Behavioural Processes 180 (2020) 104241

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Audible calls and their ontogenetic relationship with ultrasonic vocalization in a rodent with a wide vocal range, the fat-tailed gerbil (*Pachyuromys duprasi*)

Alexandra S. Zaytseva [a,b], Ilya A. Volodin [a,c,*], Olga G. Ilchenko [b], Elena V. Volodina [c]

[a] *Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Vorobievy Gory, 1/12, Moscow, 119234, Russia*
[b] *Department of Small Mammals, Moscow Zoo, B. Gruzinskaya, 1, Moscow, 123242, Russia*
[c] *Department of Behaviour and Behavioural Ecology of Mammals, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky Prospect, 33, Moscow, 119071, Russia*

A R T I C L E I N F O

Keywords:
Mammal
Vocalization
Isolation calls
Acoustic variables
Ontogeny

A B S T R A C T

Ontogeny of audible and ultrasonic calls is poorly studied in Gerbillinae rodents. In this study, analysis of calls, emitted by pup and adult fat-tailed gerbils *Pachyuromys duprasi* during 420-s isolation-and-handling procedures, allowed testing two hypotheses. Hypothesis1 predicted that audible squeaks and clicks follow the same ontogenetic pathway (towards higher-frequency and shorter calls) that has been previously documented for the ultrasonic calls of fat-tailed gerbil. Hypothesis2 predicted that the audible call types would alternate with the ultrasonic call types along ontogeny in this species. Hypothesis1 was tested with comparison of acoustic variables of audible calls (squeaks and clicks), emitted by 1–10-day old pups and by adults. Clicks of 8.3–8.7 kHz and high-frequency squeaks of 1.92–3.57 kHz were present in pups and adults, whereas mid-frequency squeaks of 0.31−0.67 kHz and low-frequency squeaks of 0.04−0.11 kHz were only present in pups. In agreement with Hypothesis1, pup high-frequency squeaks were longer, lower in fundamental frequency and higher in peak frequency. Against predictions, clicks did not differ acoustically between pups and adults. Hypothesis2 was tested with comparison of percentages of test trials containing the audible and/or ultrasonic call types of pups, repeatedly tested in 15 age classes along ontogeny from 1 to 40 days of age and in adults. The audible calls occurred in all age classes, whereas the ultrasonic calls emerged from day five of pup life and then prevailed over the audible squeaks in all age classes. We discuss that, in fat-tailed gerbil, ontogenetic pathways of acoustic variables of audible and ultrasonic calls (towards higher-frequency and shorter calls) are unusual for rodents although are typical for social and echolocation calls of bats. The is another parallelism of acoustic communication between bats and rodents aside from the recently discovered similarity between bat ultrasonic echolocation and echo-based navigation with bouts of ultrasonic calls in blind leaping rodents.

1. Introduction

Studies of rodent vocalization are mainly focused on ultrasonic calls (over 20 kHz) (Riede, 2011, 2013, 2018; Brudzynski, 2014; Pasch et al., 2017), however, many species of rodents produce human-audible calls below 20 kHz. In addition, some rodents produce audible through ultrasonic vocalizations (Pasch et al., 2011; Kobayasi and Riquimaroux, 2012; Campbell et al., 2014).

For adult rodents, the audible calls have been reported e.g. in voles (Kapusta, 2012; Rutovskaya, 2019a, 2019b), hamsters (Kapusta et al., 2006), gerbils (Bridelance, 1989; Volodin et al., 1994; Randall et al., 2005; Ter-Mikaelian et al., 2012), ground-dwelling sciurids (Shelley and Blumstein, 2005; Matrosova et al., 2012; Schneiderová and Policht, 2012), cavies (Monticelli and Ades, 2013), grasshopper mice (Campbell et al., 2014) and birch mice (Volodin et al., 2019a). For pup rodents, the audible calls have been reported e.g. in laboratory rats (Ihnat et al., 1995; LaFollette et al., 2018), mice (Ehret and Bernecker, 1986), voles (Terleph, 2011), hamsters (Hashimoto et al., 2001) and in wild-living ground-dwelling sciurids (Matrosova et al., 2007; Volodina et al., 2010; Schneiderová et al., 2015).

* Corresponding author at: Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Vorobievy Gory, 1/12, Moscow, 119234, Russia.
E-mail address: volodinsvoc@gmail.com (I.A. Volodin).

https://doi.org/10.1016/j.beproc.2020.104241
Received 6 May 2020; Received in revised form 26 August 2020; Accepted 28 August 2020
Available online 21 September 2020
0376-6357/

In rodents, relationship between ultrasonic and audible vocalization was studied within age classes (D'Udine et al., 1982; Jourdan et al., 1995; Hashimoto et al., 2001; Han et al., 2005; Kapusta et al., 2006; Williams et al., 2008; Kapusta, 2012; LaFollette et al., 2018), between age classes (Terleph, 2011), and between sexes (Lupanova and Egorova, 2015). However, the ontogenetic emergence of audible versus ultrasonic call types has yet to be investigated in rodents. So far, the alternation of different call types along ontogeny has only been studied for a single shrew species lacking the ultrasonic calls (Zaytseva et al., 2015).

The fat-tailed gerbil is a medium-sized North African desert rodent, kept at laboratories (Felt et al., 2008) and zoos (Zaytseva et al., 2016). Body mass in breeding adults is 60.0 ± 24.3 g and the head length 39.6 ± 2.1 mm, without significant differences between sexes (Zaytseva et al., 2016). Body mass in 7-day old unsexed pups is 5.3 ± 0.7 g and the head length 18.4 ± 0.8 mm (Zaytseva et al., 2016). Fat-tailed gerbil serves as a model for studying tropical diseases (Felt et al., 2008; Hanafi et al., 2013) and thermoregulation (Refinetti, 1998, 1999).

Fat-tailed gerbil is remarkable with the largest among rodents tympanal drums and respectively very low-frequency hearing sensitivity (Lay, 1972; Müller et al., 1991; Plassmann and Kadel, 1991). Nevertheless, the vocal repertoire of fat-tailed gerbil envelopes a broad range of frequencies from audible to ultrasonic (Bridelance, 1989; Zaytseva et al., 2017, 2019).

Adult fat-tailed gerbils produce both audible and ultrasonic calls when two unfamiliar males, females or male-female dyads are placed in the one cage (Bridelance, 1989). Both adult and 5–9-day old pup fat-tailed gerbils of both sexes produce both audible and ultrasonic calls when tested singly with a 420-s isolation-and-handling procedure (Zaytseva et al., 2019).

In a preceding study (Zaytseva et al., 2019), 26 types of ultrasonic calls (18 in pups, 24 in adults) were identified based on combination of six different contour shapes and six different note compositions; 16 call types were common in pups and adults (Zaytseva et al., 2019). Pup calls were overall longer and lower-frequency than adult ones, distinctive to rats and mice and reminiscent of the ontogenetic trajectory in bats (Zaytseva et al., 2019). For audible calls of adult fat-tailed gerbils, only a few published spectrograms is available (Bridelance, 1989), whereas the acoustic variables of audible calls have yet to be investigated. In this study, we advance and test a Hypothesis1, predicting that variables of audible squeaks and clicks will change towards higher-frequency and shorter calls, following the ontogenetic trajectory of ultrasonic calls previously revealed in fat-tailed gerbil (Zaytseva et al., 2019).

In fat-tailed gerbil, the ultrasonic calls emerge from day five of pup life, with maximum of ultrasound emission in 12–15-day old pups, so, a comparative analysis of ultrasonic calls between pups and adults is only possible starting with the 5 days of age (Zaytseva et al., 2017, 2019). Unlike ultrasonic call types, the audible call types emerge from the first day of pup life (Zaytseva et al., 2017, 2019). So, in this study we advance and test a Hypothesis2 predicting that audible call types would alternate with ultrasonic call types along ontogeny in fat-tailed gerbil.

In this study, we develop a categorization of fat-tailed gerbil audible calls and compare their acoustic variables between 1–10-day old pups and adults. This analysis is used for testing the Hypothesis1, predicting that variables of audible squeaks and clicks will change towards higher-frequency and shorter calls. In addition, we investigate the occurrence of audible and ultrasonic call types along ontogeny from the 1st to 40st day of pup life and in adults. This analysis is used for testing the Hypothesis2, predicting that audible and ultrasonic call types would alternate along ontogeny in fat-tailed gerbil.

2. Material and methods

2.1. Study site and animals

Audible and ultrasonic calls were recorded from members of a captive colony of fat-tailed gerbils at Moscow Zoo, Moscow, Russia, in 2013–2014. Our study animals were 20 adults from 110 to 711 (mean ± SD = 353.7 ± 182.2) days of age with breeding experience (10 males, 10 females) and 19 litters containing a total of 66 pups (17 males, 23 females, 26 unsexed) at the ages from 1 to 40 days. Nineteen litters originated from 17 different females, fifteen mothers with one litter per female and two females gave birth to two litters. The litter size varied from 1 to 6 pups (mean ± SD = 3.47 ± 1.50).

Before parturition, females were checked once a day for the appearance of a litter, and birth dates as well as the number of pups were recorded. Study pups were sexed from day 14 of age (on average at 16 ± 2.2 days of age) based on the appearance of nipples in females (Volodin et al., 1996; Zaytseva et al., 2016, 2019). The small size of pups also prevented individual chip marking for ethical reasons until 18–20 days of age.

