

RESEARCH ARTICLE

Ultrasonic vocalization of pup and adult fat-tailed gerbils (*Pachyuromys duprasi*)

Alexandra S. Zaytseva^{1,2}, Ilya A. Volodin^{1,2*}, Olga G. Ilchenko², Elena V. Volodina²

1 Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Moscow, Russia, **2** Scientific Research Department, Moscow Zoo, Moscow, Russia

* volodinsvoc@gmail.com



Abstract

Ultrasonic vocalizations (USVs) of laboratory rodents indicate animal emotional arousal and may serve as models of human disorders. We analysed spectrographically USV calls of pup and adult fat-tailed gerbils *Pachyuromys duprasi* during 420-s tests, including isolation, touch and handling. Based on combination of six different USV syllable contour shapes and six different note compositions, we classified 782 USV syllables of 24 pups aged 5–10 days to 18 types and 232 syllables of 7 adults to 24 types. Pups and adults shared 16 of these 26 USV types. Percentages of USV syllables with certain contour shapes differed between pups and adults. The contour shape and note composition significantly affected most acoustic variables of USV syllables in either pups or adults. The 1-note USV syllables were most common in either pups or adults. Pup USV syllables were overall longer and higher-frequency than adult ones, reminiscent of the USV ontogenetic pathway of bats and distinctive to rats and mice. We discuss that the USV syllable types of fat-tailed gerbils were generally similar in contour shapes and note compositions with USV syllable types of mice and rats, what means that software developed for automated classifying of mice ultrasound might be easily adapted or re-tuned to gerbil USV calls. However, using fat-tailed gerbils as model for biomedical research including control of USV vocalization is only possible since 6th day of pup life, because of the delayed emergence of USV calls in ontogeny of this species.

OPEN ACCESS

Citation: Zaytseva AS, Volodin IA, Ilchenko OG, Volodina EV (2019) Ultrasonic vocalization of pup and adult fat-tailed gerbils (*Pachyuromys duprasi*). PLoS ONE 14(7): e0219749. <https://doi.org/10.1371/journal.pone.0219749>

Editor: Elke Zimmermann, Tierärztliche Hochschule Hannover, GERMANY

Received: April 27, 2019

Accepted: July 1, 2019

Published: July 29, 2019

Copyright: © 2019 Zaytseva et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: This work was supported by Russian Science Foundation (<http://www.rscf.ru/>) funding to IAV and EVV, grant number 19-14-00037. This research received no additional funding from any public, commercial or not-for-profit sectors. The funder had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Introduction

Ultrasonic vocalizations (USV) indicate emotional arousal and impairments in rodents [1–5]. Classifying discomfort-related ultrasonic calls is an important prerequisite for their applicability as indicators of emotional arousal and welfare [2,6–13]. In addition, rodent USV are widely used in biomedical experiments modeling human affective and communicative disorders [11,14–18].

Although current biomedical research is primarily based on studying laboratory mice and rats [1,19], other rodent species may possess by peculiar features, which would make them especially suitable as test animals for modeling certain diseases. For example, the Mongolian gerbil *Meriones unguiculatus* represents an especially convenient animal model for human epilepsy [20,21] because of absence of connecting arteries between the basilar and carotid systems

Competing interests: The authors have declared that no competing interests exist.

[22]. The Norway rat *Rattus norvegicus* model is the exclusive model of vocal negative and positive emotional correlates embedded in the 22 kHz and 50-kHz USV calls [1,23], which are not clearly distinctive in the mice model [4]. The prairie vole *Microtus oregonus* is a particularly useful animal model for examining social effects on the relationship between heart rate and USV fundamental frequency because of a low and variable heart rate and the very simple acoustic structure of the USV calls [24,25] as well as an unusually large functional and anatomical representation of auditory cortex [26]. Further analyses of USV in different rodent species (hamsters, voles, gerbils) are therefore advantageous for searching new exclusive animal models for various behavioural and medical research [27].

Rodents produce USV in various contexts [28,29]. Pup rodents produce USV during social play [30–32], isolation from the lactating mother and littermates [12,33–40], pain [41] and handling [34,39,42].

Adult rodents produce USV at pair bonding [43–51], novelty [52,53], territorial defense [54], social encounters [55–57], alarm [52,58–61], spontaneously during various everyday activities [62], echo-based orientation [63,64] and at pain [65]. During isolation procedure in the lab, adult rodents either emit USV, as do e.g. *Glaucomys* flying squirrels [66], domestic mice *Mus musculus* [4] and *Scotinomys* singing mice [67], or may remain silent, as e.g. Mongolian gerbils [68,69]. During handling in the lab, the USV calls were reported in adult laboratory rats [70].

Distinctive to the audible calls, which are generated by passive flow-induced vocal fold oscillations [71], studies on mice and rats show that the most likely mechanism for producing rodent USV is so called “jet” or “whistle”, mechanism [72–76]. The jet mechanism generates USV calls because of an obstruction in the path of air jet, such as sharp edge, a hole, or a side branch [72]. The jet mechanism is probably responsible for the variability of the fundamental frequency (f_0) contours (flat, chevron, wave, upward, downward) observed in rodent USV syllables [6–8,35,73,77–79]. In addition, the USV syllable contours can be either continuous (1-note) or can be broken to 2, 3, or more notes by frequency jumps [6,7,10].

Gerbils are widely used as animal models in biomedical research [80–83]. The fat-tailed gerbil (*Pachyuromys duprasi*) represents a perspective animal model for studying USV calls [39]. This is a North African rodent species kept at laboratories and zoos [39,80,84]. Fat-tailed gerbils were used for studying ear morphology and hearing [85–87], tropical diseases [80,81], thermoregulation [88,89] and physical development [84]. The fat-tailed gerbil is a medium-sized gerbil, with body mass in adults (with breeding experience) of 60.0 ± 24.3 g and head length of 39.6 ± 2.1 mm, without significant differences between sexes [84]. In 7-d pups, body mass is 5.3 ± 0.7 g and head length is 18.4 ± 0.8 mm [84].

Pup and adult fat-tailed gerbils produce both audible and USV calls [39,55]. In adults, the low-frequency wideband chirrs along to harmonic audible calls and USV calls up to 60 kHz were registered when two unfamiliar animals (male-male, female-female or male-female) were placed together in the one cage [55]. In pups, both audible and USV calls occur during isolation and handling procedure [39]. Variables of pup “joint calls” (representing a sum of all USV calls emitted within a test trial with cut-off inter-call intervals) reflect a degree of discomfort in 8-40-d fat-tailed gerbil pups [39].

Whereas the audible calls of fat-tailed gerbils emerge since 1st day of pup life, first USV calls emerge only since 5th day of pup life, with maximum of ultrasound emission in 12-15-d pups [39]. This ontogenetic delay of USV emergence is unusual. In other rodents (gerbils, mice, California mice, voles, rats, hamsters), the isolation-induced USV calls emerge since 1st-3rd day of life, depending on the species [33,37,38,42,90–102].

The classifying of USV syllables to types and measuring their acoustic variables have not yet been done for fat-tailed gerbils. The aim of this study was to develop a categorization of fat-

tailed gerbil USV syllables and to compare their acoustics between pups and adults. As soon as USV calls of fat-tailed gerbils are missing until 5th day of pup life [39], we selected for the comparative analyses of pup and adult USV calls only those acoustic recordings collected from 5-9-d pups.

Material and methods

Ethics statement

This study was part of the research program of the Scientific Research Department of Moscow Zoo. All the four authors are zoo staff members, so no special permission was required for them to work with animals in Moscow Zoo. All study animals belonged to the laboratory collection of Moscow Zoo. The experimental procedure has been approved by the Committee of Bio-ethics of Lomonosov Moscow State University, research protocol # 2011–36. We adhered to the ‘Guidelines for the treatment of animals in behavioural research and teaching’ (Anim. Behav., 2006, 71, 245–253) and to the laws on animal welfare for scientific research of the Russian Federation, where the study was conducted. No one single animal suffered due to data collection.

Study site and subjects

The USV calls were collected from members of a captive colony of fat-tailed gerbils at Moscow Zoo, Moscow, Russia, in May–July 2013 and in June–August 2014. Our study animals were 40 6-10-d pups (17 males and 23 females from 11 litters) and 20 adults with breeding experience (10 males, 10 females). Study pups were sexed between 12 and 19 days of age, on average at 15.1 ± 2.0 days of age based on the appearance of nipples in females [84,103]. The small size of pups also prevented individual chip marking for ethical reasons until 18–20 days of age.

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. The 11 study litters, containing in total 40 study pups, originated from 10 different mothers: nine mothers with one litter per female and one female gave birth to two litters. The litter size varied from 2 to 6 pups (mean \pm SD = 4.00 ± 1.34). The day of birth was considered zero day of pup life.

Animal housing

The animals were kept under a natural light regime at room temperature (24–26°C), in family groups consisting of two parents and littermates, because a male is non-aggressive to pups and the appearance of a second litter is possible without separation of the first one [39,84]. The animals were housed in wire-and-glass cages of 51x42.5x41.5 cm, with a bedding of sawdust and hay, various 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.

Experimental procedure and USV recording

All acoustic recordings were conducted in a separate room where no other animals were present, at room temperature 23–28°C (mean \pm SD = 25.1 ± 2.4) during daytime, at the same level of background noise. For USV recordings (sampling rate 384 kHz, 16 bit resolution) we used a Pettersson D1000X recorder with built-in microphone (Pettersson Elektronik AB, Uppsala, Sweden). The microphone was established stationary at distance 15 cm above the tested

animal. The obtained recordings had a high signal/noise ratio, the reverberation practically lacked.

Both pups and adults were tested singly. In total, each individual pup participated in 3 experimental trials (one trial per pup per age), at ages of 4–5, 6–7, and 8–9 days after birth; for details see [39]. Each individual adult participated in one trial per animal. Immediately before an experimental trial, the focal pup was taken 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 an experimental trial did not exceed 60 s. The experimental trial started, when the focal animal was placed to the experimental setup. Duration of each experimental trial was 420 s (7 min). Each trial took place in three stages: the isolation stage (120 s) followed by the touch stage (105 s), handling stage (105 s) and measurement stage (120 s). The duration of tests in this study was within range typical for those used in medical tests with rodent pups, 2–15 min [104].

For the duration of the isolation stage, a focal animal was located either in a clean plastic hutch (190x130x70 mm for pups) or in a plastic cylinder without bottom (diameter 193 mm, high 170 mm for adults), standing on even plastic table surface. Both the plastic hutch 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 [105] 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, continuing keeping it in hands; the measurements were used in the study [84]. The end of measurements was the end of the trial. Although the experimenter hand surface temperature (28–30°C, [106]) was slightly higher than the temperature in the experimental room, a pup was held by fingers, so a possibility of additional warming the pup from the hand lacked. In contrast to pups, the adults were hand-held during the handling and measurement stages.

After the end of a trial, the focal pup was placed to a heating hutch with a bedding of a cotton fabric, standing in the neighboring room. Experimental 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 USV of the next focal animal in the next experimental trial [68,107]. Each trial was recorded as a wav-file.

Call samples

Visual inspection of spectrograms of acoustic files using Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany) showed that USV calls lacked in the study sample of fat-tailed gerbil pups until the 5th day of life [39]. Therefore, we selected for analysis only the acoustic files recorded from 5th to 9th day of pup life. For some pups at some ages, recording trials were missing by refusals of equipment or for other reasons. As a result, 110 trials of the potential 120 (40 pups at 3 ages) recording trials were included in analysis. For the 20 study adults, we included in the visual inspection all available 20 files corresponding to the trials, one file per adult individual.

Visual inspection of spectrograms of pup acoustic files revealed that only 37 of the 110 audio files contained USV calls (4 of the 38 files for the 5-d pups, 11 of the 37 files for the 7-d pups and 22 of the 35 files for the 9-d pups). In total, USV calls were available for 24 of the 40 study pups, from 10 of the 11 litters; 13 of the 37 audio files were from repeated recording trials of the same pups at different ages. For the 11th litter, pup USV calls were only available since 10th day of pup life, therefore we did not include it in the analysis.

Visual inspection of spectrograms of adult acoustic files revealed that only 7 of the 20 audio files contained USV calls. Therefore, the USV calls were available from 7 individual adults (3 males and 4 females).

For analyses, we took all measurable (high quality) USV syllables of pups and adults. The USV syllables contained from one to a few notes. We defined a note as USV contour either continuous without breaks or with breaks shorter 10 ms and frequency jumps less than 10 kHz. We defined a syllable as one to a few USV notes separated with frequency jumps over 10 kHz [7,8]. If the separation break between notes exceeded 10 ms, we considered that the notes belong to different syllables. This syllable separation criterion was adjusted after [10], applied the 12.75-ms syllable separation criterion for USV syllables in domestic mice.

For pups, we measured in total 782 USV syllables (from 3 to 102 USV syllables per trial, on average 21.1 ± 22.5 USV syllables per trial). For adults, we measured in total 232 USV syllables (from 14 to 90 syllables per trial, on average 33.1 ± 26.0 USV per trial). For 5-d pups, we analysed 17 USV syllables from 4 trials; for 7-d pups 177 USV syllables from 11 trials; for 9-d pups 588 USV syllables from 22 trials.

Acoustic analysis

Measurements of acoustic variables of pup and adult USV syllables have been conducted with Avisoft SASLab Pro software and exported to Microsoft Excel (Microsoft Corp., Redmond, WA, USA). As minimum fundamental frequency (f_{0min}) of USV calls always exceeded 10 kHz, before measurements all wav-files were subjected to 10 kHz high-pass filtering, to remove low-frequency noise.

For each USV syllable, we measured, in the spectrogram window of Avisoft (sampling frequency 384 kHz, Hamming window, FFT 1024 points, frame 50%, overlap 93.75%, providing frequency resolution 375 Hz and time resolution 0.17 ms), the duration with the standard marker cursor, and the maximum fundamental frequency (f_{0max}), the minimum fundamental frequency (f_{0min}), the start fundamental frequency (f_{0beg}) and the end fundamental frequency (f_{0end}) with the reticule cursor (Fig 1 and S1 Table). For each USV syllable, we measured, in the power spectrum window of Avisoft, the frequency of maximum amplitude (f_{peak}) from the syllable's mean power spectrum and the bandwidth (bndw) of the f_{peak} at the distance of 10 dB from the maximum (Fig 1 and S1 Table).

