habitats of *Microtus brandtii* in the East Khangai. Zool Zh 59:274–282 [in Russian]

Dong Q, Shi L, Li Y et al (2018) Differential responses of *Lasiopodomys mandarinus* and *Lasiopodomys brandtii* to chronic hypoxia: a cross-species brain transcriptome analysis. BMC Genomics 19:901. https://doi.org/10.1186/s12864-018-5318-1

Dvořáková V, Hrouzková E, Šumbera R (2016) Vocal repertoire of the social Mashona mole-rat (*Fukomys darlingi*) and how it compares with other mole-rats. Bioacoustics 25:253–266. https://doi.org/10.1080/09524622.2016.1141117

Ey E, Fischer J (2009) The 'acoustic adaptation hypothesis' – a review of the evidence from birds, anurans and mammals. Bioacoustics 19:21–48. https://doi.org/10.1080/09524622.2009.9753613

Fitch WT, Hauser MD (2002) Unpacking "Honesty": Vertebrate vocal production and the evolution of acoustic signals. In: Simmons A, Fay RR, Popper AN (eds) Acoustic Communication. Springer, New York, pp 65–137

Frey R, Volodin IA, Fritsch G, Volodina EV (2016) Potential sources of high frequency and biphonic vocalization in the dhole (*Cuon alpinus*). PLoS ONE 11:e0146330. https://doi.org/10.1371/journal.pone.0146330

Gerhardt P, Henning Y, Begall S, Malkemper EP (2017) Audiograms of three subterranean rodent species (genus *Fukomys*) determined by auditory brainstem responses reveal extremely poor high-frequency hearing. J Exp Biol 220:4377–4382. https://doi.org/10.1242/jeb.164426

Heffner RS, Heffner HE (1985) Hearing in mammals: the least weasel. J Mammal 66:745–755. https://doi.org/10.2307/1380801

Heffner RS, Heffner HE (1992) Hearing and sound localization in blind mole rats (*Spalax ehrenbergi*). Hearing Res 62:206–216. https://doi.org/10.1016/0378-5955(92)90188-s

Heth G, Frankenberg E, Nevo E (1986) Adaptive optimal sound for vocal communication in tunnels of a subterranean mammal (*Spalax ehrenbergi*). Experientia 42:1287–1289. https://doi.org/10.1007/BF01946426

Hrouzková E, Bernasová E, Šklíba J (2020) Eavesdropping on a heterospecific alarm call in the giant root-rat (*Tachyorytes macrocephalus*), an important prey of the Ethiopian wolf (*Canis simensis*). J Ethol 38:121–124. https://doi.org/10.1007/s10164-019-00618-1

Jiao H, Hong W, Nevo E, Li K, Zhao H (2019) Convergent reduction of *V1R* genes in subterranean rodents. BMC Evol Biol 19:176. https://doi.org/10.1186/s12862-019-1502-4

Khruscelevsky VP, Kopylova OA (1957) Materials on ecology of Brandt's vole. Report 5. Peculiarities of seasonal and daily activity. Trans Antiplague Inst Siberia Far East 16:69–76 [in Russian]

Klenova AV, Volodin IA, Ilchenko OG, Volodina EV (2021) Discomfort-related changes of call rate and acoustic variables of ultrasonic vocalizations in adult yellow steppe lemmings *Eolagurus luteus*. Sci Rep 11:14969. https://doi.org/10.1038/s41598-021-94489-7

Knotková E, Veitl S, Šumbera R, Sedláček F, Burda H (2009) Vocalisations of the silvery mole-rat: comparison of vocal repertoires in subterranean rodents with different social systems. Bioacoustics 18:241–257. https://doi.org/10.1080/09524622.2009.9753604

Kozhevnikova JD (2021) Comparative analysis of parameters of ultrasonic calls in adults and pups of four Gerbillinae species. MSc thesis, Moscow State University [in Russian]