The animals were kept under a natural light regime at room temperature (24–26 °C), in family groups consisting of two parents and littermates (Zaytseva et al., 2016, 2017). The animals were housed in wire-and-glass cages of 51 × 42.5 × 41.5 cm, with a bedding of sawdust and hay, at least two wooden shelters, cardboard boxes and tree branches as enrichment. They received custom-made small desert rodent chow with insect and mineral supplements and fruits and vegetables *ad libitum* as a source of water. All study animals were descendants of 8 animals (5 males and 3 females), obtained by Moscow Zoo in December 2007 from a natural population in Egypt. Before parturition, a female of a parental pair was becoming aggressive toward a male, displacing it to another wooden shelter; but in the second week of litter life, a male participated in parental care. Pups were kept together with parents during the entire 40-day period of call collection and were separated from the parents later, either after appearance of a second litter or in cases when parents were becoming aggressive toward them.

2.2. Experimental procedure and acoustic recording

A unified experimental procedure for collecting the audible and ultrasonic calls was applied to collect data on vocal development and body variables of 1–40-day old pups and adult fat-tailed gerbils. The recorded audible calls of 1–10-day old pups and of adults were used for testing the prediction of Hypothesis1. The recorded audible and ultrasonic calls of 1–40-day old pups and adult fat-tailed gerbils were used for testing the prediction of Hypothesis2.

All acoustic recordings were conducted in a separate room where no other animals were present, at room temperature 23–28 °C (mean ± SD = 25.1 ± 2.4) during daytime, at the same level of background noise. Both audible and ultrasonic calls were recorded simultaneously with two different sets of equipment. For the audible recordings (sampling rate 48 kHz, 24-bit resolution) we used a Fostex FR-2LE professional digital recorder (Fostex Company, Tokyo, Japan) and a Sennheiser K6-ME64 condenser microphone (Sennheiser electronic, Wedemark, Germany), flat frequency response from 0.04 to 20 kHz. For the ultrasonic recording (sampling rate 386 kHz, 16-bit resolution) we used a Pettersson D1000X recorder with built-in microphone (Pettersson Elektronik AB, Uppsala, Sweden), frequency response from 5 to 235 kHz.

Both microphones (for audible and ultrasonic recording) were established stationary at distance 15 cm above the tested animal. The obtained recordings had a high signal/noise ratio, the reverberation practically lacked. Each trial was recorded as two wav-files, one with audible and one with ultrasonic calls.

Each individual pup or adult was tested alone. Immediately before a test trial, the focal pup was taken out from the nest and transferred in a small clean plastic hutch to the experimental room within the same floor of the building. Time from removal of the focal pup from the nest to the start of a trial did not exceed 60 s. The trial started, when the focal animal was placed to the experimental setup. Duration of each trial was 420 s. Each trial took place in four stages: the isolation stage (120 s); the touch stage (90 s), the handling stage (90 s) and the measurement stage (120 s).

For the duration of the isolation stage, a focal animal was located either in a clean plastic hutch (190 × 130 × 70 mm for pups) or in a plastic cylinder without bottom (diameter 193 mm, high 170 mm for adolescents and adults), standing on even plastic table surface. Both the plastic huge and cylinder were open from above, i.e. from the side where the microphone was placed. For the duration of the touch stage, the experimenter (ASZ) gently touched the focal animal with a cotton bug, approximately two times per second. For the duration of the handling stage, the experimenter took the focal animal in hands and rotated it following the study (Hahn and Schanz 2002) on its back. For the duration of the measurement stage, the experimenter thrice measured body length, head length, foot length the tail length with an electronic caliper (Kraf Tool Co., Lenexa, Kansas, US, accurate to 0.01 mm), continuing keeping it in hands. The end of measurements was the end of the trial. After the trial, the focal animal was weighed on G&G TS-100 electronic scales (G&G GmbH, Neuss, Germany, accurate to 0.01 g). We used log body mass as a proxy measure for body size for comparison between pups and adults.

After weighing, the focal pup was placed to a heating hutch with a bedding of a cotton fabric, standing in the neighboring room. Trials with all littermates were done consequently in the same manner. Then all the litter in total was returned to their home cage to their parents; the time of pup stay out of the nest did not exceed 40 min. Although pups were not individually identified, the sequential trials with littermates allowed controlling that each pup participated in experiments only once per age. The adults were taken from their home cages before experiments with a clean plastic glass and returned to the cage after the test trial. The experimental setup was rubbed with napkin wetted with alcohol after each experimental trial, to avoid effect of smell on vocalization of the next focal animal in the next experimental trial (Thiessen et al., 1978; Lemasson et al., 2005).

2.3. Selection of audio files

Forty of 66 study pups were tested repeatedly at 15 experimental trials (one trial per pup per age) respective to 15 age classes, of 1–2, 3–4, 5–6, 7–8, 9–10, 11–12, 13–14, 15–16, 17–18, 19–20, 21–24, 25–28, 29–32, 33–36 and 37–40 days of age. Remaining 26 pups participated only at 1–2 trials per animal at age classes of 1–2, 3–4, 5–6 days of age. Each adult individual participated in one trial. Some recordings were damaged by some technical reasons, so only 1167 audio files were available for analysis from pups (611 in the audible, 556 in the ultrasonic range) and only 39 audio files were available for analysis from adults (20 in the audible, 19 in the ultrasonic range).

Description of acoustic variables of audible calls and their comparison between pups and adults were done based on 220 audio files, recorded in the audible range from 66 pups aged between 1–10 days, and based on 20 audio files from 20 adults. From 40 of the 66 pups, recordings were available at 5 trials per individual (age classes 1–2, 3–4, 5–6, 7–8, 9–10 days of age). From remaining 26 pups, recordings were available from 1 to 2 trials per individual (age classes 1–2, 3–4, 5–6 days of age). From each of the 20 adults, one recording (= one trial per individual) was available.

Inspection of spectrograms of the total of 240 audible audio files created using Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany) showed that only 13 (7 from males, 6 from females) of the 20 audio files available from adults contained calls. From the 220 audio files from pups, only 118 (from 54 pups) contained calls (55 of 57 files for age-class 1–2 days of age, 21 of 43 files for age-class 3–4 days of age, 17 of 45 files for age-class 5–6 days of age, 13 of 38 files for age-class 7–8 days of age and 12 of 37 files for 9–10 days of age).

To estimate the occurrence of ultrasonic and audible calls across age classes, we used audio files of 40 pups (17 males, 23 females) from 11 litters, repeatedly tested 15 times across 15 age classes up to 40 days of age. In addition, we used audio files from 20 adults (10 males, 10 females). Because some recordings were damaged by some technical reasons, for pups, we used the 581 audio files recorded in the audible range and 529 audio files recorded in the ultrasonic range. For adults, we used 20 audio files recorded in the audible range and 19 audio files recorded in the ultrasonic range. Percentages of audio files (= recording trials) in which a given call type was present were used as the measure of the occurrence of different call types for pups at different ages and for adults. We did not calculate call rates for each call type, because a preliminary inspection of spectrograms of audio recordings revealed that individual gerbils differed in vocal activity during test trials from zero to many hundreds of ultrasonic and/or audible calls within a minute, what should result in enormously large standard deviations.

2.4. Call analysis

For analysis, we selected the audible calls of good quality, appropriate for measurements of all acoustic variables. For reducing potential pseudoreplication, we avoided to take calls following each other in monotypic series. We considered sound utterances as separate calls if they were separated with a silent interval longer than 100 ms.

For pups, we measured in total 2113 audible calls (from 1 to 112 calls per audio file, 17.9 ± 18.0 calls per audio file on average). For 1–2-day old pups, we measured 1065 calls from 55 audio files; for 3–4-day old pups, we measured 557 calls from 21 audio files; for 5–6-day old pups, we measured 286 calls from 17 audio files; for 7–8-day old pups, we measured 76 calls from 13 audio files; for 9–10-day old pups, we measured 129 calls from 12 audio files. For adults, we measured in total 122 audible calls (from 2 to 51 calls per audio file, 9.4 ± 13.6 calls per audio file on average).

Measurements of acoustic variables of audible calls of adults and of 1–10-day old pups have been conducted with Avisoft SASLab Pro software and exported to Microsoft Excel (Microsoft Corp., Redmond, WA, USA). Before measurements, all wav-files were subjected to 0.2 kHz high-pass filtering, to remove low-frequency noise. For each audible call of any type, we measured, in the spectrogram window of Avisoft (sampling frequency 48 kHz, Hamming window, Fast Fourier Transform 1024 points, frame 50 %, overlap 96.87 %) the duration with the standard marker cursor. For each audible call of any type, we measured, in the power spectrum window of Avisoft, the frequency of maximum amplitude (fpeak), the bandwidth (bnd) of the fpeak at the distance of 10 dB from the maximum, and the lower (q25), medium (q50) and upper (q75) quartiles of power spectrum (covering respectively 25, 50 and 75 % of call energy) (Fig. 1).

For squeaks in which the f0 was visible as a continuous fundamental frequency (f0) contour, we measured the maximum fundamental frequency (f0max) and the minimum fundamental frequency (f0min), with the reticule cursor in the spectrogram window of Avisoft (Fig. 1). For squeaks in which the f0 was visible as a series of pulses, we measured the shortest period between pulses (t_1) as a measure of the maximum fundamental frequency (f0max = $1/t_1$) and the largest period between pulses (t_2) as a measure of the minimum fundamental frequency (f0min = $1/t_2$), with the standard marker cursor in the main window of Avisoft (Fig. 1). In calls displaying a transition from one type of squeak to another, the measured duration was equal to the total duration of a call, but the f0max, f0min, fpeak, bandwidth and quartiles were measured over the higher-frequency call part.

For each click, we measured the f0 as an inverse value of the average period of sound wave, visible on a strongly extended waveform, by using the standard marker cursor in the main window of Avisoft (Fig. 1). This value was taken as both f0max and f0min values of the clicks for subsequent statistical analyses.