USV syllable types

In the spectrogram window of Avisoft, we classified USV syllables accordingly to the six possible f_0 contour shapes: flat, chevron, downward, upward, short, complex (Fig 2 and S1 Audio). This classification was based (with modifications) on classifications developed for domestic mice by [6–8]. The flat contour was denoted when the difference between f_{0min} and f_{0max} was less than 6 kHz [7]. The short contour was denoted when the duration was shorter 4 ms [6,7]. In addition, when the difference between f_{0min} and f_{0max} exceeded 6 kHz, the denoted syllable contours could be the chevron (up-down one time), downward (descending from start to end), upward (ascending from start to end) or complex (up-down many times).

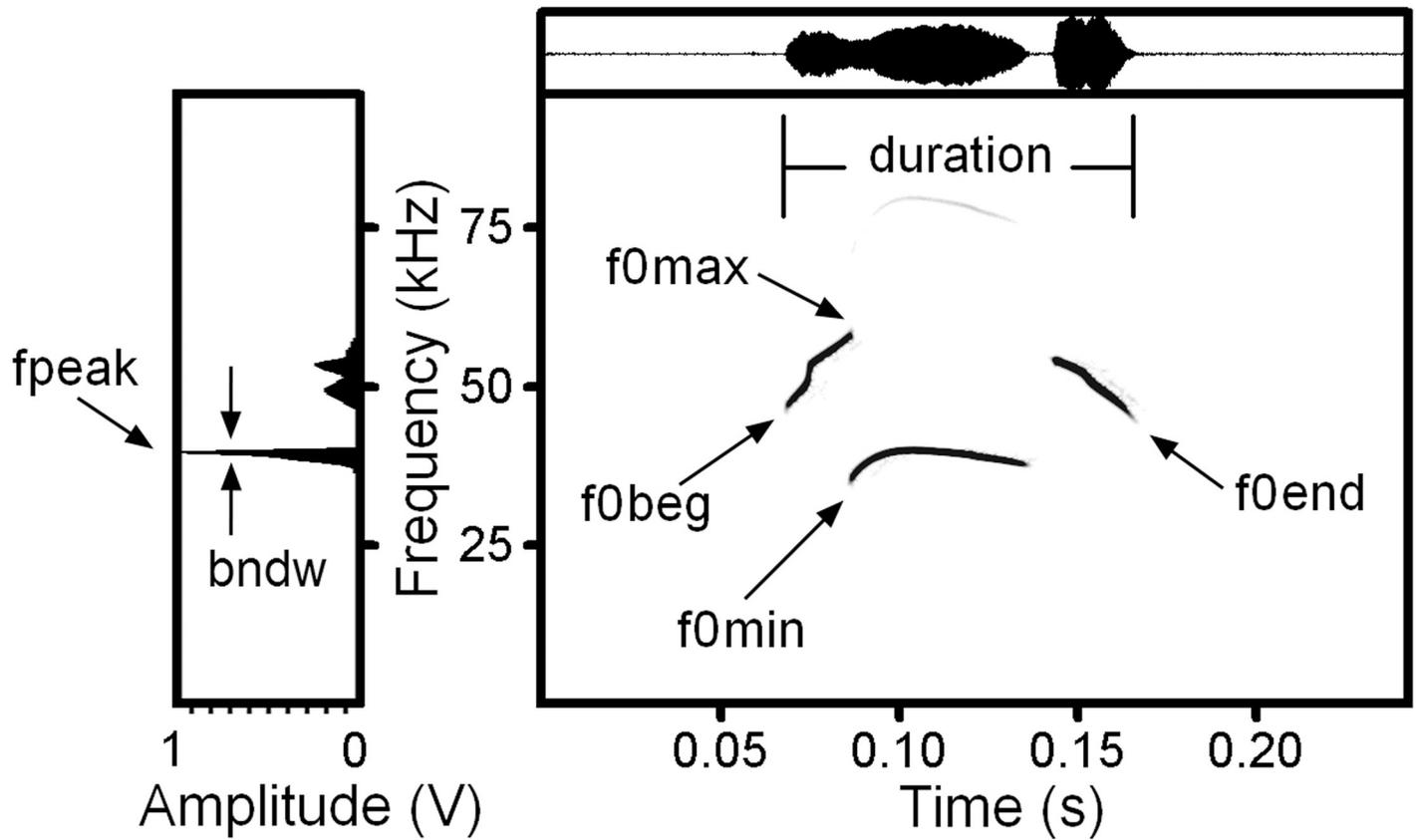


Fig 1. Measured variables for fat-tailed gerbils USV syllables exemplified by a pup 3-note down-up USV syllable with Chevron contour. Spectrogram (right) and mean power spectrum of the entire call (left). Designations: duration—syllable duration; f0beg—the fundamental frequency at the onset of a call; f0end—the fundamental frequency at the end of a call; f0max—the maximum fundamental frequency; f0min—the minimum fundamental frequency; fpeak—the frequency of maximum amplitude within a syllable; bndw—the bandwidth of the fpeak at the distance of 10 dB from the maximum. Spectrogram was created using sampling frequency 192 kHz Hamming window, FFT 1024 points, frame 50% and overlap 93.75%.

<https://doi.org/10.1371/journal.pone.0219749.g001>

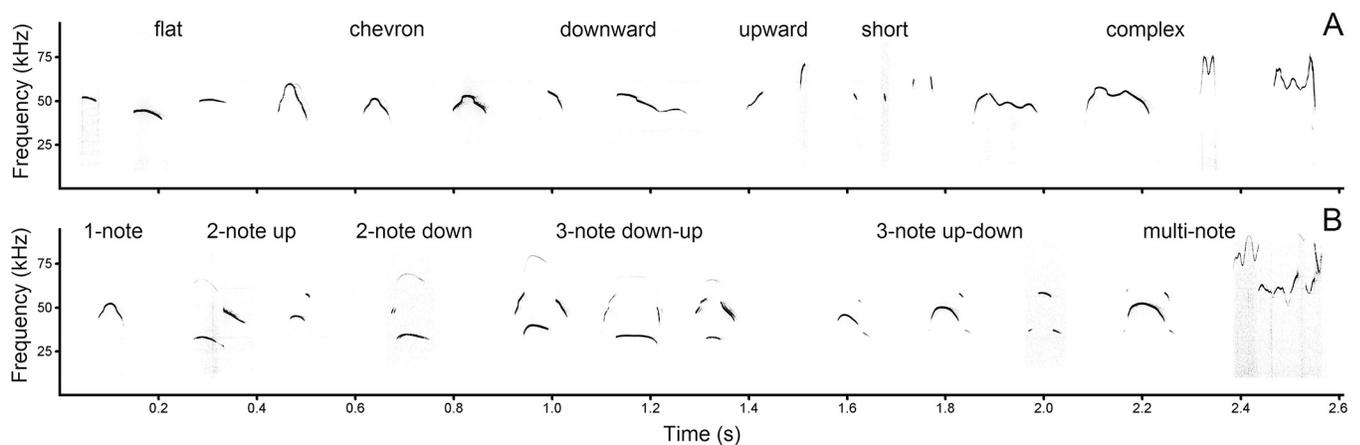


Fig 2. Six contour shapes (A, upper panel) and six note compositions (B, lower panel). Based on their combinations, USV syllables of fat-tailed gerbils were classified to distinct types (S1 Audio). Spectrogram was created using sampling frequency 192 kHz Hamming window, FFT 1024 points, frame 50%, overlap 87.5%.

<https://doi.org/10.1371/journal.pone.0219749.g002>

In addition to classifying by contour shape, we classified the USV syllables accordingly to the six possible note compositions (1-note, 2-note up, 2-note down, 3-note down-up, 3-note up-down, multi-note) based on the number of notes within syllable and presence of up or/and down frequency jumps over 10 kHz (Figs 1 and 2). The 1-note syllables lacked frequency jumps; the 2-note up syllables had one frequency jump up; the 2-note down syllables had one frequency jump down; the 3-note down-up syllables had two frequency jumps, first down and then up; the 3-note up-down syllables had two frequency jumps, first up and then down; and the multi-note syllables had three or more frequency jumps (Fig 2 and S1 Audio).

Statistical analyses

Statistical analyses were made with STATISTICA, v. 8.0 (StatSoft, Tulsa, OK, USA), all means are given as mean \pm SD. Significance levels were set at 0.05, and two-tailed probability values are reported. We used a nested design ANOVA with individual nested in age (with age as fixed factor and individual as random factor) to compare USV variables between pups and adults. We used one-way ANOVA with Tukey HSD (Honestly Significant Difference) test to estimate the effect of syllable contour shape and syllable composition on USV variables of pups and adults. In the case when not all sample sizes fitted to ANOVA assumptions for inclusion in analysis of groups differing in size not more than ten times, we calculated ANOVA results both for all groups in total and separately for the groups fitting this ANOVA assumptions.

Results

Types of USV syllables in pups and adults

Of the 36 distinct USV syllable types potentially possible by combining the six syllable contours and six note compositions, in pups we detected only 18 types and in adults only 24 types; 16 types were shared by pups and adults (Tables 1 and 2). In pups, most frequent was the 1-note syllable (600 of the total 782 USV syllables) with contours either flat (299 USV syllables) or chevron (193 USV syllables). Another frequent type in pups was the 3-note down-up syllable type with the contour chevron (96 USV syllables) (Table 1). In adults, as in pups, most frequent was the 1-note syllable (178 of the total 232 USV syllables) with the contours chevron (55 USV syllables), flat (34 USV syllables) or short (32 USV syllables) (Table 2). In addition, two USV syllables of two individual pups and four USV syllables of two individual adults contained the nonlinear phenomenon biphonation (interaction between the USV fundamental frequency and the audible fundamental frequency).

The contours flat and chevron were more frequent in pups than in adults (Fig 3). The contours upward, short and complex were more frequent in adults than in pups. The downward contour equally frequently occurred in pups and adults (Fig 3).

Percentages of the most frequent 1-note syllables were the same in pups and adults (Fig 4). The 2-note syllables were more frequent in adults than in pups, whereas the 3-note syllables were more frequent in pups than in adults and the multi-note syllables were more frequent in adults than in pups.

Acoustic variables of pup and adult USV syllables

On the total sample of USV syllables of all types, the syllable duration was found longer in pups than in adults, whereas the f_{peak} , bandw and all f_0 variables were lower in pups than in adults (Table 3). Similar results for comparisons between pups and adults were obtained on separately taken samples of all 1-note USV syllables (Table 4) and separately for flat 1-note USV syllables (Table 5) and chevron 1-note USV syllables (Table 6).

Table 1. Number and percentage of 18 distinct USV syllable types of pups, classified based on combination of contour shape and note composition.

Note composition	Number pups, litters	Contour shape						Total USV syllables
		flat	chevron	downward	upward	short	complex	
		23 pups, 9 litters	22 pups, 9 litters	18 pups, 9 litters	8 pups, 8 litters	6 pups, 4 litters	4 pups, 3 litters	
1-note	24 pups, 10 litters	299	193	87	6	9	6	600 (76.73%)
2-note up	7 pups, 7 litters	7	16	7	0	0	0	30 (3.84%)
2-note down	8 pups, 6 litters	11	16	0	3	0	0	30 (3.84%)
3-note down-up	12 pups, 7 litters	0	96	0	0	0	0	96 (12.28%)
3-note up-down	3 pups, 3 litters	1	17	4	0	0	0	22 (2.81%)
multi-note	3 pups, 3 litters	0	2	0	1	0	0	4 (0.51%)
Total USV syllables		318 (40.66%)	340 (43.48%)	99 (12.66%)	10 (1.28%)	9 (1.15%)	6 (0.77%)	782 (100%)

<https://doi.org/10.1371/journal.pone.0219749.t001>

Unexpectedly, although pup calls were overall longer by duration and lower-frequency than in adults, the longest USV syllable was found in an adult individual. Similarly, the USV syllable with the maximal value of f_0 was found in a pup individual (Table 3).

In pup 1-note USV syllables, the syllable contour shape affected all acoustic variables (Table 7). Compared to other syllable contour shapes, the USV syllables with the complex contour had the longest duration and the lowest f_{0min} and f_{0beg} . The USV syllables with the short contour had the shortest duration and the lowest f_{0max} , f_{peak} and $bndw$. The USV syllables with the upward contour had the highest f_{0max} , f_{0min} , f_{0end} and f_{peak} . The USV syllables with the downward contour had the highest f_{0beg} and $bndw$. The USV syllables with the chevron contour had the lowest f_{0end} , whereas the USV syllables with the flat contour had intermediate values of acoustic variables compared to other syllable contour shapes (Table 7). For USV syllables with three most frequently occurring contour shapes (flat, chevron and downward), one-way ANOVA results with Tukey HSD test coincided with results of their comparison in Table 7.

In adults, distinctive to pups, the contour shape affected not all acoustic variables of 1-note USV syllables, but only the duration, f_{0beg} , f_{0end} and $bndw$ (Table 8). Compared to other syllable contour shapes, the USV syllables with the complex contour had the longest duration and the highest f_{0max} and f_{peak} . The USV syllables with the short contour had the shortest duration. The USV syllables with the upward contour had the highest f_{0end} and the lowest f_{0beg} . The USV syllables with the downward contour had the highest f_{0beg} and $bndw$ (as in pups) and the lowest f_{0min} . The USV syllables with the chevron contour had the lowest f_{0end} .

Table 2. Number and percentage of 24 distinct USV syllable types of adults, classified based on combination of contour shape and note composition.