Kozhevnikova JD, Volodin IA, Zaytseva AS, Ilchenko OG, Volodina EV (2021) Pup ultrasonic isolation calls of six gerbil species and the relationship between acoustic traits and body size. R Soc Open Sci 8:201558. https://doi.org/10.1098/rsos.201558

Lacey EA, Patton JL, Cameron GN (eds) (2000) Life underground: The biology of subterranean rodents. The University of Chicago Press, Chicago

Lange S, Burda H, Wegner RE, Dammann P, Begall S, Kawalika M (2007) Living in a "stethoscope": burrow-acoustics promote auditory specializations in subterranean rodents. Naturwissenschaften 94:134–138. https://doi.org/10.1007/s00114-006-0168-0

Lebedev VS, Bannikova AA, Ya A, Shar S, Surov AV (2016) A revised checklist of Mongolian mammal species. Explor Biol Resour Mongolia 13:349–360

Lenth RV (2021) Emmeans: estimated marginal means, aka least-squares means. R package version 1.6.1. https://cran.r-project.org/web/packages/emmeans/index.html

Lesch R, Orozco A, Shilling M, Zimmerberg B, Fitch WT (2020) Selection on ultrasonic call rate in neonatal rats affects low frequency, but not ultrasonic, vocalizations in adults. Ethology 126:1007–1018. https://doi.org/10.1111/eth.13075

Li K, Kohn MH, Zhang S, Wan X, Shi D, Wang D (2017) The colonization and divergence patterns of Brandt's vole (*Lasiopodomys brandtii*) populations reveal evidence of genetic surfing. BMC Evol Biol 17:145. https://doi.org/10.1186/s12862-017-0995-y

Kössl M, Frank G, Burda H, Müller M (1996) Acoustic distortion products from the cochlea of the blind African mole rat, *Cryptomys* spec. J Comp Physiol A 178:427–434. https://doi.org/10.1007/BF00193979

Malkemper EP, Topinka V, Burda H (2015) A behavioral audiogram of the red fox (*Vulpes vulpes*). Hear Res 320:30–37. https://doi.org/10.1016/j.heares.2014.12.001

Matrosova VA, Volodin IA, Volodina EV, Babitsky AF (2007) Pups crying bass: Vocal adaptation for avoidance of age-dependent predation risk in ground squirrels? Behav Ecol Sociobiol 62:181–191. https://doi.org/10.1007/s00265-007-0452-9

Matrosova VA, Blumstein DT, Volodin IA, Volodina EV (2011) The potential to encode sex, age, and individual identity in the alarm calls of three species of Marmotinae. Naturwissenschaften 98:181–192. https://doi.org/10.1007/s00114-010-0757-9

McGee JA, Nelson PB, Ponder JB, Marr J, Redig P, Walsh EJ (2019) Auditory performance in bald eagles and red-tailed hawks: a comparative study of hearing in diurnal raptors. J Comp Physiol A 205:793–811. https://doi.org/10.1007/s00359-019-01367-9

Müller M, Burda H (1989) Restricted hearing range in a subterranean rodent, *Cryptomys hottentotus*. Naturwissenschaften 76:134–135. https://doi.org/10.1007/BF00366611

Musolf K, Penn DJ (2012) Ultrasonic vocalizations in house mice: a cryptic mode of acoustic communication. In: Macholan M, Baird SJE, Munclinger P, Pialek J (eds) Evolution of the house mouse. Cambridge University Press, Cambridge, pp 253–277

Nevo E (1999) Mosaic evolution of subterranean mammals: regression, progression and global convergence. Oxford University Press, Oxford

Nevo E, Heth G, Beiles A, Frankenberg E (1987) Geographic dialects in blind mole rats: role of vocal communication in active speciation. P Natl Acad Sci USA 84:3312–3315. https://doi.org/10.1073/pnas.84.10.3312

Nikolskii AA (2007) Comparative analyses of the alarm call frequency in different age rodent groups. Zool Zh 86:499–504 [in Russian]