2.5. Statistics

Statistical analyses were conducted using STATISTICA v. 8.0 (StatSoft, Tulsa, OK, USA) and R v. 3.0.1 (R Core Team, 2017). Means are given as mean ± SD, all tests were two-tailed, and differences were

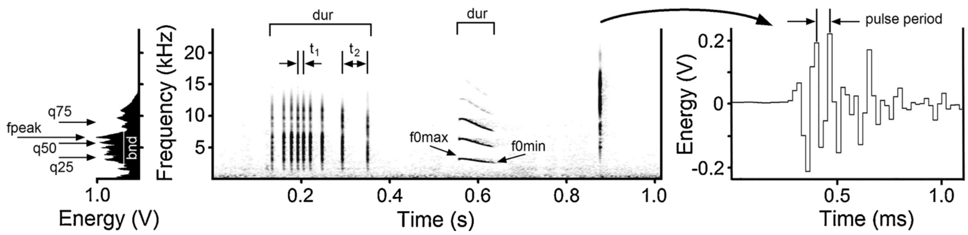

Fig. 1. Measured acoustic variables for audible calls of fat-tailed gerbils: LF (low-frequency) squeak, HF (high-frequency) squeak, click. Spectrogram (middle) and power spectrum of the entire LF squeak (left) and the waveform of the click (right). Designations: dur – call duration; f0max – the maximum fundamental frequency; f0min – the minimum fundamental frequency; fpeak – the frequency of maximum amplitude; q25, q50, q75 – the lower, the medium and the upper power quartiles; bnd – the bandwidth of the fpeak at the distance of 10 dB from the maximum; t_1 – the shortest fundamental frequency period of the low-frequency squeak; t_2 – the largest fundamental frequency period of the low-frequency squeak; pulse period – click fundamental frequency period. Spectrogram was created using sampling frequency 48 kHz, Hamming window, FFT 1024 points, frame 50 % and overlap 96.87 %.

considered significant whenever $p < 0.05$. We used a one-way ANOVA with Tukey Honest Significance Difference (HSD) post-hoc test to compare the values of acoustic variables between call types and pups and adults. We used Discriminant Function Analysis (DFA) standard procedure to calculate the probability of the assignment of calls to the correct call type. We used Wilks' Lambda values to estimate how strongly acoustic variables of calls contribute to the discrimination of call types. To validate our DFA results, we calculated the random values of correct assignment of calls to call types by applying randomization procedure with macros, created in R. The random values were averaged from DFAs performed on 1000 randomized permutations on the data sets as described by Solow (1990).

3. Results

3.1. Call types of pups and adults

Based on visual inspection of spectrograms, we subdivided audible calls by their acoustic structure into four types: squeaks (three types: LF squeaks, MF squeaks, HF squeaks) and clicks (one type) (Fig. 2). Two of the four call types were shared by 1–10-day old pups and adults, and other two call types were only found in pups. Table 1 presents mean values of measured acoustic variables for call types of pups and adults.

3.1.1. LF (low-frequency) squeak (Fig. 2a)

The fundamental frequency of LF squeaks is very low, so this call sounds as a creak. On a narrowband spectrogram, it is looking like a series of pulses with irregular intervals between them. The LF squeaks emerge from the first day of pup life and are present in all ages excluding the adults. This is the longest (up to 500 ms in duration) squeak, ranging in fundamental frequency from 0.01 to 0.37 kHz. The inter-pulse intervals vary strongly, from 3 to 80 ms. The bandwidth of peak frequency is the widest among the three types of squeaks (Table 1).

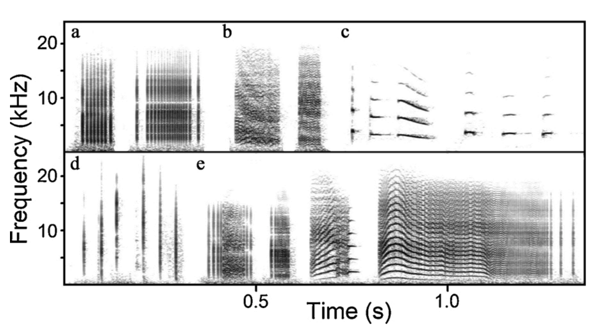

Fig. 2. Spectrogram illustrating audible calls of 2-day old pup and adult fat-tailed gerbils: (a) two pup LF (low-frequency) squeaks; (b) two pup MF (mid-frequency) squeaks; (c) three pup and three adult HF (high-frequency) squeaks; (d) three pup and three adult clicks; (e) four pup transitional calls between the LF, MF and HF squeaks. Spectrogram was created using sampling frequency 48 kHz, Hamming window, FFT 1024 points, frame 50 % and overlap 96.87 %. Audio wav-file to this spectrogram is available at Supplementary Materials Audio S1.

3.1.2. MF (mid-frequency) squeak (Fig. 2b)

The MF squeak is a tonal call intermediate in fundamental frequency between the LF and HF squeaks. On the narrowband spectrogram, the MF squeaks are looking like a combination of pulses with insertions of the fundamental frequency band with its harmonics. Like LF squeaks, MF squeaks emerge from the first day of pup life and are present in all ages excluding the adults. The duration is shorter than those of LF squeaks (Table 1), but it can reach up to 500 ms in some individual MF squeaks. Fundamental frequency ranges from 0.10 kHz to 1.30 kHz. The bandwidth of peak frequency is intermediate between the three types of squeaks (Table 1). There are transitional calls between the MF squeaks and LF squeaks (Fig. 2e). During acoustic analyses, the transitional calls were treated as MF squeaks, i.e. duration was measured over the entire call but frequency variables were only measured over the MF part.

3.1.3. HF (high-frequency) squeak (Fig. 2c)

The HF squeak is a short tonal call with harmonics well visible on the narrowband spectrogram. This call type was registered from the first day of pup life in all age classes including the adults. The duration is shorter than those of LF squeaks (up to 390 ms in pups and up to 250 ms in adults) but it does not differ from those of MF squeaks in the pups (Table 1). The HF squeak is the highest in fundamental frequency call type among the three types of squeaks. The fundamental frequency ranges from 0.65 kHz to 6.80 kHz in pups and from 0.93 kHz to 4.80 kHz in adults. The contour of fundamental frequency is weakly modulated. The bandwidth of peak frequency is the narrowest among the three types of squeaks (Table 1). There are transitional calls between HF and MF squeaks or between HF and LF squeaks (Fig. 2e); such calls were treated as HF squeaks, i.e. duration was measured over the entire call but frequency variables were only measured over the HF part.

3.1.4. Click (Fig. 2d)

The clicks represent soft sound pulses with a wideband spectrum. The clicks are produced from the first day of pup life and are present in all ages including adults. The duration is very short, not exceeding 10 ms in either pups or adults. The fundamental frequency ranges from 2.2 to 16.7 kHz. The clicks display 3–4 periods of fundamental frequency, steadily fading to the end of a call (Fig. 1); the values of fundamental

Table 1
Values (mean ± *SD*) of the acoustic variables of call types produced by 1-10-day old pup and in adult fat-tailed gerbils, one-way ANOVA results for comparison of the acoustic variables of four call types of pups, and one-way ANOVA results for comparison of the acoustic variables of two call types shared by pups and adults. Designations: LF squeak – low-frequency squeak; MF squeak – mid-frequency squeak; HF squeak – high-frequency squeak; N – number of audio files; n – number of calls; duration – call duration; f0max – the maximum fundamental frequency; f0min – the minimum fundamental frequency; fpeak – the maximum amplitude frequency; q25 – the lower quartile; q50 – the medium quartile; q75 – the upper quartile; bnd – bandwidth of the maximum amplitude frequency. Significant *p*-values for ANOVA results for comparison between four call types of pups are shown in bold, the values labeled with different letters are significantly different ($p < 0.05$, Tukey post-hoc test). Significant *p*-values for ANOVA results for comparison between pups and adults ($p < 0.025$ after Bonferroni correction) are shown in bold.

Call type	Age	N/n	duration (s)	f0max (kHz)	f0min (kHz)	fpeak (kHz)	q25 (kHz)	q50 (kHz)	q75 (kHz)	bnd (kHz)
LF squeak	Pup	63/154	0.116 ± 0.083^{a}	0.11 ± 0.08^{a}	0.04 ± 0.03^{a}	4.75 ± 2.06^{a,b}	3.45 ± 0.81^{a}	5.65 ± 1.15^{a}	8.06 ± 1.34^{a}	3.32 ± 1.59^{a}
MF squeak	Pup	78/304	0.090 ± 0.074^{b}	0.67 ± 0.28^{b}	0.31 ± 0.17^{b}	4.90 ± 2.40^{a}	3.50 ± 0.77^{a}	5.98 ± 1.12^{a}	8.52 ± 1.27^{a}	2.29 ± 1.33^{b}
HF squeak	Pup	98/1129	0.088 ± 0.074^{b}	2.99 ± 0.77^{c}	1.92 ± 0.67^{c}	4.39 ± 2.16^{b}	3.60 ± 0.93^{a}	5.74 ± 1.52^{a}	8.34 ± 1.69^{a}	0.97 ± 0.97^{c}
Click	Pup	103/526	0.007 ± 0.001^{c}	8.26 ± 3.72^{d}	8.26 ± 3.72^{d}	6.04 ± 3.40^{c}	4.57 ± 1.94^{b}	6.88 ± 2.42^{b}	9.28 ± 2.83^{b}	3.32 ± 2.01^{a}
ANOVA pup calls		$F_{3,2109}$=	229.4, ***p*<0.001**	1440.3, ***p*<0.001**	1752.8, ***p*<0.001**	50.7, ***p*<0.001**	87.6, ***p*<0.001**	55.8, ***p*<0.001**	31.7, ***p*<0.001**	409.6, ***p*<0.001**
HF squeak	Adult	6/90	0.058 ± 0.046	3.57 ± 0.41	2.96 ± 0.49	3.42 ± 0.87	3.16 ± 0.69	3.95 ± 1.21	5.89 ± 2.11	0.41 ± 0.20
ANOVA pup *vs* adult calls		$F_{1,1217}$=	14.29, ***p*<0.001**	50.20, ***p*<0.001**	207.22, ***p*<0.001**	18.09, ***p*<0.001**	19.56, ***p*<0.001**	118.07, ***p*<0.001**	166.70, ***p*<0.001**	30.36, ***p*<0.001**
Click	Adult	10/32	0.007 ± 0.001	8.70 ± 3.74	8.70 ± 3.74	6.70 ± 3.15	5.22 ± 1.75	7.76 ± 2.09	10.49 ± 2.61	2.80 ± 2.49
ANOVA pup *vs* adult calls		$F_{1,556}$=	2.63, *p*=0.11	0.41, *p*=0.52	0.41, *p*=0.52	1.15, *p*=0.28	3.42, *p*=0.06	4.00, *p*=0.046	5.53, ***p*=0.019**	2.01, *p* = 0.16