Note composition	Number adults	Contour shape						Total USV syllables
		flat	chevron	downward	upward	short	complex	
		7 adults	7 adults	7 adults	7 adults	5 adults	6 adults	
1-note	7 adults	34	55	25	26	32	6	178 (76.72%)
2-note up	6 adults	2	9	2	2	0	1	16 (6.90%)
2-note down	6 adults	6	2	3	3	0	4	18 (7.79%)
3-note down-up	4 adults	0	3	1	0	0	2	6 (2.59%)
3-note up-down	4 adults	1	3	0	0	0	0	4 (1.72%)
multi-note	5 adults	0	6	1	0	0	3	10 (4.31%)
Total USV syllables		43 (18.53%)	78 (33.62%)	32 (13.79%)	31 (13.36%)	32 (13.79%)	16 (6.90%)	232 (100%)

<https://doi.org/10.1371/journal.pone.0219749.t002>

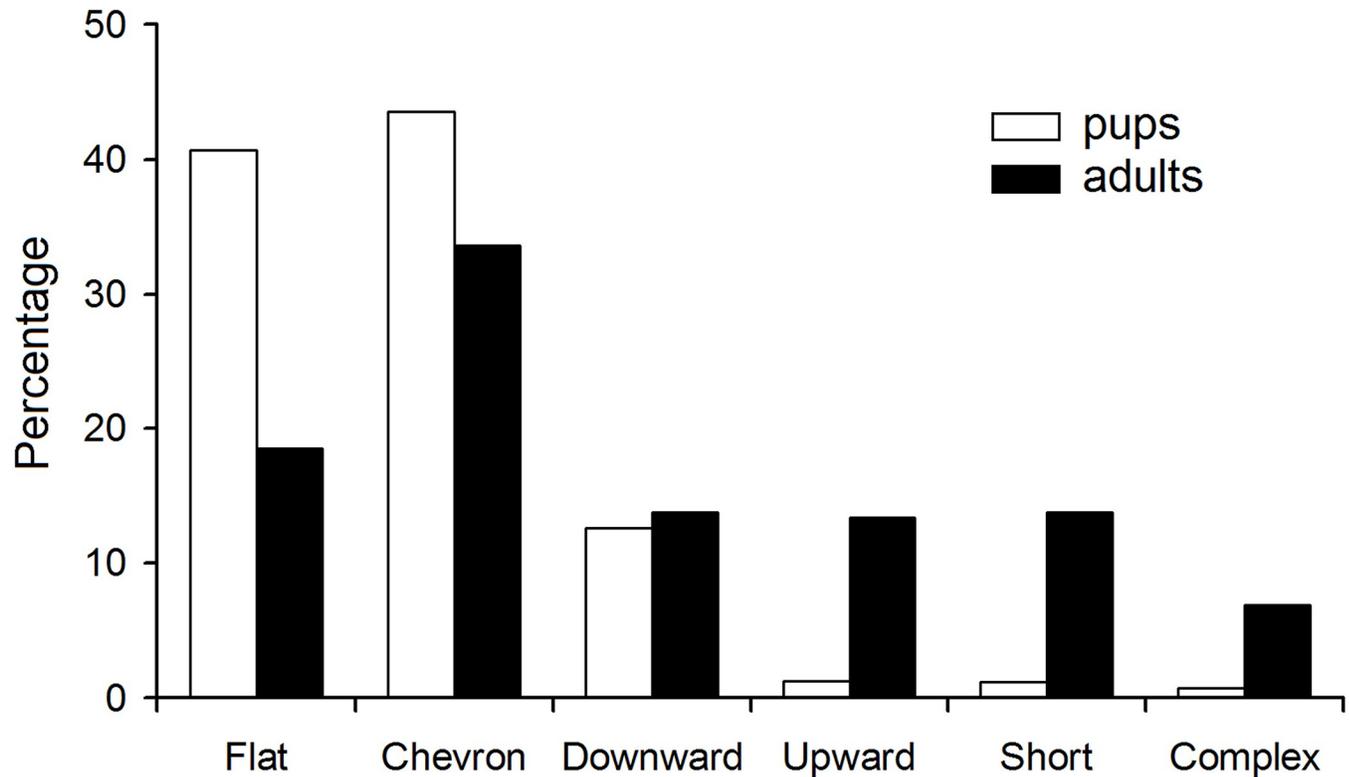


Fig 3. Percentages of pup and adult USV syllables with different contour shapes.

<https://doi.org/10.1371/journal.pone.0219749.g003>

The USV syllables with the flat contour had the highest f_{0min} and the lowest f_{0max} , f_{peak} and $bndw$ (Table 8).

Number of notes within USV syllable affected all USV acoustic variables for the exclusion of $bndw$ in pups (Table 9) and for the exclusion of f_{0beg} and f_{peak} in adults (Table 10). In both pups and adults, the highest values of duration and f_{0max} were found in the 3-note and in the multi-note syllables (Tables 9 and 10). In both pups and adults, the shortest duration, the lowest f_{0max} and the highest f_{0min} were found in the 1-note USV syllables (Tables 9 and 10). The intermediate values of acoustic variables were found in the 2-note USV syllables.

Discussion

General findings

This study revealed a rich repertoire of ultrasonic syllables in fat-tailed gerbils. Based on contour shape and note composition, we identified 24 distinct USV syllable types in adults and 18 in pups; 16 of these 26 types were shared by adults and pups. Percentages of syllables with certain number of notes were similar between pups and adults. In both pups and adults, 1-note syllables were most common. The prevalence of 1-note USV calls was also reported in hamsters [108,109].

In fat-tailed gerbils, pup USV syllables differed from adult USV syllables by the occurrence of different contour shapes. Similarly, the developmental changes in the proportions of different syllable types were reported for domestic mice [7], Norway rats [35,110] and *Scotinomys* singing mice [67]. Age-related differences in the proportion of 22-kHz and 50-kHz calls were reported in rats [111].

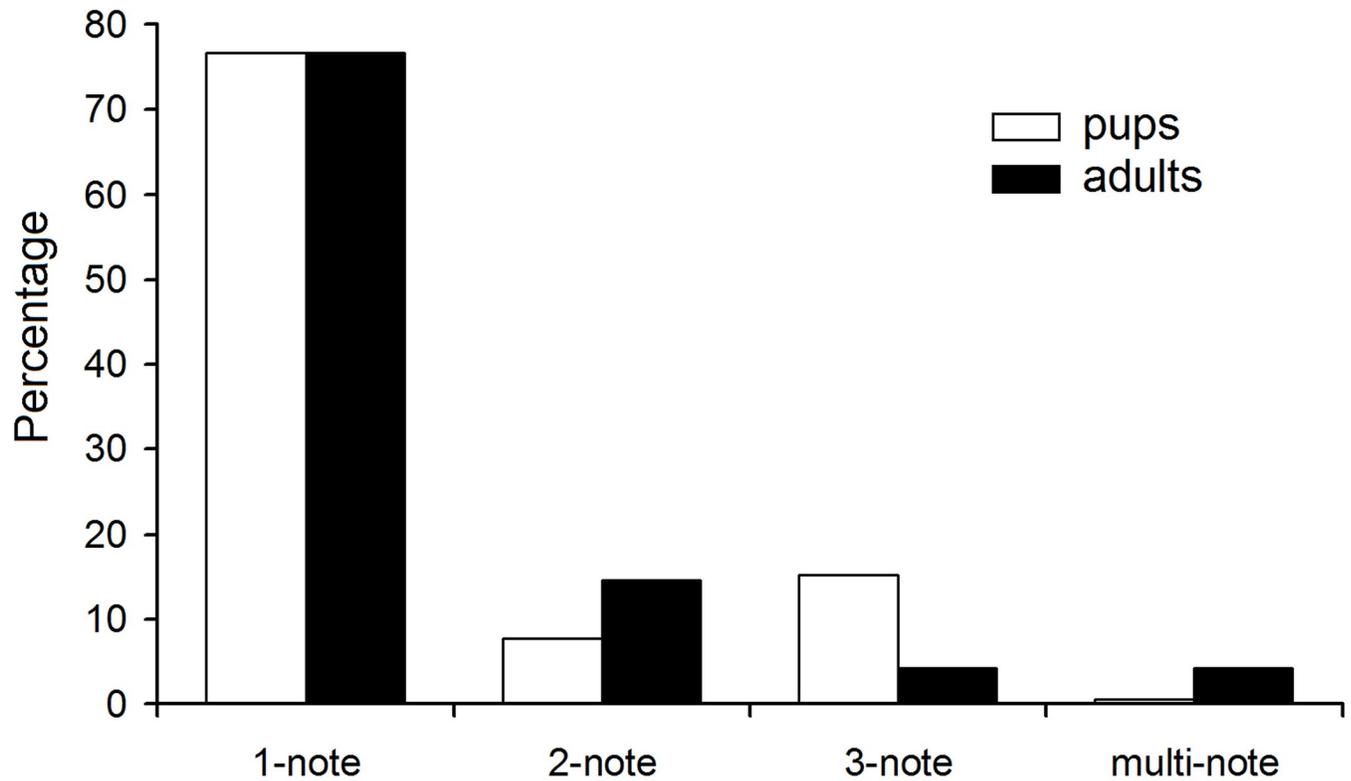


Fig 4. Percentages of pup and adult USV syllables with different note compositions.

<https://doi.org/10.1371/journal.pone.0219749.g004>

Overall, pup USV syllables were of longer duration and lower-frequency than adult USV syllables. The USV syllable contour shape and note composition significantly affected most temporal, frequency and power variables in both pups and adults, similarly with findings in domestic mice [7,112].

In fat-tailed gerbils, the overall USV fundamental frequency range was from 18 kHz to 120 kHz, and the duration of USV calls ranges from 2 ms to 350 ms. This frequency range is

Table 3. Values (mean±SD, min-max) of acoustic variables of pup and adult USV syllables and nested ANOVA results for their comparison.

Acoustic variable	Pups (n = 782 USV syllables)	Adults (n = 232 USV syllables)	ANOVA
duration (ms)	50.0±31.0 (2.4–154.7)	22.0±32.7 (1.7–354.3)	$F_{1,983} = 81.2, p < 0.001$
f0max (kHz)	52.2±5.7 (32.6–120.0)	66.8±13.9 (23.6–113.3)	$F_{1,983} = 367.8, p < 0.001$
f0min (kHz)	41.9±6.7 (19.1–80.6)	51.1±9.6 (18.4–97.9)	$F_{1,983} = 136.2, p < 0.001$
f0beg (kHz)	47.1±5.7 (19.5–120.0)	57.3±10.2 (21.8–103.2)	$F_{1,983} = 186.8, p < 0.001$
f0end (kHz)	44.6±5.5 (29.6–80.2)	55.7±13.4 (18.4–113.3)	$F_{1,983} = 319.9, p < 0.001$
fpeak (kHz)	47.9±6.1 (30.7–87.7)	60.0±10.5 (20.6–108.3)	$F_{1,983} = 262.9, p < 0.001$
bndw (kHz)	3.1±1.5 (1.5–20.6)	6.5±6.1 (1.8–31.8)	$F_{1,983} = 114.5, p < 0.001$

<https://doi.org/10.1371/journal.pone.0219749.t003>

Table 4. Values (mean±SD) of acoustic variables of fat-tailed gerbil pup and adult 1-note USV syllables and nested ANOVA results for their comparison.

Acoustic variable	Pups (<i>n</i> = 600 USV syllables)	Adults (<i>n</i> = 178 USV syllables)	ANOVA
duration (ms)	41.8±27.2	16.6±29.3	$F_{1,747} = 59.9, p < 0.001$
f0max (kHz)	50.9±5.2	63.8±11.5	$F_{1,747} = 230.0, p < 0.001$
f0min (kHz)	44.7±4.5	52.3±9.6	$F_{1,747} = 214.1, p < 0.001$
f0beg (kHz)	47.6±5.5	57.5±9.8	$F_{1,747} = 130.5, p < 0.001$
f0end (kHz)	45.3±4.8	55.1±11.9	$F_{1,747} = 109.8, p < 0.001$
fpeak (kHz)	49.2±4.4	60.1±9.3	$F_{1,747} = 241.6, p < 0.001$
bndw (kHz)	3.0±1.3	6.1±5.6	$F_{1,747} = 79.3, p < 0.001$

<https://doi.org/10.1371/journal.pone.0219749.t004>

comparable with those reported in rats, from 20 kHz to over 90 kHz, whereas the duration range of USV calls in rats is different, from approximately 10 ms to over 3500 ms [113].

No evidence for vocal learning in fat-tailed gerbils

In mammals whose vocal repertoires are assumed to be fixed at birth, the same call types can be found in pups and adults [114,115]. Our results confirm therefore that ultrasonic vocalizations of fat-tailed gerbils are innate, as the same 16 USV syllables occurred in both pups and adults. Similar findings were obtained for other rodents and insectivores. In *Scotinomys* singing mice, their ultrasonic long FM down-sweeps that comprise adult advertisement song were produced from birth [67]. In the piebald shrew *Diplomesodon pulchellum*, seven of the eight call types were shared by pups and adults [116,117]. In the Asian house shrew *Suncus murinus*, five of seven call types found in pups were also found in adults [118]. In rats, creation of strains with high or low rates of isolation-induced USV evokes corresponding changes in ontogeny of acoustic parameters, suggesting that traits of USV calls are genetically predetermined [119]. In domestic mice, pups produced 10 of 11 USV syllable types recorded from adults [7].

In addition, in domestic mice, embryo-transfer and cross-fostering experiments suggest that USV calls are innate [47,120,121]. Research suggests that Foxp2 gene plays a crucial role in vocal development in mammals [122] and in particular in mice [123]. In mice, the chevron and short contours of USV syllables are coupled respectively with two genotypically different strains and are inherited by the Mendelian law of independent assortment [124].

We should point however, that in spite of this apparently very strict genetic control of vocalization, another study reports some level of developmental plasticity of mice vocalization [8]. This level of plasticity is well comparable to those in mammals with innate vocal repertoires vocalizing in the audible range of frequencies [125–127].

Table 5. Values (mean±SD) of acoustic variables of fat-tailed gerbil pup and adult flat 1-note USV syllables and nested ANOVA results for their comparison.