Okanoya K, Screven LA (2018) Rodent vocalizations: adaptations to physical, social, and sexual factors. In: Dent M, Fay R, Popper A (eds) Rodent Bioacoustics. Springer, Cham, pp 13–41

Okanoya K, Yosida S, Barone CM, Applegate DT, Brittan-Powell EF, Dooling RJ, Park TJ (2018) Auditory-vocal coupling in the naked mole-rat, a mammal with poor auditory thresholds. J Comp Physiol A 204:905–914. https://doi.org/10.1007/s00359-018-1287-8

Pandourski I (2011) Case of alarm vocalization in a colony of *Microtus guentheri* (Danford & Alston, 1880) (Mammalia, Rodentia, Arvicolidae) from Southern Bulgaria. ZooNotes 20:1–3

Park TJ, Reznick J, Peterson BL et al (2017) Fructose-driven glycolysis supports anoxia resistance in the naked mole-rat. Science 356:307–311. https://doi.org/10.1126/science.aab3896

Pepper JW, Stanton HB, Lacey EA, Sherman PW (2017) Vocalization of the naked mole-rat. In: Sherman PW, Jarvis JUM, Alexander RD (eds) The biology of the naked mole-rat. Princeton University Press, Princeton, NJ, pp 243–274

Peterson EA, Heaton WC, Wruble SD (1969) Levels of auditory response in fissiped carnivores. J Mammal 50:566–578. https://doi.org/10.2307/1378784

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2021) nlme: linear and nonlinear mixed effects models. R package version 3.1–153, https://CRAN.R-project.org/package=nlme

Potier S, Mitkus M, Kelber A (2020) Visual adaptations of diurnal and nocturnal raptors. Semin Cell Dev Biol 106:116–126. https://doi.org/10.1016/j.semcdb.2020.05.004

R Development Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org

Riede T (2011) Subglottal pressure, tracheal airflow, and intrinsic laryngeal muscle activity during rat ultrasound vocalization. J Neurophysiol 106:2580–2592. https://doi.org/10.1152/jn.00478.2011

Riede T, Zhao Y, LeDoux MS (2015) Vocal development in dystonic rats. Physiol Rep 3:12350. https://doi.org/10.14814/phy2.12350

Rutovskaya MV (2011) Acoustic communication in the Mandarin vole (*Lasiopodomys mandarinus*, Rodentia). Biol Bull 38:911–918. https://doi.org/10.1134/S1062359011090068

Rutovskaya MV (2012) The sound signals of Brandt's vole (*Lasiopodomys brandti*). Sens Systems 26:31–38 [In Russian]

Rutovskaya MV (2018) Audible acoustic communication in voles of Arvicolinae subfamily. KMK Press, Moscow [In Russian]

Rutovskaya MV (2019a) Sound communication in social voles (subgenus *Sumeriomys*). Bioacoustics 28:503–521. https://doi.org/10.1080/09524622.2018.1482787

Rutovskaya MV (2019b) Vocal communication in *Microtus* (*Terricola*) *schelkovnikovi* and *M*. (*T*.) *daghestanicus* in the audible range of frequencies. J Ethol 37:187–195. https://doi.org/10.1007/s10164-019-00587-5

Rutovskaya MV (2019c) Inheritance of the acoustic signal parameters in interspecific hybrids of the bank (*Myodes glareolus*) and the Tien Shan (*M. centralis*) voles. BMC Evol Biol 19:44. https://doi.org/10.1186/s12862-019-1374-7

Sahm A, Platzer M, Koch P et al (2021) Increased longevity due to sexual activity in mole-rats is associated with transcriptional changes in the HPA stress axis. eLife 10:57843. https://doi.org/10.7554/eLife.57843

Schleich CE, Antenucci DC (2009) Sound transmission and burrow characteristics of the subterranean rodent *Ctenomys talarum* (Rodentia: Ctenomyidae). Acta Theriol 54:165–170. https://doi.org/10.1007/BF03193172