frequency can coincide with values of peak frequency. The peak frequency varies from 1.5 kHz to 19 kHz in pups and from 2.1 kHz to 11.3 kHz in adults. The bandwidth of peak frequency is very wide and did not differ from those of LF squeak in pups (Table 1). The low intensity of the clicks enables to reliably distinguish them from animal strikes over table surface only when the level of background noise is low.

3.2. Comparison of acoustic variables between calls types in pups

Based on ANOVA results, we found, that in 1–10-day old pups, all acoustic variables were significantly related to call type (Table 1). The duration did not differ between MF and HF squeaks, being in both significantly lower than in LF squeaks and significantly longer than in the clicks. The values of fundamental frequency variables were minimal in LF squeaks, intermediate in MF squeaks and maximal in HF squeaks; all differences were found significant (Table 1). The f0max and f0min of the clicks were a few times higher than those of the squeaks. The values of peak frequency and of the three power quartiles were higher for the clicks than for the squeaks and did not differ between types of squeaks, for the exclusion of fpeak, which was significantly higher in MF squeaks than in HF squeaks (Table 1). The bandwidth of peak frequency was the highest in the clicks and LF squeaks (and did not differ between them), intermediate in MF squeaks and the lowest in HF squeaks (Table 1).

As ANOVA revealed a significant effect of pup call type on all measured acoustic variables (Table 1), we could include in DFA all the eight measured variables of all the four call types of 1–10-day old pup audible calls. As sample sizes differed between call types (Table 1), we balanced the data set. We took the available 154 LF squeaks and randomly choose 154 calls from MF squeaks, HF squeaks and clicks (Table 2).

DFA correctly classified 82.47 % audible calls of the total number of 616 audible calls to call type (Table 2, Fig. 3). The average value of correct classifying was significantly higher ($p < 0.001$) than the random value (31.17 ± 1.57 %). The values of correct classifying to call type varied from 92.9 % for the clicks to 73.4 % for MF squeaks. Analysis of misclassifications showed that LF squeaks were misclassified with MF

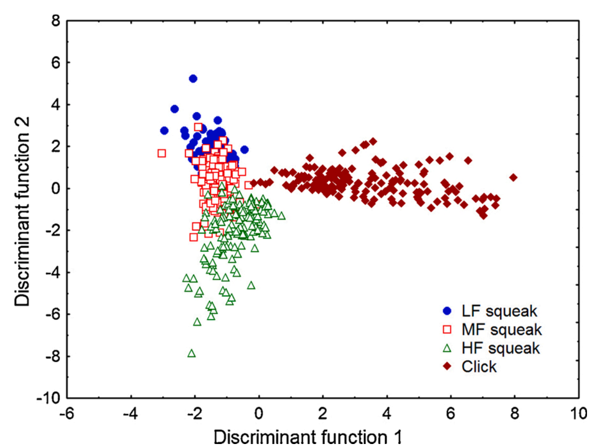

Fig. 3. Scatterplot showing separation produced by the first two discriminant functions of DFA for four call types of 1-10-day old pup fat-tailed gerbils. Designations: LF squeak – low-frequency squeak; MF squeak – mid-frequency squeak; HF squeak – high-frequency squeak; Click – click.

Table 2
Classifying the audible calls of 1-10-day old pups to correct call type with Discriminant Function Analysis (DFA) based on eight measured acoustic variables. Designations: LF squeak – low-frequency squeak; MF squeak – mid-frequency squeak; HF squeak – high-frequency squeak; Click – click.

Call type	Assignment to the predicted call type				Total calls	Percentage of calls correctly classified
	LF squeak	MF squeak	HF squeak	Click		
LF squeak	121	33	0	0	154	78.57
MF squeak	29	113	12	0	154	73.38
HF squeak	0	23	131	0	154	85.06
Click	0	11	0	143	154	92.86
Total calls	150	180	143	143	616	82.47

squeaks, MF squeaks were misclassified with LF and HF squeaks, and clicks were misclassified with MF squeaks (Table 2). Plot based on the first two discriminant functions indicated that LF squeaks and MF squeaks are substantially mixed, what could be the reason of the relatively low value of correct classifying between these call types (Fig. 3). Variables mainly introducing to discrimination, in order of decreasing importance, were f0min, f0max and duration (Table 2).

3.3. Comparison of acoustic variables between calls types shared by pups and adults

Based on ANOVA results, we compared acoustic variables of two call types (HF squeaks and clicks) shared by pups and adults (Table 1). The HF squeaks differed acoustically between 1–10-day old pups and adults in all measured variables. Pup HF squeaks were longer, lower in f0max and f0min, higher in fpeak, and had the higher three power quartiles and the wider bandwidth of the peak frequency (Table 1). Distinctively, the values of acoustic variables of the clicks did not differ between pups and adults, excluding the medium quartile, which was lower in pups than in adults (Table 1). Relationships between the f0max and logarithm body mass in pup and adult HF squeaks and clicks are indicated on Fig. 4.

3.4. Percentages of audible call types and ultrasonic calls across age classes

Percent of audio files (=recording trials) in which the given call type was registered, was used as a proxy measure for the occurrence of different call types in 1−40-day old pups and in adults (Fig. 5). All the four audible call types (LF squeaks, MF squeaks, HF squeaks and clicks) along with ultrasonic calls were registered in pups of all the 11 litters. Only two audible call types (HF squeaks and clicks) along with ultrasonic calls were registered in adults. Both pups and adults produced primarily the clicks (84 % and 60 % audio files in pups and adults, respectively) and secondarily the ultrasonic calls (46 % and 37 % audio files in pups and adults, respectively) and the HF squeaks (46 % and 30 % audio files in pups and adults, respectively) (Fig. 5). The LF squeaks and MF squeaks were the rarest call types and occurred only in pups (Fig. 5).

Detailed analysis of percentage of audio files, containing particular call types in particular age classes, showed that substantial numbers of LF squeaks occurred only in the youngest age classes, decreased steadily to a minimum in 21–24-days old pups and completely lacked in adults (Fig. 6). Percent of audio files containing MF squeaks, displayed a similar trend of age-related changes. Percent of audio files containing HF squeaks, varied from 27 to 63 %. Distinctive to any squeaks, the clicks occurred at high rates in all age classes, with maximum of 100 % audio files in 19–20 days-old pups, followed by a decrease down to 60 % of audio files in adults (Fig. 6). The ultrasonic calls emerged in pups between 5 and 6 days of age; percent of audio files with them increased up to 78 % at 13–14 days of age and then decreased steadily down to 30 % of audio files in adults (Fig. 6).

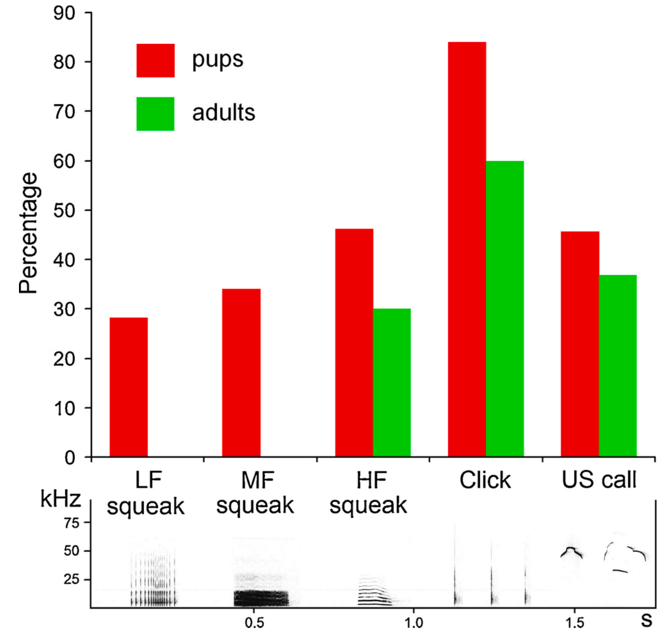

Fig. 5. Percent of audio files (one file per 420-s test trial), containing the given call type in 1-40-day old pup and in adult fat-tailed gerbils (upper panel). For pups, the total number of audio files was 1110 (581 with audible calls and 529 with ultrasonic calls). For adults, the total number of audio files was 39 (20 with audible calls, and 19 with ultrasonic calls). Lower panel provides illustrative spectrograms of respective call types. Designations: LF squeak – low-frequency squeak; MF squeak – mid-frequency squeak; HF squeak – high-frequency squeak; Click – click; US call – ultrasonic call.