Acoustic variable	Pups (<i>n</i> = 299 USV syllables)	Adults (<i>n</i> = 34 USV syllables)	ANOVA
duration (ms)	30.2±19.5	19.3±13.0	$F_{1,304} = 4.99, p = 0.03$
f0max (kHz)	49.0±4.4	59.1±8.1	$F_{1,304} = 117.8, p < 0.001$
f0min (kHz)	45.8±4.3	54.8±7.6	$F_{1,304} = 112.2, p < 0.001$
f0beg (kHz)	47.5±4.5	56.4±7.3	$F_{1,304} = 95.1, p < 0.001$
f0end (kHz)	46.3±4.5	56.0±8.6	$F_{1,304} = 126.4, p < 0.001$
fpeak (kHz)	48.0±4.3	58.2±7.7	$F_{1,304} = 125.4, p < 0.001$
bndw (kHz)	2.4±0.6	2.7±0.8	$F_{1,304} = 7.52, p = 0.007$

<https://doi.org/10.1371/journal.pone.0219749.t005>

Table 6. Values (mean±SD) of acoustic variables of fat-tailed gerbil pup and adult chevron 1-note USV syllables and nested ANOVA results for their comparison.

Acoustic variable	Pups (<i>n</i> = 193 USV syllables)	Adults (<i>n</i> = 55 USV syllables)	ANOVA
duration (ms)	64.8±23.5	17.8±14.3	$F_{1,222} = 89.5, p < 0.001$
f0max (kHz)	52.5±3.3	65.8±11.2	$F_{1,222} = 26.6, p < 0.001$
f0min (kHz)	43.1±3.2	50.2±8.7	$F_{1,222} = 4.09, p = 0.04$
f0beg (kHz)	45.4±3.3	56.8±8.9	$F_{1,222} = 34.7, p < 0.001$
f0end (kHz)	43.8±3.3	50.6±8.9	$F_{1,222} = 4.32, p = 0.04$
fpeak (kHz)	50.3±3.3	61.4±9.1	$F_{1,222} = 22.7, p < 0.001$
bndw (kHz)	3.5±1.3	7.6±6.5	$F_{1,222} = 9.25, p = 0.003$

<https://doi.org/10.1371/journal.pone.0219749.t006>

USV call types in rodent species

The overall richness of USV syllable types, found in fat-tailed gerbils in this study (26 distinct calls types), was comparable with those reported for bats (28 distinct call types) [128,129]. The acoustic variation of USV syllable types in pup fat-tailed gerbils (18 USV syllable types) was comparable with level of variation (10–12 USV syllable types) in pup domestic mice [6–8,50,130] and in pup Norway rats [16,35,131]. At the same time, seven USV call types were identified in pup short-tailed field voles *Microtus agrestis* [132]. Six USV call types were identified in pup *Scotinomys* [67] and in pup Mongolian gerbils [133,134]. In *Peromyscus* pups, the three identified USV call types were shared with adults but did not have clear boundaries between the types and could grade into one another [102]. Two USV call types were identified in pup Djungarian hamsters *Phodopus sungarus* [99]. One USV call type was identified in pup Syrian hamsters *Mesocricetus auratus*, in pup Chinese hamsters *Cricetulus griseus* [99], in pup Key Largo woodrats *Neotoma floridana smalli* [135], but further analyses most probable will identify more types.

Among adult rodents, 15 distinct USV call types were identified in Norway rats [77,136]; some of these call types were shared between the Norway and 8 other poorly investigated bio-acoustically *Rattus* species [137]. Eight USV call types were identified in adult African woodland dormice *Graphiurus murinus* [138]. Five USV call types were identified in adult hazel dormice *Muscardinus avellanarius* [139]; 4 USV call types were identified in adult *Peromyscus* [140]. Three USV call types were identified in Mongolian gerbils [141], but these analyses were limited with sexual behaviour. One USV call type was identified in adult Key Largo woodrats [135].

Overall, the USV calls of fat-tailed gerbils displayed many similar acoustic traits with USV calls of domestic mice, Norway rats and other rodents. Therefore, from the applied perspective, mice USV databases [142] and the automated software for detection, clustering and analyses of mice USV syllables [10,143–145], can potentially be adapted, re-tuned or modified for calls of fat-tailed gerbils and other laboratory rodent participating in biomedical experiments. For example, frequency jumps are also characteristic for domestic mice [7,8,146–149], Norway rats [16,61], short-tailed field voles [132] and collared lemmings *Dicrostonyx groenlandicus* [95]. Short notes within 5 ms are also characteristic for domestic mice [6,7] and Norway rats [14]. The different USV syllable contour shapes of fat-tailed gerbils are also similar with those reported in mice [6–8,148], Norway rats [14,16] and in short-tailed field voles [132]. Therefore, for classifying USV calls of fat-tailed gerbils in this study, we mostly followed the categorization scheme of USV syllables developed for domestic mice [6–8,148]. Although the categorization scheme of bat USV syllables [128,129] was previously applied by for classifying USV syllables of Mongolian gerbils [78], we did not use it in this study, because the USV syllable

Table 7. Values (mean±SD) of acoustic variables of pup 1-note USV syllables with different contour shapes (flat, chevron, downward, upward, short, complex) and one-way ANOVA results for their comparison.

Acoustic variable	Contour shape						ANOVA
	flat	chevron	downward	upward	short	complex	
duration (ms)	30.2±19.5 ^a	64.8±23.5 ^b	32.5±18.6 ^a	19.7±14.9 ^{a,c}	3.7±0.5 ^c	97.2±38.1 ^d	$F_{5,594} = 84.4, p < 0.001$
f0max (kHz)	49.0±4.4 ^{a,d}	52.5±3.3 ^b	53.5±7.7 ^{b,c}	58.2±8.1 ^c	46.6±7.5 ^a	54.1±3.2 ^{b,c,d}	$F_{5,594} = 23.0, p < 0.001$
f0min (kHz)	45.8±4.3 ^{a,c}	43.1±3.2 ^b	44.2±5.7 ^b	50.7±7.7 ^c	44.7±7.0 ^{a,b,c}	41.2±4.9 ^{a,b}	$F_{5,594} = 12.2, p < 0.001$
f0beg (kHz)	47.5±4.5 ^a	45.4±3.3 ^b	53.0±7.7 ^c	50.8±8.0 ^{a,b,c}	46.3±7.4 ^{a,b}	43.4±6.6 ^{a,b}	$F_{5,594} = 31.0, p < 0.001$
f0end (kHz)	46.3±4.5 ^a	43.8±3.3 ^b	44.3±5.7 ^b	57.8±8.6 ^c	45.0±7.1 ^{a,b}	44.0±4.0 ^{a,b}	$F_{5,594} = 17.6, p < 0.001$
fpeak (kHz)	48.0±4.3 ^a	50.3±3.3 ^b	50.5±4.8 ^b	55.1±7.3 ^b	45.8±7.2 ^a	50.7±3.0 ^{a,b}	$F_{5,594} = 12.9, p < 0.001$
bndw (kHz)	2.4±0.6 ^a	3.5±1.3 ^b	4.3±1.8 ^c	2.7±0.6 ^{a,b}	2.3±0.6 ^a	3.6±1.8 ^{a,b,c}	$F_{5,594} = 50.8, p < 0.001$

Note: The same superscripts indicate which values did not differ significantly ($p > 0.05$, Tukey HSD test).

<https://doi.org/10.1371/journal.pone.0219749.t007>

contour shapes reported in bats are rather distinctive from those produced by fat-tailed gerbils.

Ontogenetic changes in USV acoustic variables

In fat-tailed gerbils, pup USV syllables were in general longer in duration and lower in frequency than adult USV syllables, and each particular call type shared the general ontogenetic pathway. The general pathway of USV ontogeny in fat-tailed gerbils (increasing fundamental frequency and call shortening) is opposed to those reported for rats (decreasing fundamental frequency and call lengthening) and strongly reminiscent of bats. In rat, the initial broad range of 30–65 kHz of pup so called 40-kHz calls USV frequencies split in adults into two non-overlapping frequency ranges, of 22 kHz and 50 kHz calls [1,35,72,150]. In particular, rat pup USV syllables decrease in fundamental frequency during first 2–3 wk of life [16,41,151]. Then they suddenly increase in fundamental frequency on 14th [152] or 30th day of pup life [16,113], depending on rat strain, and split to the adult-like 22-kHz and 50-kHz calls [136]. Then, since approximately 4 wks up to senescence, the fundamental frequency decreases in both 22-kHz and 50-kHz calls, irrespectively to the USV syllable contour [153–155]. At the same time, duration of rat USV calls remains stable until 3 wks, then suddenly decreases [16] and increases again from 6 wks up to senescence [153–155].

In bats, the ontogenetic changes of USV variables are similar to fat-tailed gerbils in spite of a distinctive to rodents mechanism for production of bat USV calls, based on vibrations of the

Table 8. Values (mean±SD) of acoustic variables of adult 1-note USV syllables with different contour shapes (flat, chevron, downward, upward, short, complex) and one-way ANOVA results for their comparison.

Acoustic variable	Contour shape						ANOVA
	flat	chevron	downward	upward	short	complex	
duration (ms)	19.3±13.0 ^a	17.8±14.3 ^a	10.7±7.2 ^a	14.3±15.6 ^a	3.2±0.6 ^a	95.1±129.2 ^b	$F_{5,172} = 14.1, p < 0.001$
f0max (kHz)	59.1±8.1	65.8±11.2	65.4±15.2	64.8±9.6	62.6±13.1	67.8±7.4	$F_{5,172} = 1.9, p = 0.10$
f0min (kHz)	54.8±7.6	50.2±8.7	49.5±12.2	54.4±7.4	53.8±11.9	51.2±5.7	$F_{5,172} = 1.9, p = 0.10$
f0beg (kHz)	56.4±7.3 ^a	56.8±8.9 ^{a,b}	63.0±13.6 ^a	54.5±7.4 ^b	57.8±11.2 ^{a,b}	57.2±2.4 ^{a,b}	$F_{5,172} = 2.4, p = 0.04$
f0end (kHz)	56.0±8.6 ^{a,b,c}	50.6±8.9 ^a	50.7±14.6 ^{a,c}	64.1±9.6 ^{b,c}	57.7±14.9 ^{b,c}	56.2±6.2 ^{a,b,c}	$F_{5,172} = 6.4, p < 0.001$
fpeak (kHz)	58.2±7.7	61.4±9.1	60.0±11.1	60.2±7.0	59.3±11.9	62.2±6.7	$F_{5,172} = 0.6, p = 0.70$
bndw (kHz)	2.7±0.8 ^a	7.6±6.5 ^{b,c}	9.3±7.9 ^c	4.7±3.0 ^{a,b}	5.7±4.4 ^{a,b,c}	7.1±3.7 ^{a,b,c}	$F_{5,172} = 6.1, p < 0.001$

Note: The same superscripts indicate which values did not differ significantly ($p > 0.05$, Tukey HSD test).

<https://doi.org/10.1371/journal.pone.0219749.t008>

Table 9. Values (mean±SD) of acoustic variables of pup USV syllables with different number of notes within syllable (1, 2, 3, multi-note) and one-way ANOVA results for their comparison.

Acoustic variable	Number of notes within USV syllable				ANOVA
	1-note	2-note	3-note	multi-note	
duration (ms)	41.8±27.2 ^a	58.6±26.3 ^b	86.5±22.9 ^c	68.0±33.7 ^{a,b,c}	$F_{3,778} = 96.1, p < 0.001$
f0max (kHz)	50.9±5.2 ^a	56.3±7.0 ^b	56.7±3.1 ^b	59.4±1.9 ^b	$F_{3,778} = 59.5, p < 0.001$
f0min (kHz)	44.7±4.5 ^a	34.9±5.4 ^b	31.6±2.2 ^c	33.9±1.9 ^{b,c}	$F_{3,778} = 367.6, p < 0.001$
f0beg (kHz)	47.6±5.5 ^a	44.4±7.9 ^b	46.1±4.9 ^b	39.9±8.4 ^b	$F_{3,778} = 9.5, p < 0.001$
f0end (kHz)	45.3±4.8 ^a	42.9±9.3 ^b	42.0±5.3 ^b	41.0±10.3 ^{a,b}	$F_{3,778} = 15.4, p < 0.001$
fpeak (kHz)	49.2±4.4 ^a	44.7±9.4 ^b	43.2±8.1 ^b	43.0±8.5 ^{a,b}	$F_{3,778} = 46.1, p < 0.001$
bndw (kHz)	3.0±1.3	3.1±2.6	3.3±1.5	2.9±0.3	$F_{3,778} = 1.1, p = 0.34$

Note: The same superscripts indicate which values did not differ significantly ($p > 0.05$, Tukey HSD test).

<https://doi.org/10.1371/journal.pone.0219749.t009>

thin vocal membranes on their vocal folds [156,157]. Throughout maturation, bats produce USV calls of the same [158] or an increasingly high fundamental frequency [159–172], in spite of the growing larynx [173]. USV calls’ shortening from pups to adults has been reported in the pomona leaf-nosed bat *Hipposideros pomona* [166], in Asian particolored bat *Vespertilio sinensis* [167], in the big brown bat *Eptesicus fuscus* [170] and in the long-fingered bat *Myotis capaccinii* [172].

In mice, USV syllables also shorten as in fat tailed gerbils, but decrease in frequency and each call type can display a specific pattern of developmental changes [6,98,174–180]. In domestic mice, as in Norway rats, the developmental analyses are complicated, because the ontogenetic trends of USV acoustic variables are strain-specific, although generally follow the species-specific pattern [181]. In ontogeny of *Peromyscus* rodents, USV syllables shortened, whereas frequency changes inconsistently [182].

USV and audible calls and hearing sensitivity

Fat-tailed gerbils have the extraordinarily inflated tympanic bullae [85–87]. It can be related with low-frequency hearing and potential detection of vibrations passing through their sandy substrate for location insects and approaching predators such as owls or snakes [183,184]. Nevertheless, this study showed that pup and adult fat-tailed gerbils produce many various USV calls. Study of hearing sensitivity suggests that in fat-tailed gerbils, the hearing in the human audible range of frequencies is shifted to the lower-frequency range compared to other gerbils

Table 10. Values (mean±SD) of acoustic variables of adult USV with different number of notes within syllable (1, 2, 3, multi-note) and one-way ANOVA results for their comparison.

