



Comparison of ultrasonic isolation calls of pure-breeding and interspecies hybrid *Phodopus* dwarf hamster pups

Semen V. Piastolov^{a,1}, Ilya A. Volodin^{a,*,2}, Nina Yu. Vasilieva^{b,3}, Anastasia M. Khrushchova^{b,4}, Olga N. Shekarova^{c,5}, Elena V. Volodina^{d,6}

^a Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Vorobievsky Gory, 1/12, Moscow 119234, Russia

^b Department of Comparative Ethology and Biocommunication, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky prospect, 33, Moscow 119071, Russia

^c Department of Population Ecology, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky prospect, 33, Moscow 119071, Russia

^d Department of Behaviour and Behavioural Ecology, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky prospect, 33, Moscow 119071, Russia

ARTICLE INFO

Keywords:

Cross-species hybrids
Hybrid vocalization
Phodopus campbelli
Phodopus sungorus
Pups
Ultrasonic vocalization

ABSTRACT

In mammalian cross-species hybrids, parameters of voice calls, produced by vocal fold vibrations, are intermediate between parental species. Inheritance of ultrasonic calls, produced by whistle mechanism, is unstudied for hybrids. We examined 4000 pup ultrasonic isolation-induced calls for peak power of call fundamental frequency and for call duration in 4–8-day-old captive hamsters of four Study Groups: pure *Phodopus sungorus*; pure *P. campbelli* of two populations (Mongolian and Kosh-Agach) and hybrids between male *P. sungorus* and female *P. campbelli* (Kosh-Agach). All Study Groups produced two categories of ultrasonic calls: Low-Frequency centered around 41 kHz and High-Frequency centered around 60 kHz, but in different percentages. Between populations, only Low-Frequency calls were shorter and higher-frequency in Mongolian *P. campbelli*. Between species, only High-Frequency calls were shorter and higher-frequency in *P. sungorus*. In hybrids, Low-Frequency calls were shorter and lower-frequency than in either parental species, whereas High-Frequency calls were longer and lower-frequency in hybrids than in pure *P. sungorus* but similar with another parental species. We discuss that interspecific hybridization may give rise to offspring with new properties of ultrasonic calls.

1. Introduction

In mammals, important drivers of evolution of acoustic communication are genetic drift (Campbell et al., 2010; Matrosova et al., 2016, 2019) and interspecies hybridization (Shmyrov et al., 2012; Kitchen et al., 2019). All previous studies exploring the inheritance of acoustic properties in mammalian interspecific hybrids have been conducted on the voice-based calls produced by phonation-based mechanism, involving the synchronous vibrations of the vocal folds in the larynx (Fitch and Hauser, 2002; Finck and Lejeune, 2010). For ultrasonic vocalizations (USVs) produced by aerodynamic whistle mechanism, based

on vorticities of airflow in the vocal tract (Mahrt et al., 2016; Riede et al., 2017; Azola et al., 2018; Håkansson et al., 2022a), population-level variation is poorly studied (Musolf et al., 2015).

The voice-based calls of mammalian hybrids are intermediate in the acoustic properties between parental species (Nikol'skiy et al., 1984; Long et al., 1998; Page et al., 2001; Shmyrov et al., 2012; Wyman et al., 2016; Kitchen et al., 2019; Rutovskaya, 2019). The intermediate pattern of inheritance for voice-based calls was described for hybrids between closely related parental species with strongly acoustically different vocalizations: between red deer *Cervus elaphus* and sika deer *C. nippon* (Long et al., 1998; Wyman et al., 2016), between little (*Spermophilus*

* Corresponding author.

E-mail address: volodinsvoc@gmail.com (I.A. Volodin).

¹ ORCID ID: 0000-0001-7482-7703

² ORCID ID: 0000-0001-6278-0354

³ ORCID ID: 0000-0001-7557-6918

⁴ ORCID ID: 0000-0002-3956-8395

⁵ ORCID ID: 0000-0003-1760-0320

⁶ ORCID ID: 0000-0001-9755-4576

pygmaeus) and speckled (*S. suslicus*) ground squirrels (Nikol'skiy et al., 1984), between russet (*S. major*) and yellow (*S. fulvus*) ground squirrels (Shmyrov et al., 2012) and between Tien Shan (*Myodes centralis*) and bank (*M. glareolus*) voles (Rutovskaya, 2019). Intermediate acoustic structure of voice calls was also reported for hybrids between Antarctic (*Arctocephalus gazella*) and subantarctic (*A. tropicalis*) fur seals (Page et al., 2001) and for hybrids between mantled (*Alouatta palliata*) and black (*A. pigra*) howler monkeys (Kitchen et al., 2019). Inheritance of USVs by cross-species hybrids is unknown and has yet to be studied for mammals.