Thus, the vocal repertoire of newborn fat-tailed gerbils included only the audible calls: three types of squeaks and the clicks. Regular emission of all the five call types (including the ultrasonic calls) in a substantial number of trials has been registered from 9–10 to 19–20 days of age. In general, adult fat-tailed gerbils were less vocal during the experimental trials than pups. Adult fat-tailed gerbils produced only three call types: HF squeaks, the clicks and the ultrasonic calls (Fig. 6).

4. Discussion

This study revealed that repertoires of audible calls in pup and adult fat-tailed gerbils, tested with isolation-and-handling procedure, comprised of squeaks and clicks. From the total of three types of squeaks, the 1–10-day old pup fat-tailed gerbils produced all the three types. At the same time, the adult fat-tailed gerbils produced only HF squeaks,

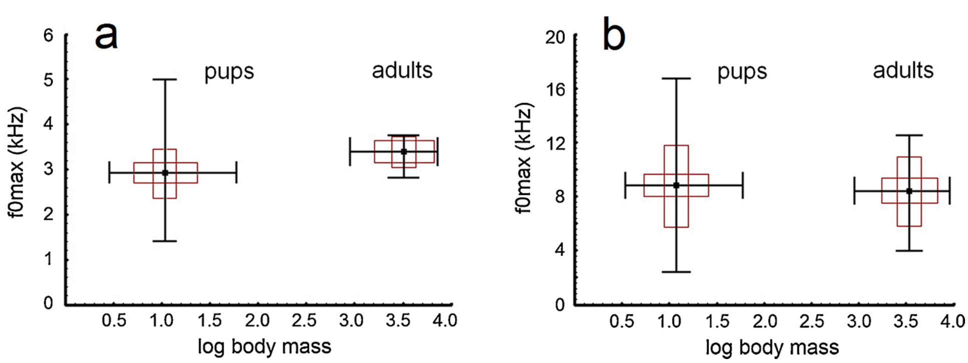

Fig. 4. Plot illustrating the relationship between the maximum fundamental frequency (f0max) and logarithm body mass in two call types shared by pups and adults: (a) HF squeaks; (b) clicks. Central points indicate the means, boxes indicate SD; whiskers indicate min-max values.

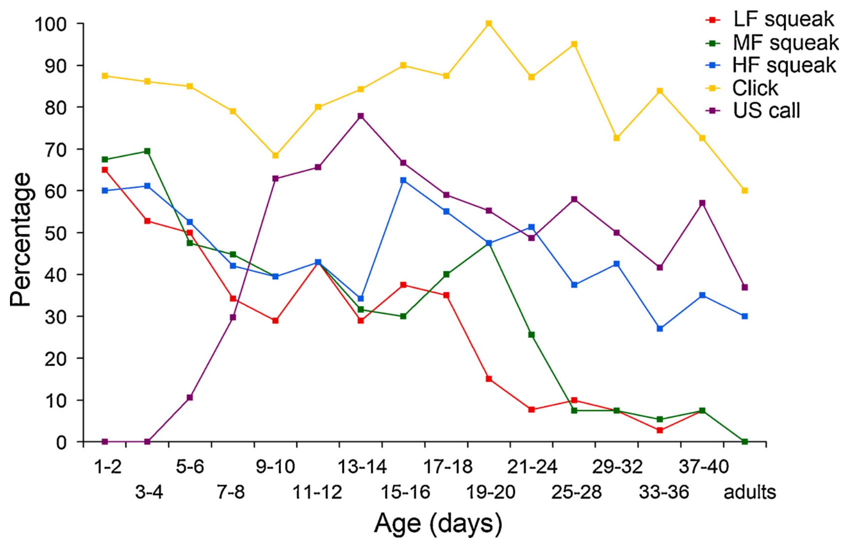

Fig. 6. Percent of audio files containing the given call type at each age class. Designations: LF squeak – low-frequency squeak; MF squeak – mid-frequency squeak; HF squeak – high-frequency squeak; Click – click; US call – ultrasonic call.

which were significantly higher-frequency and shorter than HF squeaks of pups. Clicks were produced by both pups and adults and did not differ acoustically between the ages, for exclusion of the medium quartile, which was lower in pups than in adults. Discriminant analysis confirmed the categorization of the audible calls to four call types.

In addition to “pure” call types, the vocal repertoire of audible calls of fat-tailed gerbils included also many calls transitional forms between the three types of squeaks. Among other rodents, repertoires of audible calls with only few "pure" call types and many transitional forms between them were found, e.g. in the northern collared lemming *Dicrostonyx groenlandicus* (Brooks and Banks, 1973), in the Uinta ground squirrel *Spermophilus armatus* (Balph and Balph, 1966), in the wild cavy *Cavia aperea* (Monticelli and Ades, 2013), in the Djungarian hamster *Phodopus sungorus* (Keesom et al., 2015), in the steppe lemming *Lagurus lagurus* (Rutovskaya, 2019a), in the yellow steppe lemming *Eolagurus luteus* (Rutovskaya, 2019a) and in a few species of voles of genus *Microtus* (Rutovskaya, 2019b).

In this study, prediction of Hypothesis1 that variables of audible calls of fat-tailed gerbils follow the ontogenetic trajectory towards higher-frequency and shorter calls, as in the ultrasonic calls of fat-tailed gerbils (Zaytseva et al., 2019), was only confirmed for HF squeaks, but was not supported for the clicks, which did not differ acoustically between pups and adults. Hypothesis2, predicting that audible and ultrasonic call types would alternate along ontogeny of fat-tailed gerbils, was only partially supported, because the audible calls occurred in all age classes, whereas the ultrasonic calls emerged only from the fifth day of pup life and then prevailed over the audible squeaks at all ages.

Along ontogeny, the audible vocalization of fat-tailed gerbils underwent substantial changes. In pups, trials containing all the three types of squeaks were approximately equally frequent between the 1–2 and 13–14 days of age. In older ages, percent of trials containing LF and MF squeaks decreased, and in adults, the trials only contained HF squeaks and clicks. In the lack of comparative data on other species is unclear, whether other species of gerbils also loss some of their audible call types with maturation.

Comparison of acoustic variables of HF squeaks between pups and adults showed that the fundamental frequency was significantly higher in adults than in pups. Previously we showed for the ultrasonic calls of fat-tailed gerbils that fundamental frequency significantly increases from pups to adults (Zaytseva et al., 2019). We conclude therefore that fat-tailed gerbil is the first rodent species in which the ontogenetic increase of fundamental frequency has been proven for both ultrasonic calls (Zaytseva et al., 2019) and audible squeaks (this study).

In contrast, in most other species of rodents, the audible vocalizations of adults are lower in fundamental frequency than those of their smaller pups (Blumstein and Munos, 2005; Matrosova et al., 2007; Campbell et al., 2014; Rutovskaya, 2019a). Nevertheless, some taxa of rodents, as e.g. ground squirrels, have undistinguishable fundamental frequencies of alarm calls between pups and adults, as in speckled ground squirrel *Spermophilus suslicus*, yellow ground squirrel *S. fulvus* (Matrosova et al., 2007; Volodina et al., 2010), Richardson’s ground squirrel *S. richardsonii* (Swan and Hare, 2008) and European ground squirrel *S. citellus* (Schneiderová et al., 2015). The ontogenetic shortening of call duration from pups to adults, as in fat-tailed gerbils, was reported for the alarm calls of degu *Octodon degu* (Nakano et al., 2013) and for the alarm calls of yellow-bellied marmots *Marmota flaviventris* (Blumstein and Munos, 2005).

The revealed in this study ontogenetic pathway towards higher-frequency and shorter calls in both audible and ultrasonic ranges of frequencies seems to be unique for fat-tailed gerbil among rodents. However, this kind of ontogenetic changes of acoustic variables is typical for social and echolocation calls of bats (Jones et al., 1991; De Fanis and Jones, 1995; Moss et al., 1997; Zhang et al., 2005; Liu et al., 2007; Hiryu and Riquimaroux, 2011; Monroy et al., 2011; Jin et al., 2011, 2012; Funakoshi et al., 2013; Wang et al., 2014; Engler et al., 2017; Mehduzadeh et al., 2018). We can conclude therefore that this study have documented another parallelism of vocal communication between Chiroptera and Rodentia, in alignment with a recently discovered parallelism between bat echolocation and echo-based orientation with bouts of ultrasonic pulses in a blind leaping rodent *Typhlomys chapensis* (Panyutina et al., 2017; Volodin et al., 2019b; Youlatos et al., 2020).

Unlike HF squeaks, the clicks did not differ in duration and fundamental frequency between pup and adult fat-tailed gerbils. The audible clicks are not well-studied in terms of acoustic structure or context in any mammal. Among rodents, the audible clicks were also described in capybaras *Hydrochoerus hydrochaeris* during group movement and at return of individuals to a group (Barros et al., 2011); in laboratory rats *Rattus norvegicus* in darkness (Thomas and Jalili, 2004), and in domestic mice at situation of pup isolation and handling (Haack et al., 1983; Shu et al., 2005; Gaub et al., 2010) as well as in the context of drop from an elevated back-down position to a padded surface (Groszer et al., 2008; Fujita et al., 2008). Aside from rodents, the clicks were described in shrews and tenrecs (Gould, 1965, 1969; Schneiderová, 2014; Volodin et al., 2015; Zaytseva et al., 2015).