Acoustic variable	Number of notes within USV syllables				ANOVA
	1-note	2-note	3-note	multi-note	
duration (ms)	16.6±29.3 ^a	31.3±31.0 ^b	45.7±25.0 ^{b,c}	64.1±54.6 ^c	$F_{3,228} = 11.1, p < 0.001$
f0max (kHz)	63.8±11.5 ^a	75.3±18.1 ^b	81.5±14.2 ^b	76.6±11.3 ^b	$F_{3,228} = 14.5, p < 0.001$
f0min (kHz)	52.3±9.6 ^a	47.8±8.4 ^b	48.3±11.8 ^{a,b}	43.2±4.7 ^b	$F_{3,228} = 5.0, p = 0.002$
f0beg (kHz)	57.5±9.8	55.5±13.0	59.8±8.5	57.7±7.9	$F_{3,228} = 0.6, p = 0.62$
f0end (kHz)	55.1±11.9 ^{a,b}	61.2±18.3 ^a	54.4±15.5 ^{a,b}	49.1±12.9 ^b	$F_{3,228} = 2.9, p = 0.03$
fpeak (kHz)	60.1±9.3	59.4±14.7	61.2±11.8	58.1±12.9	$F_{3,228} = 0.2, p = 0.91$
bndw (kHz)	6.1±5.6 ^a	6.0±5.6 ^a	11.5±10.6 ^b	10.2±8.1 ^{a,b}	$F_{3,228} = 4.0, p = 0.009$

Note: The same superscripts indicate which values did not differ significantly ($p > 0.05$, Tukey HSD test).

<https://doi.org/10.1371/journal.pone.0219749.t010>

[85]. Data on ultrasonic hearing of fat-tailed gerbils are unavailable. At the same time, studies on domestic mice showed that neurons in the dorsal cochlear nucleus, designed for responsiveness to USV calls below 30 kHz, are also responsive to social USV calls over 50 kHz [185], probably because of sound distortion when passing cochlea [186]. Fat-tailed gerbils with their low-frequency sensitivity can serve a potential convenient model for testing this hypothesis of hearing distorted ultrasound by rodents.

There is a preliminary evidence that during the isolation and handling procedure, pup and adult fat-tailed gerbils produce also very low-frequency audible calls [39]. Vocalization in both audible and ultrasonic frequency ranges occurs during experimental isolation and handling procedures in many species of rodents [26,109]. Further research should investigate the acoustic structure and use of the audible calls produced by pup and adult fat-tailed gerbils during isolation and handling procedure and alternation in their use with the USV calls.

In gerbils, ontogenetic emergence of USV calls is ahead substantially the opening of ears and eyes. Pup Mongolian gerbils produce USV calls since the 1st day of pup life, with maximum of ultrasound emission in 2-6-day pups [33,96,174]. In pup fat-tailed gerbils, first USV calls emerge since 5th day of pup life, with maximum of ultrasound emission in 11-14-day pups [39]. At the same time, in gerbils, the ear opening occurs between 12 and 28 postnatal day depending on the species and the eye opening occurs between 14 and 24 postnatal day depending on the species, see review in [review in 84]. In pup fat-tailed gerbils, the ears open very late, at postnatal day 27, whereas the eyes open between 16 and 24 postnatal days [80,84]. As in rats and mice, pup isolation USV calls are directed to their mothers at situations when pup USV calls promote retrieval by the pups by their mothers [36].

This study provides an additional evidence about the wide acoustic variation of USV calls in pup and adult gerbils. These variable calls may potentially play an important role in different social contexts. Further studies are necessary to reveal the relationships between the acoustics structure and the attending behaviours in the fat-tailed gerbil.

Supporting information

S1 Table. Acoustic measurements of USV syllables of fat-tailed gerbils for describing the acoustics of call types and for estimating the effects of age, contour shape and note composition on the acoustic variables.

(XLS)

S1 Audio. USV syllables of fat-tailed gerbils. Order as on Fig 2. Sampling frequency of the acoustic file is 192 kHz.

(WAV)

Acknowledgments

We thank the staff of Moscow Zoo for their help and support. We are appreciate to N. Vasilieva for her courteous consulting in statistics and to the two anonymous reviewers for their useful and constructive comments.

Author Contributions

Conceptualization: Ilya A. Volodin, Elena V. Volodina.

Data curation: Alexandra S. Zaytseva, Ilya A. Volodin, Olga G. Ilchenko.

Formal analysis: Alexandra S. Zaytseva, Ilya A. Volodin, Elena V. Volodina.

Funding acquisition: Ilya A. Volodin, Elena V. Volodina.

Investigation: Alexandra S. Zaytseva, Ilya A. Volodin, Olga G. Ilchenko, Elena V. Volodina.

Methodology: Ilya A. Volodin, Olga G. Ilchenko.

Project administration: Ilya A. Volodin.

Resources: Alexandra S. Zaytseva, Ilya A. Volodin, Olga G. Ilchenko.

Validation: Ilya A. Volodin.

Writing – original draft: Alexandra S. Zaytseva, Ilya A. Volodin, Olga G. Ilchenko, Elena V. Volodina.

Writing – review & editing: Ilya A. Volodin, Elena V. Volodina.

References

1. Brudzynski SM. Ethotransmission: communication of emotional states through ultrasonic vocalization in rats. *Curr Opin Neurobiol.* 2013; 23: 310–317. <https://doi.org/10.1016/j.conb.2013.01.014> PMID: 23375168
2. Brudzynski SM. Pharmacology of ultrasonic vocalizations in adult rats: significance, call classification and neural substrate. *Curr Neuropharmacol.* 2015; 13: 180–192. <https://doi.org/10.2174/1570159X13999150210141444> PMID: 26411761
3. Wöhr M, Schwarting RK. Affective communication in rodents: ultrasonic vocalizations as a tool for research on emotion and motivation. *Cell Tissue Res.* 2013; 354: 81–97. <https://doi.org/10.1007/s00441-013-1607-9> PMID: 23576070
4. Grimsley JMS, Sheth S, Vallabh N, Grimsley CA, Bhattal J, Latsko M, et al. Contextual modulation of vocal behavior in mouse: newly identified 12 kHz “mid-frequency” vocalization emitted during restraint. *Front Behav Neurosci.* 2016; 10: 38. <https://doi.org/10.3389/fnbeh.2016.00038> PMID: 27014000
5. Jouda J, Wöhr M, del Rey A. Immunity and ultrasonic vocalization in rodents. *Ann N Y Acad Sci.* 2019; 1437: 68–82. <https://doi.org/10.1111/nyas.13931> PMID: 30062701
6. Scattoni ML, Gandhi SU, Ricceri L, Crawley JN. Unusual repertoire of vocalizations in the BTBR T+tf/J mouse model of autism. *PLoS ONE* 2008; 3(8): e3067. <https://doi.org/10.1371/journal.pone.0003067> PMID: 18728777
7. Grimsley JMS, Monaghan JJM, Wenstrup JJ. Development of social vocalizations in mice. *PLoS ONE* 2011; 6(3): e17460. <https://doi.org/10.1371/journal.pone.0017460> PMID: 21408007
8. Arriaga G, Jarvis ED. Mouse vocal communication system: Are ultrasounds learned or innate? *Brain Lang.* 2013; 124: 96–116. <https://doi.org/10.1016/j.bandl.2012.10.002> PMID: 23295209
9. Heckman J, McGuinness B, Celikel T, Englitz B. Determinants of the mouse ultrasonic vocal structure and repertoire. *Neurosci Biobehav Rev.* 2016; 65: 313–325. <https://doi.org/10.1016/j.neubiorev.2016.03.029> PMID: 27060755
10. Dou X, Shirahata S, Sugimoto H. Functional clustering of mouse ultrasonic vocalization data. *PLoS ONE* 2018; 13(5): e0196834. <https://doi.org/10.1371/journal.pone.0196834> PMID: 29742174
11. Granon S, Faure A, Chauveau F, Cressant A, Ey E. Why should my mouse call me? Acoustic communication in mouse models of social disorders: ultrasonic vocalizations as an index of emotional and motivational states. In: Brudzynski SM, editor. *Handbook of Ultrasonic Vocalization*. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 423–431. <https://doi.org/10.1016/B978-0-12-809600-0.00040-8>
12. Shair HN. Factors affecting emission of infantile vocalizations and vocal expression of emotional states. In: Brudzynski SM, editor. *Handbook of Ultrasonic Vocalization*. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 157–168. <https://doi.org/10.1016/B978-0-12-809600-0.00015-9>
13. Simola N, Granon S. Ultrasonic vocalizations as a tool in studying emotional states in rodent models of social behavior and brain disease. *Neuropharmacology* 2019. <https://doi.org/10.1016/j.neuropharm.2018.11.008>
14. Gulia KK, Patel N, Radhakrishnan A, Kumar VM. Reduction in ultrasonic vocalizations in pups born to rapid eye movement sleep restricted mothers in rat model. *PLoS ONE* 2014; 9(1): e84948. <https://doi.org/10.1371/journal.pone.0084948> PMID: 24454768

15. Zeskind PS, McMurray MS, Cox Lippard ET, Grewen KM, Garber KA, Johns JM. Translational analysis of effects of prenatal cocaine exposure on human infant cries and rat pup ultrasonic vocalizations. *PLoS ONE* 2014; 9(10): e110349. <https://doi.org/10.1371/journal.pone.0110349> PMID: 25338015
16. Riede T, Zhao Y, LeDoux MS. Vocal development in dystonic rats. *Physiol Rep*. 2015; 3(4): e12350. <https://doi.org/10.14814/phy2.12350> PMID: 25907786
17. Esposito G, Hiroi N, Scattoni ML. Cry, baby, cry: expression of distress as a biomarker and modulator in autism spectrum disorder. *Int J Neuropsychopharmacol*. 2017; 20: 498–503. <https://doi.org/10.1093/ijnp/pyx014>
18. Scattoni M.L, Michetti C., Ricceri L. Rodent vocalization studies in animal models of the autism spectrum disorder. In: Brudzynski SM, editor. *Handbook of Ultrasonic Vocalization*. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 445–456. <https://doi.org/10.1016/B978-0-12-809600-0.00042-1>
19. Ellenbroek B, Youn J. Rodent models in neuroscience research: is it a rat race? *Disease Models & Mechanisms* 2016; 9: 1079–1087. <https://doi.org/10.1242/dmm.026120>
20. Bertorelli R, Adami M, Ongeni E. The Mongolian gerbil in experimental epilepsy. *Ital J Neurol Sci*. 1995; 16: 101–106 PMID: 7642342
21. Ito U, Hakamata Y, Yamaguchi T, Ohno K. 2013. Cerebral ischemia model using Mongolian gerbils—comparison between unilateral and bilateral carotid occlusion models. *Acta Neurochir Suppl*. 2013; 118: 17–21. https://doi.org/10.1007/978-3-7091-1434-6_3
22. Somova LI, Gregory MA, Nxumalo EN. Mongolian gerbil (*Meriones unguiculatus*) as a model of cerebral infarction for testing new therapeutic agents. *Methods Find Exp Clin Pharmacol*. 2000; 22: 203–210. <https://doi.org/10.1358/mf.2000.22.4.584452> PMID: 10939031
23. Furtak SC, Brown TH. Limbic-system involvement in rat ultrasonic communications. In: Brudzynski SM, editor. *Handbook of Ultrasonic Vocalization*. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 95–108. <https://doi.org/10.1016/B978-0-12-809600-0.00009-3>
24. Stewart AM, Lewis GF, Yee JR, Kenkel WM, Davila MI, Carter CS, et al. Acoustic features of prairie vole (*Microtus ochrogaster*) ultrasonic vocalizations covary with heart rate. *Physiol Behav*. 2015; 138: 94–100. <https://doi.org/10.1016/j.physbeh.2014.10.011> PMID: 25447483
25. Kolacz J, Lewis GF, Porges SW. The integration of vocal communication and biobehavioral state regulation in mammals: a polyvagal hypothesis. In: Brudzynski SM, editor. *Handbook of Ultrasonic Vocalization*. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 23–34. <https://doi.org/10.1016/B978-0-12-809600-0.00003-2>
26. Terleph T. A comparison of prairie vole audible and ultrasonic pup calls and attraction to them by adults of each sex. *Behaviour* 2011; 148: 1277–1296. <https://doi.org/10.2307/41445245>
27. Hashimoto H, Moritani N, Aoki-Komori S, Tanaka M, Saito TR. Comparison of ultrasonic vocalizations emitted by rodent pups. *Exp Anim*. 2004; 53(5): 409–416. <https://doi.org/10.1538/expanim.53.409> PMID: 15516788
28. Constantini F, D'Amato R. Ultrasonic vocalizations in mice and rats: social contexts and functions. *Acta Zool Sinica* 2006; 52: 619–633.
29. Portfors CV. Types and functions of ultrasonic vocalizations in laboratory rats and mice. *J Am Assoc Lab Anim Sci*. 2007; 46: 28–34. PMID: 17203913
30. Brunelli SA, Nie R, Whipple C, Winiger V, Hofer MA, Zimmerberg B. The effects of selective breeding for infant ultrasonic vocalizations on play behavior in juvenile rats. *Physiol Behav*. 2006; 200687: 527–536. <https://doi.org/10.1016/j.physbeh.2005.11.020>
31. Kisko TM, Braun MD, Michels S, Witt SH, Rietschel M, Culmsee C, et al. Sex-dependent effects of Cacna1c haploinsufficiency on juvenile social play behavior and pro-social 50-kHz ultrasonic communication in rats. *Genes Brain Behav*. 2018; e12552. <https://doi.org/10.1111/gbb.12552> PMID: 30592145
32. Pellis SM, Burke CJ, Kisko TM, Euston DR. 50-kHz Vocalizations, play and the development of social competence. In: Brudzynski SM, editor. *Handbook of Ultrasonic Vocalization*. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 117–126. <https://doi.org/10.1016/B978-0-12-809600-0.00011-1>
33. Broom DM, Elwood RW, Lakin J, Willy SJ, Pretlove AJ. Developmental changes in several parameters of ultrasonic calling by young Mongolian gerbils (*Meriones unguiculatus*). *J Zool*. 1977; 183: 281–290. <https://doi.org/10.1111/j.1469-7998.1977.tb04187.x>
34. Sales GD, Smith JC. Comparative studies of the ultrasonic calls of infant murid rodents. *Devel Psychobiol*. 1978; 11: 595–619. <https://doi.org/10.1002/dev.420110609>
35. Brudzynski SM, Kehoe P, Callahan M. Sonographic structure of isolation-induced ultrasonic calls of rat pups. *Devel Psychobiol*. 1999; 34: 195–204. [https://doi.org/10.1002/\(SICI\)1098-2302\(199904\)34:33.0.CO;2-S](https://doi.org/10.1002/(SICI)1098-2302(199904)34:33.0.CO;2-S)