Schleich CE, Francescoli G (2018) Three decades of subterranean acoustic communication studies. In: Dent M, Fay R, Popper A (eds) Rodent Bioacoustics. Springer, Cham, pp 43–69

Schneiderová I (2014) Vocal repertoire ontogeny of the captive Asian house shrew *Suncus murinus* suggests that the male courtship call develops from the caravanning call of the young. Acta Theriol 59:149–164. https://doi.org/10.1007/s13364-013-0141-1

Schneiderová I, Schnitzerova P, Uhlıkova J, Brandl P, Zouhar J, Mateju J (2015) Differences in alarm calls of juvenile and adult European ground squirrels (*Spermophilus citellus*): findings on permanently marked animals from a semi-natural enclosure. Zoo Biol 34:503–512. https://doi.org/10.1002/zoo.21233

Shi L, Liu L, Li X, Wu Y, Tian X, Shi Y, Wang Z (2021) Phylogeny and evolution of *Lasiopodomys* in subfamily Arvivolinae based on mitochondrial genomics. Peer J 9:e10850. https://doi.org/10.7717/peerj.10850

Sibiryakova OV, Volodin IA, Volodina EV (2021) Polyphony of domestic dog whines and vocal cues to body size. Curr Zool 67:165–176. https://doi.org/10.1093/cz/zoaa042

Smith AT, Xie Y (2008) A Guide to the Mammals of China. Princeton University Press, Princeton, NJ

Smorkatcheva AV (1999) The social organization of the mandarin vole, *Lasiopodomys mandarinus*, during the reproductive period. Z Saugetierkd 64:344–355

Smorkatcheva AV, Aksenova TG, Zorenko TA (1990) The ecology of *Lasiopodomys mandarinus* (Rodentia, Cricetidae) in the Transbaical area. Zool Zh 69:115–124 [in Russian]

Sun H, Zhang Y, Wang B, LiY XuW, Mao R, Wang Z (2019) Investigation on oxygen and carbon dioxide fluctuations in *Lasiopodomys mandarinus* burrows. Pakistan J Zool 51:1519–1526. https://doi.org/10.17582/journal.pjz/2019.51.4.1519.1526

Sun H, Ye K, Liu D, Pan D, Gu S, Wang Z (2020) Evolution of hemoglobin genes in a subterranean rodent species (*Lasiopodomys mandarinus*). Biology 9:106. https://doi.org/10.3390/biology9050106

Swan DC, Hare JF (2008) Signaler and receiver ages do not affect responses to Richardson's ground squirrel alarm calls. J Mammal 89:889–894. https://doi.org/10.1644/07-MAMM-A-228.1

Tai F, Wang T (2001) Social organization of mandarin voles in burrow system. Acta Theriol Sin 21:50–56

Terleph T (2011) A comparison of prairie vole audible and ultrasonic pup calls and attraction to them by adults of each sex. Behaviour 148:1277–1296. https://doi.org/10.1163/000579511X600727

Vejmělka F, Okrouhlík J, Lövy M, Šafa G, Nevo E, Bennett NC, Šumbera R (2021) Heat dissipation in subterranean rodents: the role of body region and social organisation. Sci Rep 11:2029. https://doi.org/10.1038/s41598-021-81404-3

Volodin IA, Zaytseva AS, Ilchenko OG, Volodina EV (2015) Small mammals ignore common rules: a comparison of vocal repertoires and the acoustics between pup and adult piebald shrews *Diplomesodon pulchellum*. Ethology 121:103–115. https://doi.org/10.1111/eth.12321

Volodin IA, Yurlova DD, Ilchenko OG, Volodina EV (2021) Ontogeny of audible squeaks in yellow steppe lemming *Eolagurus luteus*:

trend towards shorter and low-frequency calls is reminiscent of those in ultrasonic vocalization. BMC Zool 6:27. https://doi.org/10.1186/s40850-021-00092-8