Compared to fat-tailed gerbils, the clicks were longer (from 0.03 to

0.06 s) in the large-sized capybara (Lacerda et al., 2014), of the same duration (from 0.008 to 0.009 s) in the same-sized Asian house shrew *Suncus murinus* (Schneiderová, 2014) and shorter (0.004 s) in the smaller-sized piebald shrew *Diplomesodon pulchellum* (Volodin et al., 2015). Interesting, that values of fundamental frequency of the clicks in capybaras (from 3.36 kHz to 7.24 kHz) (Lacerda et al., 2014) and in piebald shrews (8.43 kHz in pups and 9.66 kHz in adults) (Volodin et al., 2015) and those of the peak frequency in Asian house shrews (4.97 kHz in pups and 6.20 kHz in adults) (Schneiderová, 2014) were practically the same as values of these acoustic variables in the clicks of fat-tailed gerbils in this study.

The delay of emergence of ultrasonic calls in fat-tailed gerbils until 5 days of age is unusual for rodents. Commonly, pup ultrasonic isolation calls are emitted from 1 to 3 days of age, as e.g. in Mongolian gerbils *Meriones unguiculatus* (de Ghett, 1974; Broom et al., 1977), domestic mice (Noirot, 1966; Okon, 1970; Hahn et al., 1998), long-tailed field mice *Apodemus sylvaticus* (Pontet et al., 1989), deer mice *Peromyscus californicus* (Vieira and Brown, 2002; Kalcounis-Rueppell et al., 2018), voles (Brooks and Banks, 1973; Yu et al., 2011; Blake, 2012), laboratory rats (Noirot, 1968; Allin and Banks, 1971; Okon, 1971) and Syrian hamsters *Mesocricetus auratus* (Okon, 1971; Hashimoto et al., 2001; Schneider and Fritzsche, 2011). Another remarkable difference of the fat-tailed gerbil from other rodents is the slight decrease of ultrasonic vocalization with maturation, whereas in other studied species of rodents, including Mongolian gerbils, the elder pups and the adults practically lack ultrasonic calls in the context of isolation (Thiessen et al., 1978; Motomura et al., 2002; Nishiyama et al., 2011; Wöhr, 2014; Weiner et al., 2016).

Fat-tailed gerbil is among a few rodent species, in which ontogeny of both acoustic variables and call types were studied for both the audible and ultrasonic vocalizations. Further research with more number of rodent species is necessary to explain the unusual findings of our study of fat-tailed gerbil: an extraordinary wide vocal range, from about 0.02 kHz (as low as in elephant rumbles) to over 110 kHz (as high as in bat echolocation); the ontogenetic delay of emission of ultrasonic calls by pups; the ontogenetic increase of fundamental frequency of the audible calls from pups to adults; and the complete disappearance of the low-frequency pup calls in adults.

Author statement

BEPROC_2020_187: Audible calls and their ontogenetic relationship with ultrasonic vocalization in a rodent with a wide vocal range, the fat-tailed gerbil (*Pachyuromys duprasi*).

CRediT authorship contribution statement

Alexandra S. Zaytseva: Conceptualization, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Funding acquisition. **Ilya A. Volodin:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Writing - review & editing, Project administration, Funding acquisition. **Olga G. Ilchenko:** Investigation, Resources, Writing - original draft, Writing - review & editing. **Elena V. Volodina:** Conceptualization, Validation, Investigation, Writing - original draft, Writing - review & editing, Funding acquisition.

Declaration of Competing Interest

The authors report no declarations of interest.

Acknowledgements

We thank the staff of Moscow Zoo for their help and support. We thank Steven Pollard for help with language correction. The experimental procedure has been approved by the Committee of Bio-ethics of Lomonosov Moscow State University, research protocol # 2011-36. During our work, we adhered to the 'Guidelines for the treatment of animals in behavioural research and teaching' (Anim. Behav., 2020, 159, I-XI) and the legal requirements about protecting animal welfare of Russian Federation, the country where the research was conducted. This study was supported by the Russian Science Foundation, grant number 19-14-00037.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.beproc.2020.104241.

References

Allin, J.T., Banks, E.M., 1971. Effects of temperature on ultrasound production by infant albino rats. Dev. Psychobiol. 4, 149–156. https://doi.org/10.1002/dev.420040206.

Balph, D.M., Balph, D.F., 1966. Sound communication of Uinta ground squirrels. J. Mammal. 47, 440–450. https://doi.org/10.2307/1377685.

Barros, K.S., Tokumaru, R.S., Pedroza, J.P., Nogueira, S.S.C., 2011. Vocal repertoire of captive capybara (*Hydrochoerus hydrochaeris*): Structure, context and function. Ethology 117, 83–93. https://doi.org/10.1111/j.1439-0310.2010.01853.x.

Blake, B.H., 2012. Ultrasonic calling in 2 species of voles, *Microtus pinetorum* and *M. pennsylvanicus*, with different social systems. J. Mammal. 93, 1051–1060. https://doi.org/10.1644/11-MAMM-A-356.2.

Blumstein, D.T., Munos, O., 2005. Individual, age and sex-specific information is contained in yellow-bellied marmot alarm calls. Anim. Behav. 69, 353–361. https://doi.org/10.1016/j.anbehav.2004.10.001.

Bridelance, P., 1989. Communication acoustique entre individus adultes des genres *Meriones*, *Pachyuromys*, *Psammomys* (Gerbillidae, Rodentia). I. Analyse des repertoires. Mammalia 53, 3–17 [in French].

Brooks, R.J., Banks, E.M., 1973. Behavioural biology of the collared lemming [*Dicrostonyx groenlandicus* (Trail)]: an analysis of acoustic communication. Anim. Behav. 6, 1–83. https://doi.org/10.1016/0003-3472(73)90003-1.

Broom, D.M., Elwood, R.W., Lakin, J., Willy, S.J., Pretlove, A.J., 1977. Developmental changes in several parameters of ultrasonic calling by young Mongolian gerbils (*Meriones unguiculatus*). J. Zool. 183, 281–290. https://doi.org/10.1111/j.1469-7998.1977.tb04187.x.

Brudzynski, S.M., 2014. Social origin of vocal communication in rodents. In: Witzany, G. (Ed.), Biocommunication of Animals. Springer, Dordrecht, pp. 63–79. https://doi.org/10.1007/978-94-007-7414-8_5.

Campbell, P., Pasch, B., Warren, A.L., Phelps, S.M., 2014. Vocal ontogeny in Neotropical singing mice (*Scotinomys*). PLoS One 9 (12), e113628. https://doi.org/10.1371/journal.pone.0113628.

D'Udine, B., Robinson, D.J., Oliverio, A., 1982. An analysis of single-gene effects on audible and ultrasonic vocalizations in the mouse. Behav. Neural Biol. 36, 197–203. https://doi.org/10.1016/s0163-1047(82)90189-3.

De Fanis, E., Jones, D.G., 1995. Post-natal growth, mother-infant interactions and development of vocalizations in the vespertilionid bat *Plecotus auritus*. J. Zool. 235, 85–97. https://doi.org/10.1111/j.1469-7998.1995.tb05130.x.

de Ghett, V.J., 1974. Developmental changes in the rate of ultrasonic vocalization in the Mongolian gerbil. Dev. Psychobiol. 7, 261–272. https://doi.org/10.1002/dev.420070311.

Ehret, G., Bernecker, C., 1986. Low-frequency sound communication by mouse pups (*Mus musculus*): wriggling calls release maternal behavior. Anim. Behav. 34, 821–830. https://doi.org/10.1016/S0003-3472(86)80067-7.

Engler, S., Rose, A., Knörnschild, M., 2017. Isolation call ontogeny in bat pus (*Glossophaga soricina*). Behaviour 154, 267–286. https://doi.org/10.1163/1568539x-00003421.

Felt, S.A., Hussein, H.I., Helmy, I.H., 2008. Biology, breeding, husbandry and diseases of the captive Egyptian fat-tailed jird (*Pachyuromys duprasi natronensis*). Lab. Anim. (NY) 37, 256–261. https://doi.org/10.1038/laban0608-256.

Fujita, E., Tanabe, Y., Shiota, A., Ueda, M., Suwa, K., Momoi, M.Y., Momoi, T., 2008. Ultrasonic vocalization impairment of *Foxp2* (R552H) knockin mice related to speech-language disorder and abnormality of Purkinje cells. Proc. Natl. Acad. Sci. U. S. A. 105, 3117–3122, 10.1073_pnas.0712298105.

Funakoshi, K., Arai, A., Inoue, T., 2013. Development of sounds during postnatal growth of the eastern bent-winged bat *Miniopterus fuliginosus*. Mammal Study 38, 49–56. https://doi.org/10.3106/041.038.0106.

Gaub, S., Groszer, M., Fisher, S.E., Ehret, G., 2010. The structure of innate vocalizations in Foxp2-deficient mouse pups. Genes Brain Behav. 9, 390–401. https://doi.org/10.1111/j.1601-183X.2010.00570.x.

Gould, E., 1965. Evidence for echolocation in the Tenrecidae of Madagascar. Proc. Am. Phil. Soc. 109, 352–360.

Gould, E., 1969. Communication in three genera of shrews (Soricidae) *Suncus*, *Blarina*, and *Cryptotis*. Commun. Behav. Biol. Part A 3, 11–31.

Groszer, M., Keays, D.A., Deacon, R.M.J., de Bono, J.P., Prasad-Mulcare, S., Gaub, S., et al., 2008. Impaired synaptic plasticity and motor learning in mice with a point mutation implicated in human speech deficits. Curr. Biol. 18, 354–362. https://doi.org/10.1016/j.cub.2008.01.060.

Haack, B., Markl, H., Ehret, G., 1983. Sound communication between parents and offspring. In: Willott, J.F. (Ed.), The Auditory Psychobiology of the Mouse. C.C. Thomas, Springfield, IL, pp. 57–97.

Hahn, M.E., Karkowski, L., Weinreb, L., Henry, A., Schanz, N., Hahn, E.M., 1998. Genetic and developmental influences on infant mouse ultrasonic calling. II. Developmental patterns in the calls of mice 2-12 days of age. Behav. Genetics 28, 315–325. https://doi.org/10.1023/a:1021679615792.