36. Hahn ME, Lavooy MJ. A review of the methods of studies on infant ultrasound production and maternal retrieval in small rodents. *Behav Genet.* 2005; 35: 31–52. <https://doi.org/10.1007/s10519-004-0854-7> PMID: 15674531
37. Schneider N, Fritzsche P. Isolation calls and retrieving behavior in laboratory and wild-derived golden hamsters—No sign for inbreeding depression. *Mammal Biol.* 2011; 76: 549–554. <https://doi.org/10.1016/j.mambio.2011.03.002>
38. Blake BH. Ultrasonic calling in 2 species of voles, *Microtus pinetorum* and *M. pennsylvanicus*, with different social systems. *J Mammal.* 2012; 93: 1051–1060. <https://doi.org/10.1644/11-MAMM-A-356.2>
39. Zaytseva AS, Volodin IA, Ilchenko OG, Volodina EV. Discomfort-related changes in pup ultrasonic calls of fat-tailed gerbils *Pachyuromys duprasi*. *Bioacoustics* 2017; 26: 1–13. <https://doi.org/10.1080/09524622.2016.1164076>
40. Marchlewska-Koj A, Kapusta J. Biology, development, and ultrasonic vocalizations of bank vole infants. In: Brudzynski SM, editor. *Handbook of Ultrasonic Vocalization*. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 169–174. <https://doi.org/10.1016/B978-0-12-809600-0.00016-0>
41. Boulanger-Bertolus J, Rincón-Cortés M, Regina M, Sullivan RM, Mouly A-M. Understanding pup affective state through ethologically significant ultrasonic vocalization frequency. *Sci Rep.* 2017; 7: 13483. <https://doi.org/10.1038/s41598-017-13518-6> PMID: 29044126
42. Okon EE. The ultrasonic responses of albino mouse pups to tactile stimuli. *J Zool.* 1970; 162: 485–492. <https://doi.org/10.1111/j.1469-7998.1970.tb01283.x>
43. Dempster ER, Perrin MR. Ultrasonic vocalizations of six taxa of Southern African gerbils (Roderitia: Gerbillinae). *Ethology* 1991; 88: 1–10. <https://doi.org/10.1111/j.1439-0310.1991.tb00258.x>
44. Dempster ER, Perrin MR. Divergence in acoustic repertoire of sympatric and allopatric gerbil species (Rodentia: Gerbillinae). *Mammalia* 1994; 58: 93–104. <https://doi.org/10.1515/mamm.1994.58.1.93>
45. Holy TE, Guo Z. Ultrasonic songs of male mice. *PLoS Biol.* 2005; 3(12): e386. <https://doi.org/10.1371/journal.pbio.0030386> PMID: 16248680
46. Miller JR, Engstrom MD. Vocal stereotypy and singing behavior in baiomyine mice. *J Mammal.* 2007; 88: 1447–1465. <https://doi.org/10.1644/06-MAMM-A-386R.1>
47. Hammerschmidt K, Reisinger E, Westekemper K, Ehrenreich L, Strenzke N, Fischer J. Mice do not require auditory input for the normal development of their ultrasonic vocalizations. *BMC Neurosci.* 2012; 13: 40. <https://doi.org/10.1186/1471-2202-13-40> PMID: 22533376
48. Musolf K, Meindl S, Larsen AL, Kalcounis-Rueppell MC, Penn DJ. Ultrasonic vocalizations of male mice differ among species and females show assortative preferences for male calls. *PLoS ONE* 2015; 10(8): e0134123. <https://doi.org/10.1371/journal.pone.0134123> PMID: 26309246
49. Zala SM, Reitschmidt D, Noll A, Balazs P, Penn DJ. Sex-dependent modulation of ultrasonic vocalizations in house mice (*Mus musculus musculus*). *PLoS ONE* 2017; 12(12): e0188647. <https://doi.org/10.1371/journal.pone.0188647> PMID: 29236704
50. Matsumoto YK, Okanoya K. Mice modulate ultrasonic calling bouts according to sociosexual context. *R Soc open sci.* 2018; 5: 180378. <https://doi.org/10.1098/rsos.180378> PMID: 30110406
51. Pultorak JD, Alger SJ, Loria SO, Johnson AM, Marler CA. Changes in behavior and ultrasonic vocalizations during pair bonding and in response to an infidelity challenge in monogamous California mice. *Front Ecol Evol.* 2018; 6: 125. <https://doi.org/10.3389/fevo.2018.00125>
52. Ter-Mikaelian M, Yapa WB, Rübsamen R. Vocal behavior of the Mongolian gerbil in a seminatural enclosure. *Behaviour* 2012; 149: 461–492. <https://doi.org/10.1163/156853912X639778>
53. Mun HS, Lipina TV, Roder JC. Ultrasonic vocalizations in mice during exploratory behavior are context-dependent. *Front Behav Neurosci.* 2015; 9: 316. <https://doi.org/10.3389/fnbeh.2015.00316> PMID: 26696847
54. Rieger NS, Marler CA. The function of ultrasonic vocalizations during territorial defense by pair-bonded male and female California mice. *Anim Behav.* 2018; 135: 97–108. <https://doi.org/10.1016/j.anbehav.2017.11.008>
55. Bridelance P. Communication acoustique ntr individus adults ds gens *Meriones*, *Pchyuroms*, *Psmmoms* (Gbillida, Rodntia). I. Analys ds reptoirs Mammalia 1989; 53: 3–17. [in French]
56. Kapusta J, Sales GD, Czuchnowski R. Aggression and vocalization behaviour of three sympatric vole species during conspecific and heterospecific same-sex encounters. *Behaviour*, 2007; 144: 283–305. <https://doi.org/10.1163/156853907780425730>
57. Kapusta J, Sales GD. Male–female interactions and ultrasonic vocalization in three sympatric species of voles during conspecific and heterospecific encounters. *Behaviour* 2009; 146: 939–962. <https://doi.org/10.1163/156853908X396818>

58. Wilson DR, Hare JF. Ground squirrel uses ultrasonic alarms. *Nature* 2004; 430: 523. <https://doi.org/10.1038/430523a> PMID: 15282596
59. Wilson DR, Hare JF. The adaptive utility of Richardson's ground squirrel (*Spermophilus richardsonii*) short-range ultrasonic alarm signals. *Can J Zool.* 2006; 84: 1322–1330. <https://doi.org/10.1139/Z06-120>
60. Matrosova VA, Schneiderová I, Volodin IA, Volodina EV. Species-specific and shared features in vocal repertoires of three Eurasian ground squirrels (genus *Spermophilus*). *Acta Theriol.* 2012; 57: 65–78. <https://doi.org/10.1007/s13364-011-0046-9>
61. Simola N, Brudzynski SM. Repertoire and biological function of ultrasonic vocalizations in adolescent and adult rats. In: Brudzynski SM, editor. *Handbook of Ultrasonic Vocalization*. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 177–186. <https://doi.org/10.1016/B978-0-12-809600-0.00017-2>
62. Griffiths S, Dow S, Burman O. Ultrasonic vocalizations and their associations with the non-vocalization behaviour of the endangered Turkish spiny mouse *Acomys cilicicus* Spitzenberger in a captive population. *Bioacoustics* 2010; 19: 143–157. <https://doi.org/10.1080/09524622.2010.9753621>
63. Panyutina AA, Kuznetsov AN, Volodin IA, Abramov AV, Soldatova IB. A blind climber: the first evidence of ultrasonic echolocation in arboreal mammals. *Integr Zool.* 2017; 12: 172–184. <https://doi.org/10.1111/1749-4877.12249> PMID: 27991725
64. Volodin IA, Panyutina AA, Abramov AV, Ilchenko OG, Volodina EV. Ultrasonic bouts of a blind climbing rodent (*Typhlomys chapensis*): acoustic analysis. *Bioacoustics* 2019. <https://doi.org/10.1080/09524622.2018.1509374>
65. Williams WO, Riskin DK, Mott KM. Ultrasonic sound as an indicator of acute pain in laboratory mice. *J Am Assoc Lab Anim Sci.* 2008; 47: 8–10.
66. Murrant MN, Bowman J, Garroway CJ, Prinzen B, Mayberry H, Faure PA. Ultrasonic vocalizations emitted by flying squirrels. *PLoS ONE* 2013; 8(8): e73045. <https://doi.org/10.1371/journal.pone.0073045> PMID: 24009728
67. Campbell P, Pasch B, Warren AL, Phelps SM. Vocal ontogeny in Neotropical singing mice (*Scotinomys*). *PLoS ONE* 2014; 9(12): e113628. <https://doi.org/10.1371/journal.pone.0113628> PMID: 25469986
68. Thiessen DD, Graham M, Davenport R. Ultrasonic signaling in the gerbil (*Meriones unguiculatus*): Social interaction and olfaction. *J Comp Physiol Psychol.* 1978; 92: 1041–1049. <https://doi.org/10.1037/h0077512>
69. Nishiyama K, Kobayasi KI, Riquimaroux H. Vocalization control in Mongolian gerbils (*Meriones unguiculatus*) during locomotion behavior. *J Acoust Soc Am.* 2011; 130: 4148–4157. <https://doi.org/10.1121/1.3651815> PMID: 22225069
70. Brudzynski SM, Ociepa D. Ultrasonic vocalization of laboratory rats in response to handling and touch. *Physiol Behav.* 1992; 52: 655–660. [https://doi.org/10.1016/0031-9384\(92\)90393-g](https://doi.org/10.1016/0031-9384(92)90393-g) PMID: 1409936
71. Titze IR. *Principles of voice production*. Englewood Cliffs, NJ: Prentice-Hall; 1994. 354 p.
72. Riede T. Subglottal pressure, tracheal airflow, and intrinsic laryngeal muscle activity during rat ultrasound vocalization. *J Neurophysiol.* 2011; 106: 2580–2592. <https://doi.org/10.1152/jn.00478.2011> PMID: 21832032
73. Riede T. Stereotypic laryngeal and respiratory motor patterns generate different call types in rat ultrasound vocalization. *J Exp Zool.* 2013; 319A: 213–224. <https://doi.org/10.1002/jez.1785>
74. Mahrt E, Agarwal A, Perkel D, Portfors C, Elemans CPH. Mice produce ultrasonic vocalizations by intra-laryngeal planar impinging jets. *Curr Biol.* 2016; 26: R865–R881. <https://doi.org/10.1016/j.cub.2016.08.032>
75. Pasch B, Tokuda IT, Riede T. Grasshopper mice employ distinct vocal production mechanisms in different social contexts. *Proc R Soc B* 2017; 284: 20171158. <https://doi.org/10.1098/rspb.2017.1158> PMID: 28724740
76. Riede T, Borgard HL, Pasch B. Laryngeal airway reconstruction indicates that rodent ultrasonic vocalizations are produced by an edge-tone mechanism. *R Soc open sci.* 2017; 4: 170976. <https://doi.org/10.1098/rsos.170976> PMID: 29291091
77. Wright JM, Gourdon JM, Clarke PB. Identification of multiple call categories within the rich repertoire of adult rat 50-kHz ultrasonic vocalizations: Effects of amphetamine and social context. *Psychopharmacology* 2010; 211: 1–13. <https://doi.org/10.1007/s00213-010-1859-y> PMID: 20443111
78. Kobayasi KI, Riquimaroux H. Classification of vocalizations in the Mongolian gerbil, *Meriones unguiculatus*. *J Acoust Soc Am.* 2012; 131: 1622–1631. <https://doi.org/10.1121/1.3672693> PMID: 22352532