Volodin IA, Dymskaya MM, Smorkatcheva AV, Volodina EV (2022) Ultrasound from underground: cryptic communication in subterranean wild-living and captive northern mole voles (*Ellobius talpinus*). Bioacoustics 31:414–434. https://doi.org/10.1080/09524622.2021.1960191

Volodina EV, Matrosova VA, Volodin IA (2010) An unusual effect of maturation on the alarm call fundamental frequency in two species of ground squirrels. Bioacoustics 20:87–98. https://doi.org/10.1080/09524622.2011.9753634

Wan X, Liu W, Wang G, Wang M, Zhong W (2006) Seasonal changes of the activity patterns of Brandt's vole (*Lasiopodomys brandtii*) in the typical steppe in Inner Mongolia. Acta Theriol Sin 26:226–234

Warren MR, Campbell D, Borie AM, Ford CL, Dharani AM, Young LJ, Liu RC (2022) Maturation of social-vocal communication in prairie vole (*Microtus ochrogaster*) pups. Front Behav Neurosci 15:814200. https://doi.org/10.3389/fnbeh.2021.814200

Wilden I, Tembrock G, Herzel H, Peters G (1998) Subharmonics, biphonation, and deterministic chaos in mammal vocalization. Bioacoustics 9:171–196. https://doi.org/10.1080/09524622.1998.9753394

Wilson DR, Hare JF (2006) The adaptive utility of Richardson's ground squirrel *Spermophilus richardsonii* short-range ultrasonic alarm signals. Can J Zool 84:1322–1330. https://doi.org/10.1139/z06-120

Yamazaki Y, Yamada H, Murofushi M, Momose H, Okanoya K (2004) Estimation of hearing range in raptors using unconditioned responses. Ornithol Sci 3:85–92. https://doi.org/10.2326/osj.3.85

Yu P, Wang J, Tai F, Broders H, An S, Zhang X, He F, An X, Wu R (2011) The effects of repeated early deprivation on ultrasonic vocalizations and ontogenetic development in mandarin vole pups. Behav Process 88:162–167. https://doi.org/10.1016/j.beproc.2011.09.001

Yurlova DD, Volodin IA, Ilchenko OG, Volodina EV (2020) Rapid development of mature vocal patterns of ultrasonic calls in a fast-growing rodent, the yellow steppe lemming (*Eolagurus luteus*). PLoS ONE 15:e0228892. https://doi.org/10.1371/journal.pone.0228892

Zaytseva AS, Volodin IA, Ilchenko OG, Volodina EV (2019) Ultrasonic vocalization of pup and adult fat-tailed gerbils (*Pachyuromys duprasi*). PLoS ONE 14:e0219749. https://doi.org/10.1371/journal.pone.0219749

Zaytseva AS, Volodin IA, Ilchenko OG, Volodina EV (2020) Audible calls and their ontogenetic relationship with ultrasonic vocalization in a rodent with a wide vocal range, the fat-tailed gerbil (*Pachyuromys duprasi*). Behav Process 180:104241. https://doi.org/10.1016/j.beproc.2020.104241

Zhong Z, Li G, Sanders D, Wang D, Holt RD, Zhang Z (2022) A rodent herbivore reduces its predation risk through ecosystem engineering. Curr Biol 32:1869–1874. https://doi.org/10.1016/j.cub.2022.02.074

Zorenko TA, Jakobsone GK (1986) Peculiarities of the postnatal development of the Brandt's vole, *Lasiopodomys brandtii* Radde. In: Zorenko TA (ed) Conservation, ecology and ethology of animals. University of Latvia, Riga, pp 25–44 [in Russian]

Zorenko TA, Smorkatcheva AV, Aksyonova TG (1994) Reproduction and postnatal ontogenesis of the mandarin vole *Lasiopodomys mandarinus* Milne-Edwards, and a comparison with Brandt's vole *L. brandti* Radde (Rodentia, Cricetidae). Laboratornye Zhyvotnye 4:5–16

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