Han, J.S., Bird, G.C., Li, W., Jones, J., Neugebauer, V., 2005. Computerized analysis of audible and ultrasonic vocalizations of rats as a standardized measure of pain-related behavior. J. Neurosci. Meth. 141, 261–269. https://doi.org/10.1016/j.jneumeth.2004.07.005.

Hanafi, H.A., Fryauff, D.J., Kittell, C.E., 2013. Evaluation of the fat-tailed gerbil, *Pachyuromys duprasi* (Rodentia: Gerbillidae), as a new animal model for studies of *Leishmania major* infection and transmission. Vector Borne Zoonotic Dis. 13, 650–656. https://doi.org/10.1089/vbz.2012.1185.

Hashimoto, H., Saito, T.R., Moritani, N., Komeda, K., Takahashi, K.W., 2001. Comparative study on isolation calls emitted from hamster pups. Exp. Anim. 50, 313–318. https://doi.org/10.1538/expanim.50.313.

Hiryu, S., Riquimaroux, H., 2011. Developmental changes in ultrasonic vocalizations by infant Japanese echolocating bats, *Pipistrellus abramus*. J. Acoust. Soc. Am. 130, EL147–EL153. https://doi.org/10.1121/1.3632044.

Ihnat, R., White, N.R., Barfield, R.J., 1995. Pup's broadband vocalizations and maternal behavior in the rat. Behav. Process. 33, 257–271. https://doi.org/10.1016/0376-6357(94)00028-f.

Jin, L., Lin, A., Sun, K., Liu, Y., Feng, J., 2011. Postnatal development of morphological features and vocalization in the pomona leaf-nosed bat *Hipposideros pomona*. Acta Theriol. 56, 13–22. https://doi.org/10.1007/s13364-010-0011-z.

Jin, L., Wang, J., Zhang, Z., Sun, K., Kanwal, J.S., Feng, J., 2012. Postnatal development of morphological and vocal features in Asian particolored bat, *Vespertilio sinensis*. Mammal Biol. 77, 339–344. https://doi.org/10.1016/j.mambio.2012.05.001.

Jones, G., Hughes, P.M., Rayner, J.M.V., 1991. The development of vocalizations in *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during post-natal growth and the maintenance of individual vocal signatures. J. Zool. 225, 71–84. https://doi.org/10.1111/j.1469-7998.1991.tb03802.x.

Jourdan, D., Ardid, D., Chapuy, E., Eschalier, A., Le Bars, D., 1995. Audible and ultrasonic vocalization elicited by single electrical nociceptive stimuli to the tail in the rat. Pain 63, 237–249. https://doi.org/10.1016/0304-3959(95)00049-x.

Kalcounis-Rueppell, M.C., Pultorak, J.D., Marler, C.A., Blake, B.H., 2018. Ultrasonic vocalizations of young mice in the genus *Peromyscus*. In: Brudzynski, S.M. (Ed.), Handbook of Ultrasonic Vocalization. V. 25. A Window into the Emotional Brain. Elsevier, pp. 149–156. https://doi.org/10.1016/B978-0-12-809600-0.00014-7.

Kapusta, J., 2012. Effect of the stage of the reproductive cycle on vocalization and behaviour in female bank voles. Acta Theriol. 57, 145–152. https://doi.org/10.1007/s13364-011-0056-7.

Kapusta, J., Szentgyorgyi, H., Surov, A., Ryurikov, G., 2006. Vocalization of two Palaearctic species of hamster: Eversmann hamster *Allocricetulus eversmanni* and grey hamster *Cricetulus migratorius*. Bioacoustics 15, 315–330. https://doi.org/10.1080/09524622.2006.9753556.

Keesom, S.M., Rendon, N.M., Demas, G.E., Hurley, L.M., 2015. Vocal behaviour during aggressive encounters between Siberian hamsters, *Phodopus sungorus*. Anim. Behav. 102, 85–93. https://doi.org/10.1016/j.anbehav.2015.01.014.

Kobayasi, K.I., Riquimaroux, H., 2012. Classification of vocalizations in the Mongolian gerbil, *Meriones unguiculatus*. J. Acoust. Soc. Am. 131, 1622–1631. https://doi.org/10.1121/1.3672693.

Lacerda, P.O., Tokumaru, R.S., da Cunha Nogueira, S.S., 2014. Vocal signature in capybara, *Hydrochoerus hydrochaeris*. Acta Ethol. 17, 77–81. https://doi.org/10.1007/s10211-013-0162-4.

LaFollette, M.R., O'Haire, M.E., Cloutier, S., Gaskill, B.N., 2018. Practical rat tickling: determining an efficient and effective dosage of heterospecific play. Appl. Anim. Behav. Sci. 208, 82–91. https://doi.org/10.1016/j.applanim.2018.08.005.

Lay, D.M., 1972. The anatomy, physiology, functional significance and evolution of specialized hearing organs of Gerbilline rodents. J. Morphol. 138, 41–120. https://doi.org/10.1002/jmor.1051380103.

Lemasson, M., Delbé, C., Gheusi, G., Vincent, J.-D., Lledo, P.-M., 2005. Use of ultrasonic vocalizations to assess olfactory detection in mouse pups treated with 3-methylindole. Behav. Process. 68, 13–23. https://doi.org/10.1016/j.beproc.2004.09.001.

Liu, Y., Feng, J., Jiang, Y.L., Wu, L., Sun, K.P., 2007. Vocalization development of greater horseshoe bat, *Rhinolophus ferrumequinum* (Rhinolophidae, Chiroptera). Folia Zool. 56, 126–136.

Lupanova, A.S., Egorova, M.A., 2015. Vocalization of sex partners in the house mouse (*Mus musculus*). J. Evol. Biochem. Phys. 51, 324–331. https://doi.org/10.1134/S0022093015040080.

Matrosova, V.A., Volodin, I.A., Volodina, E.V., Babitsky, A.F., 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, V.A., Schneiderová, I., Volodin, I.A., Volodina, E.V., 2012. Species-specific and shared features in vocal repertoires of three Eurasian ground squirrels (genus *Spermophilus*). Acta Theriol. 57, 65–78. https://doi.org/10.1007/s13364-011-0046-9.

Mehduzadeh, R., Eghbali, H., Sharifi, M., 2018. Postnatal growth and vocalization development in the long-fingered bat, *Myotis capaccinii* (Chiroptera, Vespertilionidae). Zool. Stud. 57, 37. https://doi.org/10.6620/ZS.2018.57-37.

Monroy, J.A., Carter, M.E., Miller, K.E., Covey, E., 2011. Development of echolocation and communication vocalizations in the big brown bat, *Eptesicus fuscus*. J. Comp. Physiol. A 197, 459–467. https://doi.org/10.1007/s00359-010-0614-5.

Monticelli, P.F., Ades, C., 2013. The rich acoustic repertoire of a precocious rodent, the wild cavy *Cavia aperea*. Bioacoustics 22, 49–66. https://doi.org/10.1080/09524622.2012.711516.

Moss, C.F., Redish, D., Gounden, C., Kunz, T.H., 1997. Ontogeny of vocal signals in the little brown bat, *Myotis lucifugus*. Anim. Behav. 54, 131–141. https://doi.org/10.1006/anbe.1996.0410.

Motomura, N., Shimizu, K., Shimizu, M., Aoki-Komori, S., Taniguchi, K., Serizawa, I., Saito, T.R., 2002. A comparative study of isolation-induced ultrasonic vocalization in rodent pups. Exp. Anim. 51, 187–190. https://doi.org/10.1538/expanim.51.187.

Müller, M., Ott, H., Bruns, V., 1991. Frequency representation and spiral ganglion cell density in the cochlea of the gerbil *Pachyuromys duprasi*. Hear. Res. 56, 191–196. https://doi.org/10.1016/0378-5955(91)90169-A.

Nakano, R., Nakagawa, R., Tokimoto, N., Okanoya, K., 2013. Alarm call discrimination in a social rodent: adult but not juvenile degu calls induce high vigilance. J. Ethol. 31, 115–121. https://doi.org/10.1007/s10164-012-0355-8.

Nishiyama, K., Kobayasi, K.I., Riquimaroux, H., 2011. Vocalization control in Mongolian gerbils (*Meriones unguiculatus*) during locomotion behavior. J. Acoust. Soc. Am. 130, 4148–4157. https://doi.org/10.1121/1.3651815.

Noirot, E., 1966. Ultrasounds in young rodents. I. Changes with age in albino mice. Anim. Behav. 14, 459–462. https://doi.org/10.1016/S0003-3472(66)80045-3.

Noirot, E., 1968. Ultrasounds in young rodents. II. Changes with age in albino rats. Anim. Behav. 16, 129–134. https://doi.org/10.1016/0003-3472(68)90123-1.

Okon, E.E., 1970. The ultrasonic responses of albino mouse pups to tactile stimuli. J. Zool. 162, 485–492. https://doi.org/10.1111/j.1469-7998.1970.tb01283.x.

Okon, E.E., 1971. The temperature relations of vocalization in infant Golden hamsters and Wistar rats. J. Zool. 164, 227–237. https://doi.org/10.1111/j.1469-7998.1971.tb01308.x.

Panyutina, A.A., Kuznetsov, A.N., Volodin, I.A., Abramov, A.V., Soldatova, I.B., 2017. A blind climber: the first evidence of ultrasonic echolocation in arboreal mammals. Integr. Zool. 12, 172–184. https://doi.org/10.1111/1749-4877.12249.