79. Riede T. Peripheral vocal motor dynamics and combinatory call complexity of ultrasonic vocal production in rats. In: Brudzynski SM, editor. Handbook of Ultrasonic Vocalization. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 45–60. <https://doi.org/10.1016/B978-0-12-809600-0.00005-6>
80. Felt SA, Hussein HI, Helmy IH. Biology, breeding, husbandry and diseases of the captive Egyptian fat-tailed jird (*Pachyuromys duprasi natronensis*). Lab Anim (NY). 2008; 37: 256–261. <https://doi.org/10.1038/labon0608-256>
81. Hanafi HA, Fryauff DJ, Kittell CE. 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. 2013; 13(9): 650–656. <https://doi.org/10.1089/vbz.2012.1185> PMID: 23697770
82. Gouaref I, Detaille D, Wiernsperger N, Khan NA, Leverve X, Koceir E-A. The desert gerbil *Psammomys obesus* as a model for metformin-sensitive nutritional type 2 diabetes to protect hepatocellular metabolic damage: Impact of mitochondrial redox state. PLoS ONE 2017; 12(2): e0172053. <https://doi.org/10.1371/journal.pone.0172053> PMID: 28222147
83. Quintar AA, Gonçalves BF, Taboga SR, Maldonado CA. The Mongolian gerbil (*Meriones unguiculatus*) as a model for inflammation-promoted prostate carcinogenesis. Cell Biol Int. 2017; 41: 1234–1238. <https://doi.org/10.1002/cbin.10789> PMID: 28493535
84. Zaytseva AS, Ilchenko OG, Volodin IA, Volodina EV. Early postnatal development of the fat-tailed gerbil (*Pachyuromys duprasi*, Rodentia, Gerbillinae) in a laboratory colony. Zool Zhurnal 2016; 95: 94–103 [in Russian]. <https://doi.org/10.7868/S0044513416010141>
85. Lay DM. The anatomy, physiology, functional significance and evolution of specialized hearing organs of Gerbilline rodents. J Morphol. 1972; 138: 41–120. <https://doi.org/10.1002/jmor.1051380103> PMID: 5069372
86. Müller M, Ott H, Bruns V. Frequency representation and spiral ganglion cell density in the cochlea of the gerbil *Pachyuromys duprasi*. Hear Res. 1991; 56: 191–196. [https://doi.org/10.1016/0378-5955\(91\)90169-A](https://doi.org/10.1016/0378-5955(91)90169-A) PMID: 1769913
87. Plassmann W, Kadel M. Low-frequency sensitivity in a gerbilline rodent, *Pachyuromys duprasi*. Brain Behav Evol. 1991; 38: 115–126. <https://doi.org/10.1159/000114382> PMID: 1742598
88. Refinetti R. Homeostatic and circadian control of body temperature in the fat-tailed gerbil. Comp Biochem Physiol A Mol Integr Physiol. 1998; 119: 295–300. [https://doi.org/10.1016/S1095-6433\(97\)00436-4](https://doi.org/10.1016/S1095-6433(97)00436-4) PMID: 11253797
89. Refinetti R. Amplitude of the daily rhythm of body temperature in eleven mammalian species. J Thermal Biol. 1999; 24: 477–481. [https://doi.org/10.1016/S0306-4565\(99\)00077-7](https://doi.org/10.1016/S0306-4565(99)00077-7)
90. Noiro E. Ultrasounds in young rodents. I. Changes with age in albino mice. Anim Behav. 1966; 14: 459–467. [https://doi.org/10.1016/S0003-3472\(66\)80045-3](https://doi.org/10.1016/S0003-3472(66)80045-3) PMID: 5972804
91. Noiro E. Ultrasounds in young rodents. II. Changes with age in albino rats. Anim Behav. 1968; 16: 129–134. [https://doi.org/10.1016/0003-3472\(68\)90123-1](https://doi.org/10.1016/0003-3472(68)90123-1) PMID: 5639891
92. Allin JT, Banks EM. Effects of temperature on ultrasound production by infant albino rats. Develop Psychobiol. 1971; 4: 149–156. <https://doi.org/10.1002/dev.420040206>
93. Okon EE. The effect of environmental temperature on the production of ultrasounds in non-handled albino mouse pups. J Zool. 1970; 162: 71–83. <https://doi.org/10.1111/j.1469-7998.1970.tb01258.x>
94. Okon EE. The temperature relations of vocalization in infant Golden hamsters and Wistar rats. J Zool. 1971; 164: 227–237. <https://doi.org/10.1111/j.1469-7998.1971.tb01308.x>
95. Brooks RJ, Banks EM. Behavioural biology of the collared lemming (*Dicrostonyx groenlandicus* (Trail)): An analysis of acoustic communication. Anim Behav. 1973; 6: 1–83. [https://doi.org/10.1016/0003-3472\(73\)90003-1](https://doi.org/10.1016/0003-3472(73)90003-1)
96. de Gheff VJ. Developmental changes in the rate of ultrasonic vocalization in the Mongolian gerbil. Develop Psychobiol. 1974; 7: 261–272. <https://doi.org/10.1002/dev.420070311>
97. Pontet A, Gyger M, Schenk F. Ontogeny of ultrasonic vocalizations in the woodmouse (*Apodemus sylvaticus* L.). I: Temporal organization. Behaviour 1989; 108: 241–261. <https://doi.org/10.1163/156853989X00321>
98. Hahn ME, Karkowski L, Weinreb L, Henry A, Schanz N, Hahn EM. Genetic and developmental influences on infant mouse ultrasonic calling. II. Developmental patterns in the calls of mice 2–12 days of age. Behav Genet. 1998; 28: 315–325. <https://doi.org/10.1023/A:1021679615792> PMID: 9803024
99. Hashimoto H, Saito TR, Moritani N, Komeda K, Takahashi KW. Comparative study on isolation calls emitted from hamster pups. Exp Anim. 2001; 50(4): 313–318. <https://doi.org/10.1538/expanim.50.313> PMID: 11515094
100. Vieira M, Brown R. Ultrasonic vocalizations and ontogenetic development in California mice (*Peromyscus californicus*). Behav Process. 2002; 59: 147–156. [https://doi.org/10.1016/S0376-6357\(02\)00089-X](https://doi.org/10.1016/S0376-6357(02)00089-X)

101. Yu P, Wang J, Tai F, Broders H, An S, Zhang X, et al. The effects of repeated early deprivation on ultrasonic vocalizations and ontogenetic development in Mandarin vole pups. *Behav Process.* 2011; 88: 162–167. <https://doi.org/10.1016/j.beproc.2011.09.001>
102. Kalcounis-Rueppell MC, Pultorak JD, Marler CA, Blake BH. Ultrasonic vocalizations of young mice in the genus *Peromyscus*. In: Brudzynski SM, editor. *Handbook of Ultrasonic Vocalization*. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 149–156. <https://doi.org/10.1016/B978-0-12-809600-0.00014-7>
103. Volodin IA, Ilchenko OG, Popov SV. Gerbils: captive management and population demography of different species in laboratory. Moscow: Moscow Zoo press; 1996. 228 p. [in Russian].
104. Groenink L, Verdouw PM, Bakker B, Wever KE. Pharmacological and methodological aspects of the separation-induced vocalization test in guinea pig pups; a systematic review and meta-analysis. *Eur J Pharmacol.* 2015; 753: 191–208. <https://doi.org/10.1016/j.ejphar.2014.10.062> PMID: 25460027
105. Hahn ME, Schanz N. The effects of cold, rotation, and genotype on the production of ultrasonic calls in infant mice. *Behav Genet.* 2002; 32: 267–273. <https://doi.org/10.1023/A:1019728813891> PMID: 12211626
106. Ceron RJ, Radwin RG, Henderson CJ. Hand skin temperature variations for work in moderately cold environments and the effectiveness of periodic rewarming. *Am Ind Hyg Assoc J.* 1995; 56: 558–567. <https://doi.org/10.1080/15428119591016782> PMID: 7778525
107. Lemasson M, Delbé C, Gheusi G, Vincent J-D, Lledo P-M. Use of ultrasonic vocalizations to assess olfactory detection in mouse pups treated with 3-methylindole. *Behav Process.* 2005; 68: 13–23. <https://doi.org/10.1016/j.beproc.2004.09.001>
108. Fernández-Vargas M, Johnston RE. Ultrasonic vocalizations in golden hamsters (*Mesocricetus auratus*) reveal modest sex differences and nonlinear signals of sexual motivation. *PLoS ONE* 2015; 10 (2): e0116789. <https://doi.org/10.1371/journal.pone.0116789> PMID: 25714096
109. Floody OR. Ultrasonic communication in hamsters. In: Brudzynski SM, editor. *Handbook of Ultrasonic Vocalization*. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 197–206. <https://doi.org/10.1016/B978-0-12-809600-0.00019-6>
110. Shair HN. Infantile vocalizations in rats. In: Brudzynski SM, editor. *Handbook of Ultrasonic Vocalization*. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 129–137. <https://doi.org/10.1016/B978-0-12-809600-0.00012-3>
111. Peterson JR, Watts CR, Morris JA, Shelton JM, Cooper BG. Laryngeal aging and acoustic changes in male rat ultrasonic vocalizations. *Devel Psychobiol.* 2013; 55: 818–828. <https://doi.org/10.1002/dev.21072>
112. Hoffmann F, Musolf K, Penn DJ. Ultrasonic courtship vocalizations in wild house mice: spectrographic analyses. *J Ethol.* 2012; 30: 173–180. <https://doi.org/10.1007/s10164-011-0312-y>
113. Kelm-Nelson CA, Lenell C, Johnson AM, Ciucci MR. Laryngeal activity for production of ultrasonic vocalizations in rats. In: Brudzynski SM, editor. *Handbook of Ultrasonic Vocalization*. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 37–43. <https://doi.org/10.1016/B978-0-12-809600-0.00004-4>
114. Janik VM, Slater PJB. The different roles of social learning in vocal communication. *Anim Behav.* 2000; 60: 1–11. <https://doi.org/10.1006/anbe.2000.1410> PMID: 10924198
115. Seyfarth RM, Cheney DL. Production, usage, and comprehension in animal vocalizations. *Brain Lang.* 2010; 115: 92–100. <https://doi.org/10.1016/j.bandl.2009.10.003> PMID: 19944456
116. Volodin IA, Zaytseva AS, Ilchenko OG, Volodina EV. Small mammals ignore common rules: A comparison of vocal repertoires and the acoustics between pup and adult piedbald shrews *Diplomesodon pulchellum*. *Ethology* 2015; 121: 103–115. <https://doi.org/10.1111/eth.12321>
117. Zaytseva AS, Volodin IA, Mason MJ, Frey R, Fritsch G, Ilchenko OG, et al. Vocal development during postnatal growth and ear morphology in a shrew that generates seismic vibrations, *Diplomesodon pulchellum*. *Behav Process.* 2015; 118: 130–141. <https://doi.org/10.1016/j.beproc.2015.06.012>
118. Schneiderová I. 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.* 2014; 59: 149–164. <https://doi.org/10.1007/s13364-013-0141-1>
119. Spence HR, Aslam AM, Hofer MA, Brunelli SA, Shair HN. Vocal coselection in rat pup ultrasonic vocalizations. *Ecol Evol.* 2016; 6: 1922–1929. <https://doi.org/10.1002/ece3.1907> PMID: 27066218
120. Wöhr M, Dahlhoff M, Wolf E, Holsboer F, Schwarting RKW, Wotjak CT. Effects of genetic background, gender, and early environmental factors on isolation-induced ultrasonic calling in mouse pups: an embryo-transfer study. *Behav Genet.* 2008; 38: 579–595. <https://doi.org/10.1007/s10519-008-9221-4> PMID: 18712592

121. Kikusui T, Nakanishi K, Nakagawa R, Nagasawa M, Mogi K, Okanoya K. Cross fostering experiments suggest that mice songs are innate. *PLoS ONE* 2011; 6(3): e17721. <https://doi.org/10.1371/journal.pone.0017721> PMID: 21408017
122. Fischer J, Hammerschmidt K. Ultrasonic vocalizations in mouse models for speech and socio-cognitive disorders: insights into the evolution of vocal communication. *Genes Brain Behav.* 2011; 10: 17–27. <https://doi.org/10.1111/j.1601-183X.2010.00610.x> PMID: 20579107
123. Castellucci GA, McGinley MJ, McCormick DA. Knockout of Foxp2 disrupts vocal development in mice. *Sci Rep.* 2016; 6: 23305. <https://doi.org/10.1038/srep23305> PMID: 26980647
124. Choi H, Park S, Kim D. Two genetic loci control syllable sequences of ultrasonic courtship vocalizations in inbred mice. *BMC Neurosci.* 2011; 12: 104. <https://doi.org/10.1186/1471-2202-12-104> PMID: 22018021
125. Briefer EF, McElligott AG. Social effects on vocal ontogeny in an ungulate, the goat, *Capra hircus*. *Anim Behav.* 2012; 83: 991–1000. <https://doi.org/10.1016/j.anbehav.2012.01.020>
126. Volodin IA, Volodina EV, Lapshina EN, Efremova KO, Soldatova NV. Vocal group signatures in the goitred gazelle *Gazella subgutturosa*. *Anim Cogn.* 2014; 17: 349–357. <https://doi.org/10.1007/s10071-013-0666-3> PMID: 23929532
127. Pasch B, Abbasi MZ, Wilson M, Zhao D, Searle JB, Webster MS, et al. Cross-fostering alters advertisement vocalizations of grasshopper mice (*Onychomys*): Evidence for the developmental stress hypothesis. *Physiol Behav.* 2016; 157: 265–269. <https://doi.org/10.1016/j.physbeh.2016.02.012> PMID: 26873411
128. Kanwal JS, Matsumura S, Ohlemiller K, Suga N. Analysis of acoustic elements and syntax in communication sounds emitted by mustached bats. *J Acoust Soc Am.* 1994; 96: 1229–1254. <https://doi.org/10.1121/1.410273> PMID: 7962992
129. Kanwal JS. Ultrasonic social communication in bats: signal complexity and its neural management. In: Brudzynski SM, editor. *Handbook of Ultrasonic Vocalization*. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 493–508. <https://doi.org/10.1016/B978-0-12-809600-0.00046-9>
130. Nakagawa R, Matsunaga E, Okanoya K. Defects in ultrasonic vocalization of Cadherin-6 knockout mice. *PLoS ONE* 2012; 7(11): e49233. <https://doi.org/10.1371/journal.pone.0049233> PMID: 23173049
131. McMurray MS, Johns JM. Effects of prenatal cocaine on maternal care and ultrasonic vocalizations of rat offspring. In: Brudzynski SM, editor. *Handbook of Ultrasonic Vocalization*. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 457–466. <https://doi.org/10.1016/B978-0-12-809600-0.00043-3>
132. Mandelli M-J, Sales G. Ultrasonic vocalizations of infant short-tailed field voles, *Microtus agrestis*. *J Mammal.* 2004; 85: 282–289. [https://doi.org/10.1644/1545-1542\(2004\)085<0282:UVOISF>2.0.CO;2](https://doi.org/10.1644/1545-1542(2004)085<0282:UVOISF>2.0.CO;2)
133. Holman SD, Seale WTC. Ontogeny of sexually dimorphic ultrasonic vocalizations in Mongolian gerbils. *Devel Psychobiol.* 1991; 24: 103–115. <https://doi.org/10.1002/dev.420240204>
134. Holman SD, Seale WTC, Hutchison JB. Ultrasonic vocalizations in immature gerbils: emission rate and structural changes after neonatal exposure to androgen. *Physiol Behav.* 1995; 57: 451–460. [https://doi.org/10.1016/0031-9384\(94\)00237-y](https://doi.org/10.1016/0031-9384(94)00237-y) PMID: 7753881
135. Soltis J, Allgood CA, Blowers TE, Savage A. The vocal repertoire of the Key Largo woodrat (*Neotoma floridana smalli*). *J Acoust Soc Am.* 2012; 132: 3550–3558. <https://doi.org/10.1121/1.4757097> PMID: 23145634
136. Stark RA. An ontogenetic profile of infant ultrasonic vocalizations using whole litter recordings: the transition from infant to adult calls in rats. A Thesis Master of Science, University of Lethbridge: Lethbridge, Alberta, Canada; 2017. 95 p. Available: <http://opus.uleth.ca/handle/10133/4992>
137. Watts CHS. Vocalizations of nine species of rat (*Rattus*; Muridae). *J Zool.* 1980; 191: 531–555. <https://doi.org/10.1111/j.1469-7998.1980.tb01484.x>
138. Ancillotto L, Russo D. Individual vs. non-individual acoustic signalling in African woodland dormice (*Graphiurus murinus*). *Mammal Biol.* 2016; 81: 410–414. <https://doi.org/10.1016/j.mambio.2016.05.001>
139. Ancillotto L, Sozio G, Mortelliti A, Russo D. Ultrasonic communication in Gliridae (Rodentia): the hazel dormouse (*Muscardinus avellanarius*) as a case study *Bioacoustics* 2014; 83: 129–141. <https://doi.org/10.1080/09524622.2013.838146>
140. Kalcounis-Rueppell MC, Pultorak JD, Marler CA. Ultrasonic vocalizations of mice in the genus *Peromyscus*. In: Brudzynski SM, editor. *Handbook of Ultrasonic Vocalization*. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 227–235. <https://doi.org/10.1016/B978-0-12-809600-0.00022-6>
141. Holman SD. Sexually dimorphic, ultrasonic vocalizations of Mongolian gerbils. *Behav Neural Biol.* 1980; 28: 183–192. [https://doi.org/10.1016/S0163-1047\(80\)91535-6](https://doi.org/10.1016/S0163-1047(80)91535-6)