Pasch, B., George, A.S., Hamlin, H.J., Guillette, L.J., Phelps, S.M., 2011. Androgens modulate song effort and aggression in Neotropical singing mice. Horm. Behav. 59, 90–97. https://doi.org/10.1016/j.yhbeh.2010.10.011.

Pasch, B., Tokuda, I.T., Riede, T., 2017. Grasshopper mice employ distinct vocal production mechanisms in different social contexts. Proc. R. Soc. B 284, 20171158. https://doi.org/10.1098/rspb.2017.1158.

Plassmann, W., Kadel, M., 1991. Low-frequency sensitivity in a gerbilline rodent, *Pachyuromys duprasi*. Brain Behav. Evol. 38, 115–126. https://doi.org/10.1159/000114382.

Pontet, A., Gyger, M., Schenk, F., 1989. Ontogeny of ultrasonic vocalizations in the woodmouse (*Apodemus sylvaticus* L.). I: temporal organization. Behaviour 108, 241–261. https://doi.org/10.1163/156853989X00321.

R Core Team, 2017. R: A Language and Environment for Statistical Computing. Vienna, Austria. Retrieved from. https://www.r-project.org/.

Randall, J.A., McCowan, B., Collins, K.C., Hooper, S.L., Rogovin, K., 2005. Alarm signals of the great gerbil: acoustic variation by predator context, sex, age, individual, and family group. J. Acoust. Soc. Am. 118, 2706–2714. https://doi.org/10.1121/1.2031973.

Refinetti, R., 1998. Homeostatic and circadian control of body temperature in the fat-tailed gerbil. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 119, 295–300. https://doi.org/10.1016/S1095-6433(97)00436-4.

Refinetti, R., 1999. Amplitude of the daily rhythm of body temperature in eleven mammalian species. J. Thermal Biol. 24, 477–481. https://doi.org/10.1016/S0306-4565(99)00077-7.

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., 2013. Stereotypic laryngeal and respiratory motor patterns generate different call types in rat ultrasound vocalization. J. Exp. Zool. A 319, 213–224. https://doi.org/10.1002/jez.1785.

Riede, T., 2018. Peripheral vocal motor dynamics and combinatory call complexity of ultrasonic vocal production in rats. In: Brudzynski, S.M. (Ed.), Handbook of Ultrasonic Vocalization. V. 25. A Window into the Emotional Brain. Elsevier, pp. 45–60. https://doi.org/10.1016/B978-0-12-809600-0.00005-6.

Rutovskaya, M.V., 2019a. Vocal communication in two lemming species (*Lagurus lagurus* and *Eolagurus luteus*). Bioacoustics 28, 42–56. https://doi.org/10.1080/09524622.2017.1361338.

Rutovskaya, M.V., 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.

Schneider, N., Fritzsche, P., 2011. Isolation calls and retrieving behavior in laboratory and wild-derived golden hamsters – no sign for inbreeding depression. Mammal. Biol. 76, 549–554. https://doi.org/10.1016/j.mambio.2011.03.002.

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., Policht, R., 2012. Acoustic analysis of the alarm call of the Anatolian ground squirrel *Spermophilus xanthoprymnus*: a description and comparison with alarm calls of the Taurus *S. taurensis* and European *S. citellus* ground squirrels. Naturwissenschaften 99, 55–64. https://doi.org/10.1007/s00114-011-0870-4.

Schneiderová, I., Schnitzerová, P., Uhlíková, J., Brandl, P., Zouhar, J., Matějů, 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.

Shelley, E.L., Blumstein, D.T., 2005. The evolution of vocal alarm communication in rodents. Behav. Ecol. 16, 169–177. https://doi.org/10.1093/beheco/arh148.
Shu, W., Cho, J.Y., Jiang, Y., Zhang, M., Weisz, D., Elder, G.A., et al., 2005. Altered ultrasonic vocalization in mice with a disruption in the *Foxp2* gene. Proc. Natl. Acad. Sci. U. S. A. 102, 9643–9648, 10.1073_pnas.0503739102.
Solow, A.R., 1990. A randomization test for misclassification probability in discriminant analysis. Ecology 71, 2379–2382. https://doi.org/10.2307/1938650.
Swan, D.C., Hare, J.F., 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.
Terleph, T.A., 2011. A comparison of prairie vole audible and ultrasonic pup calls and attraction to them by adults of each sex. Behaviour 148, 1275–1294. https://doi.org/10.1163/000579511X600727.
Ter-Mikaelian, M., Rübsamen, R., Yapa, W.B., 2012. Vocal behavior of the Mongolian gerbil in a seminatural enclosure. Behaviour 149, 461–492. https://doi.org/10.1163/156853912x639778.
Thiessen, D.D., Graham, M., Davenport, R., 1978. Ultrasonic signaling in the gerbil (*Meriones unguiculatus*): social interaction and olfaction. J. Comp. Physiol. Psychol. 92, 1041–1049. https://doi.org/10.1037/h0077512.
Thomas, J.A., Jalili, M., 2004. Review of echolocation in insectivores and rodents. In: Thomas, J.A., Moss, C., Vater, V. (Eds.), Echolocation in Bats and Dolphins. The University of Chicago Press, pp. 547–564.
Vieira, M.L., Brown, R.E., 2002. Ultrasonic vocalizations and ontogenetic development in California mice (*Peromyscus californicus*). Behav. Process. 59, 147–156. https://doi.org/10.1016/S0376-6357(02)00089-X.
Volodin, I.A., Goltsman, M.E., Borisova, N.G., 1994. Situational changes in vocalization of Great gerbils (*Rhombomys opimus* Licht.) during defensive behavior. Dokl. Biol. Sci. 334, 65–68.
Volodin, I.A., Ilchenko, O.G., Popov, S.V., 1996. Gerbils: Captive Management and Population Demography of Different Species in Laboratory. Moscow Zoo press, Moscow [in Russian].
Volodin, I.A., Zaytseva, A.S., Ilchenko, O.G., Volodina, E.V., 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, I.A., Klenova, A.V., Ilchenko, O.G., Volodina, E.V., 2019a. High frequency audible calls in northern birch mice *Sicista betulina* in response to handling: effects of individuality, sex and body mass on the acoustics. BMC Res. Notes 12, 677. https://doi.org/10.1186/s13104-019-4719-9.
Volodin, I.A., Panyutina, A.A., Abramov, A.V., Ilchenko, O.G., Volodina, E.V., 2019b. Ultrasonic bouts of a blind climbing rodent (*Typhlomys chapensis*): acoustic analysis. Bioacoustics 28, 575–591. https://doi.org/10.1080/09524622.2018.1509374.
Volodina, E.V., Matrosova, V.A., Volodin, I.A., 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.
Wang, L., Lin, A., Xiao, Y., Jiang, T., Feng, J., 2014. Postnatal development in the big-footed bat, *Myotis macrodactylus*: wing morphology, echolocation calls, and flight. Acta Theriol. 59, 435–441. https://doi.org/10.1007/s13364-014-0182-0.
Weiner, B., Hertz, S., Perets, N., London, M., 2016. Social ultrasonic vocalization in awake head-restrained mouse. Front. Behav. Neurosci. 10, 236. https://doi.org/10.3389/fnbeh.2016.00236.
Williams, W.O., Riskin, D.K., Mott, A.K., 2008. Ultrasonic sound as an indicator of acute pain in laboratory mice. J. Am. Assoc. Lab. Anim. Sci. 47, 8–10.
Wöhr, M., 2014. Ultrasonic vocalizations in Shank mouse models for autism spectrum disorders: detailed spectrographic analyses and developmental profiles. Neurosci. Biobeh. Rev. 43, 199–212. https://doi.org/10.1016/j.neubiorev.2014.03.021.
Youlatos, D., Panyutina, A.A., Tsinoglou, M., Volodin, I.A., 2020. Locomotion and postures of the Vietnamese pygmy dormouse *Typhlomys chapensis* (Platacanthomyidae, Rodentia): climbing and leaping in the blind. Mammal. Biol. https://doi.org/10.1007/s42991-020-00043-9.
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.
Zaytseva, A.S., Volodin, I.A., Mason, M.J., Frey, R., Fritsch, G., Ilchenko, O.G., Volodina, E.V., 2015. Vocal development during postnatal growth and ear morphology in a shrew that generates seismic vibrations, *Diplomesodon pulchellum*. Behav. Process. 118, 130–141. https://doi.org/10.1016/j.beproc.2015.06.012.
Zaytseva, A.S., Ilchenko, O.G., Volodin, I.A., Volodina, E.V., 2016. Early postnatal development of the fat-tailed gerbil (*Pachyuromys duprasi*, Rodentia, Gerbillinae) in a laboratory colony. Zool. Zhurnal 95, 94–103. https://doi.org/10.7868/S0044513416010141 [in Russian].
Zaytseva, A.S., Volodin, I.A., Ilchenko, O.G., Volodina, E.V., 2017. Discomfort-related changes in pup ultrasonic calls of fat-tailed gerbils *Pachyuromys duprasi*. Bioacoustics 26, 1–13. https://doi.org/10.1080/09524622.2016.1164076.
Zaytseva, A.S., Volodin, I.A., Ilchenko, O.G., Volodina, E.V., 2019. Ultrasonic vocalization of pup and adult fat-tailed gerbils (*Pachyuromys duprasi*). PLoS One 14, e0219749. https://doi.org/10.1371/journal.pone.0219749.
Zhang, L., Jones, G., Parsons, S., Liang, B., Zhang, S., 2005. Development of vocalizations in the flat-headed bats, *Tylonycteris pachypus* and *T. robustula* (Chiriptera: Vespertilionidae). Acta Chiropt. 7, 91–99. https://doi.org/10.3161/1733-5329(2005)7[91:DOVITF]2.0.CO;2.