142. Ferhat AT, Torquet N, Le Sourd AM, de Chaumont F, Olivo-Marin JC, Faure P, et al. Recording mouse ultrasonic vocalizations to evaluate social communication. *J Vis Exp*. 2016; 112: e53871. <https://doi.org/10.3791/53871>
143. Zala SM, Reitschmidt D, Noll A, Balazs P, Penn DJ. Automatic mouse ultrasound detector (A-MUD): A new tool for processing rodent vocalizations. *PLoS ONE* 2017; 12(7): e0181200. <https://doi.org/10.1371/journal.pone.0181200> PMID: 28727808
144. Ivanenko A, Watkins P, van Gerven MAJ, Hammerschmidt K, Englitz B. Classification of mouse ultrasonic vocalizations using deep learning. *bioRxiv*, 2018; 358143. <https://doi.org/10.1101/358143>
145. Coffey KR, Masx RG, Neumaier JF. DeepSqueak: a deep learning-based system for detection and analysis of ultrasonic vocalizations. *Neuropsychopharmacology* 2019; 44: 859–868. <https://doi.org/10.1038/s41386-018-0303-6> PMID: 30610191
146. Gaub S, Groszer M, Fisher SE, Ehret G. The structure of innate vocalizations in Foxp2-deficient mouse pups. *Genes Brain Behav*. 2010; 9: 390–401. <https://doi.org/10.1111/j.1601-183X.2010.00570.x> PMID: 20132318
147. Gaub S, Fisher SE, Ehret G. Ultrasonic vocalizations of adult male Foxp2-mutant mice: behavioral contexts of arousal and emotion. *Genes Brain Behav*. 2016; 15: 243–259. <https://doi.org/10.1111/gbb.12274> PMID: 26566793
148. Grimsley JMS, Gadziola MA, Wenstrup JJ. Automated classification of mouse pup isolation syllables: from cluster analysis to an Excel-based “mouse pup syllable classification calculator”. *Front Behav Neurosci*. 2013; 6: 89. <https://doi.org/10.3389/fnbeh.2012.00089> PMID: 23316149
149. Ehret G. Characteristics of vocalization in adult mice. In: Brudzynski SM, editor. *Handbook of Ultrasonic Vocalization*. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 187–195. <https://doi.org/10.1016/B978-0-12-809600-0.00018-4>
150. Brudzynski SM. Principles of rat communication: Quantitative parameters of ultrasonic calls in rats. *Behav Genet*. 2005; 35: 85–92. <https://doi.org/10.1007/s10519-004-0858-3> PMID: 15674535
151. Hashimoto H, Moritani N, Katou M, Nishiya T, Kromkhun P, Yokosuka M, et al. Ontogenetic changes of ultrasonic vocalizations emitted from infant rats. *Exp Anim*. 2007; 56: 315–318. <https://doi.org/10.1538/expanim.56.315> PMID: 17660687
152. Kromkhun P, Katou M, Hashimoto H, Terada M, Moon C, Saito TR. Quantitative and qualitative analysis of rat pup ultrasonic vocalization sounds induced by a hypothermic stimulus. *Lab Anim Res*. 2013; 29(2): 77–83. <https://doi.org/10.5625/lar.2013.29.2.77> PMID: 23825480
153. Basken JN, Connor NP, Ciucci MR. Effect of aging on ultrasonic vocalizations and laryngeal sensorimotor neurons in rats. *Exp Brain Res*. 2012; 219: 351–361. <https://doi.org/10.1007/s00221-012-3096-6> PMID: 22562586
154. Inagaki H, Takeuchi Y, Mori Y. Close relationship between the frequency of 22-kHz calls and vocal tract length in male rats. *Physiol Behav*. 2012; 106: 224–228. <https://doi.org/10.1016/j.physbeh.2012.01.018> PMID: 22326645
155. Johnson AM, Grant LM, Schallert T, Ciucci MR. Changes in rat 50-kHz ultrasonic vocalizations during dopamine denervation and aging: relevance to neurodegeneration. *Curr. Neuropharm*. 2015; 13: 211–219. <https://doi.org/10.2174/1570159X1302150525122416>
156. Novick A, Griffin DR. Laryngeal mechanisms in bats for the production of orientation sounds. *J Exp Zool*. 1961; 148: 125–145. <https://doi.org/10.1002/jez.1401480203> PMID: 14480574
157. Suthers RA, Fattu JM. Mechanisms of sound production by echolocating bats. *Amer Zool*. 1973; 13: 1215–1226. <https://doi.org/10.1093/icb/13.4.1215>
158. Carter RT, Shaw JB, Adams RA. Ontogeny of vocalization in Jamaican fruit bats with implications for the evolution of echolocation *J Zool*. 2014; 293: 25–32. <https://doi.org/10.1111/jzo.12097>
159. Jones G, Hughes PM, Rayner JMV. The development of vocalizations in *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during post-natal growth and the maintenance of individual vocal signatures. *J Zool*. 1991; 225: 71–84. <https://doi.org/10.1111/j.1469-7998.1991.tb03802.x>
160. De Fanis E, Jones DG. Post-natal growth, mother-infant interactions and development of vocalizations in the vespertilionid bat *Plecotus auritus*. *J Zool*. 1995; 235: 85–97. <https://doi.org/10.1111/j.1469-7998.1995.tb05130.x>
161. Moss CF, Redish D, Gounden C, Kunz TH. Ontogeny of vocal signals in the little brown bat, *Myotis lucifugus*. *Anim Behav*. 1997; 54: 131–141. <https://doi.org/10.1006/anbe.1996.0410> PMID: 9268443
162. Zhang L, Jones G, Parsons S, Liang B, Zhang S. Development of vocalizations in the flat-headed bats, *Tylonycteris pachypus* and *T. robustula* (Chiroptera: Vespertilionidae). *Acta Chiropt*. 2005; 7: 91–99. [https://doi.org/10.3161/1733-5329\(2005\)7\[91:DOVITF\]2.0.CO;2](https://doi.org/10.3161/1733-5329(2005)7[91:DOVITF]2.0.CO;2)
163. Liu Y, Feng J, Jiang YL, Wu L, Sun KP. Vocalization development of greater horseshoe bat, *Rhinolophus ferrumequinum* (Rhinolophidae, Chiroptera). *Folia Zool*. 2007; 56: 126–136.

164. Hiryu S, Riquimaroux H. Developmental changes in ultrasonic vocalizations by infant Japanese echolocating bats, *Pipistrellus abramus*. *J Acoust Soc Am*. 2011; 130(4): EL149. <https://doi.org/10.1121/1.3632044>
165. Monroy JA, Carter ME, Miller KE, Covey E. Development of echolocation and communication vocalizations in the big brown bat, *Eptesicus fuscus*. *J Comp Physiol A* 2011; 197: 459–467. <https://doi.org/10.1007/s00359-010-0614-5>
166. Jin L, Lin A, Sun K, Liu Y, Feng J. Postnatal development of morphological features and vocalization in the pomona leaf-nosed bat *Hipposideros pomona*. *Acta Theriol*. 2011; 56: 13–22. <https://doi.org/10.1007/s13364-010-0011-z>
167. Jin L, Wang J, Zhang Z, Sun K, Kanwal JS, Feng J. Postnatal development of morphological and vocal features in Asian particolored bat, *Vespertilio sinensis*. *Mammal Biol*. 2012; 77: 339–344. <https://doi.org/10.1016/j.mambio.2012.05.001>
168. Funakoshi K, Arai A, Inoue T. Development of sounds during postnatal growth of the eastern bent-winged bat *Miniopterus fuliginosus*. *Mammal Study* 2013; 38: 49–56. <https://doi.org/10.3106/041.038.0106>
169. Wang L, Lin A, Xiao Y, Jiang T, Feng J. Postnatal development in the big-footed bat, *Myotis macrodactylus*: wing morphology, echolocation calls, and flight. *Acta Theriol*. 2014; 59: 435–441. <https://doi.org/10.1007/s13364-014-0182-0>
170. Mayberry HW, Faure PA. Morphological, olfactory, and vocal development in big brown bats. *Biol Open* 2015; 4: 22–34. <https://doi.org/10.1242/bio.201410181>
171. Engler S, Rose A, Knörnschild M. Isolation call ontogeny in bat pup (*Glossophaga soricina*). *Behaviour* 2017; 154: 267–286. <https://doi.org/10.1163/1568539x-00003421>
172. Mehduzadeh R, Eghbali H, Sharifi M. Postnatal growth and vocalization development in the long-fingered bat, *Myotis capaccinii* (Chiroptera, Vespertilionidae). *Zool Stud*. 2018; 57: 37. <https://doi.org/10.6620/ZS.2018.57-37>
173. Carter RT, Adams RA. Ontogeny of the larynx and flight ability in Jamaican fruit bats (Phyllostomidae) with considerations for the evolution of echolocation. *Anat Rec*. 2014; 297: 1270–1277. <https://doi.org/10.1002/ar.22934>
174. Motomura N, Shimizu K, Shimizu M, Aoki-Komori S, Taniguchi K, Serizawa I, et al. A comparative study of isolation-induced ultrasonic vocalization in rodent pups. *Exp Anim*. 2002; 51: 187–190. <https://doi.org/10.1538/expanim.51.187> PMID: 12012730
175. Liu RC, Miller KD, Merzenich MM, Schreiner CE. Acoustic variability and distinguishability among mouse ultrasound vocalizations. *J Acoust Soc Am*. 2003; 114: 3412–3422. <https://doi.org/10.1121/1.1623787> PMID: 14714820
176. Noiro E, Pye D. Sound analysis of ultrasonic distress calls of mouse pups as a function of their age. *Anim Behav*. 1969; 17: 340–349. [https://doi.org/10.1016/0003-3472\(69\)90020-7](https://doi.org/10.1016/0003-3472(69)90020-7)
177. Lahvis GP, Alleva E, Scattoni ML. Translating mouse vocalizations: prosody and frequency modulation. *Genes Brain Behav*. 2011; 10: 4–16. <https://doi.org/10.1111/j.1601-183X.2010.00603.x> PMID: 20497235
178. Ey E, Torquet N, Le Sour AM, Leblond CS, Boeckers TM, Faure P, et al. The Autism ProSAP1/Shank2 mouse model displays quantitative and structural abnormalities in ultrasonic vocalisations. *Behav Brain Res* 2013; 256: 677–689. <https://doi.org/10.1016/j.bbr.2013.08.031> PMID: 23994547
179. Lai JKY, Sobala-Drozdowski M, Zhou L, Doering LC, Faure PA, Foster JA. Temporal and spectral differences in the ultrasonic vocalizations of fragile X knock out mice during postnatal development. *Behav Brain Res*. 2014; 259: 119–130. <https://doi.org/10.1016/j.bbr.2013.10.049> PMID: 24211451
180. Caruso A, Sabbioni M, Scattoni ML, Branchi I. Quantitative and qualitative features of neonatal vocalizations in mice. In: Brudzynski SM, editor. *Handbook of Ultrasonic Vocalization*. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 139–147. <https://doi.org/10.1016/B978-0-12-809600-0.00013-5>
181. Wiaderkiewicz J, Glowacka M, Grabowska M, Barski J-J. Ultrasonic vocalizations (USV) in the three standard laboratory mouse strains: developmental analysis. *Acta Neurobiol Exp*. 2013; 73: 557–563.
182. Johnson SA, Painter MS, Javurek AB, Murphy CR, Howald EC, Khan ZZ, et al. Characterization of vocalizations emitted in isolation by California mouse (*Peromyscus californicus*) pups throughout the postnatal period. *J Comp Psychol*. 2017; 131: 30–39. <https://doi.org/10.1037/com0000057> PMID: 28182483
183. Mason MJ. Structure and function of the mammalian middle ear. I: Large middle ears in small desert mammals. *J Anat*. 2016; 228: 284–299. <https://doi.org/10.1111/joa.12313> PMID: 26104342

184. Dempster ER. Ultrasonic vocalizations in 10 taxa of Southern African Gerbilline rodents. In: Brudzynski SM, editor. Handbook of Ultrasonic Vocalization. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 207–216. <https://doi.org/10.1016/B978-0-12-809600-0.00020-2>
185. Roberts PD, Portfors CV. Responses to social vocalizations in the dorsal cochlear nucleus of mice. *Front Syst Neurosci*. 2015; 9: 172. <https://doi.org/10.3389/fnsys.2015.00172> PMID: 26733824
186. Portfors CV. Processing of ultrasonic vocalizations in the auditory midbrain of mice. In: Brudzynski SM, editor. Handbook of Ultrasonic Vocalization. V. 25. A window into the emotional brain. Elsevier, 2018. pp. 73–82. <https://doi.org/10.1016/B978-0-12-809600-0.00007-X>