Both whistle and voice-based calls can be sonic or ultrasonic, i.e., produced in a human-audible range of frequencies (below 20 kHz) or in the ultrasonic range (above 20 kHz) (Fernández-Vargas et al., 2022). In large mammals, the whistle calls are audible, as in cervids (Reby et al., 2016; Volodin et al., 2016), bovids (Volodin et al., 2017), camelids (Volodin et al., 2022), canids (Frey et al., 2016; Sibiryakova et al., 2021), Asian elephants *Elephas maximus* (Beeck et al., 2021) and humans (Azola et al., 2018). In small mammals like bats, calls produced by phonation mechanism may be nevertheless ultrasonic (Suthers and Fattu, 1973, 1982; Håkansson et al., 2022b). Voice and whistle-based mechanisms of call production may coexist within species (Frey et al., 2016; Beeck et al., 2021; Sibiryakova et al., 2021; Fernández-Vargas et al., 2022; Riede et al., 2022).

For rodents, experiments in light gases showed that USVs of all studied species were produced by whistle mechanism (Riede, 2011; Riede and Pasch, 2020; Fernández-Vargas et al., 2022; Riede et al., 2022). For mice and rats, the whistle mechanism of USV production was confirmed experimentally, by combining in-vitro larynx physiology and individual-based 3D airway reconstructions with fluid dynamics simulations (Håkansson et al., 2022a). For cricetids, the whistle mechanism for USVs was confirmed by experiments in light gases for three species of grasshopper mice *Onychomys* (Pasch et al., 2017), for northern pygmy mice *Baiomys taylori* (Riede and Pasch, 2020) and for three species of *Peromyscus* deer mice (Riede et al., 2022). Switching between voice and whistle mechanisms has been documented for *Onychomys* and *Peromyscus* species of cricetid rodents (Pasch et al., 2017; Riede et al., 2022).

The ontogenetic development of USVs in rodents does not require the auditory feedback, which is necessary for production vocal learning in mammals (Janik and Slater, 2000; Janik and Knörnschild, 2021; Lattenkamp et al., 2021). Rearing genetically deaf and normally hearing pup laboratory mice by deaf mothers indicates the lack of differences in the ontogenetic development of pups in terms of the number, structure and usage of USVs (Hammerschmidt et al., 2012). Consistently, when these pups became mature, no difference was found between the ultrasonic courtship songs of deaf and normally hearing male mice (Hammerschmidt et al., 2012). Experimental deafening of laboratory pup mice at 2 days (d) of age did not affect subsequent adult male courtship song compared to normally hearing males in terms of the temporal structure of vocal sequences, call type, syllable structure and the acoustics (Mahrt et al., 2013).

Hybrids of closely-related species of dwarf hamsters (*Phodopus campbelli* and *P. sungorus*) may serve as a convenient model for studying inheritance of USVs. Interspecific hybrids can be obtained experimentally in captivity (Sokolov, Vasil'eva, 1993a; Brekke and Good, 2014). Female hybrids of *P. campbelli* and *P. sungorus* are fertile, but male hybrids are sterile because of problems with meiosis and underdevelopment of their reproductive system (Safronova et al., 1992, 1999; Sokolov, Vasil'eva, 1993a; Safronova, Vasil'eva, 1996; Ishishita et al., 2015; Bikchurina et al., 2018). Hybrids between male *P. sungorus* and female *P. campbelli* can be obtained easier than hybrids of male *P. campbelli* and female *P. sungorus*. In the first combination, hybrid newborns are comparable in body size with pups of *P. campbelli*, whereas hybrid newborns of male *P. campbelli* and female *P. sungorus* are much larger, resulting in problems during parturitions (Sokolov, Vasil'eva, 1993a; Brekke and Good, 2014; Ishishita and Matsuda, 2016).

In the wild, these species are allopatric: *P. campbelli* inhabits arid

steppes from North-East China (Inner Mongolia) throughout Mongolia to Tuva and Altai; *P. sungorus* inhabits the steppes of Central and East Kazakhstan to the North from Lake Balkhash and to West Siberia in the southern extent of its range (Ross, 1995, 1998). Males of both species provide parental care to pups (Wynne-Edwards, 1995, 1998), however, male presence only enhances litter survival in *P. campbelli* (Wynne-Edwards, 1987; Wynne-Edwards and Lisk, 1989) under conditions of water scarcity (Scribner and Wynne-Edwards, 1994), which is attributable to pup consumption of glandular secretions produced by sires (Vasilieva and Khruschova, 2010). In both species, pups grow fast: 4-d pups are still naked, but 8-d pups have some fur, can stand on paws and are ambulatory, with eyes opening between 10 and 11 d of age (Ross, 1995, 1998). In the wild, 18-d pups leave their natal burrow and become independent, and their mother deliver the next litters (Sokolov, Vasil'eva, 1993b).

Both pup and adult *Phodopus* dwarf hamsters produce USVs along with audible voice calls (Pierce et al., 1989; Hashimoto et al., 2001; Keesom et al., 2015; Rendon et al., 2015). Adult *P. sungorus* produce four types of USVs (classified based on presence of frequency jumps and harmonics) during same-sex encounters (Keesom et al., 2015). The fundamental frequency (f₀) of USVs ranges from 33.6 to 91.0 kHz, with average duration of 92.9 ± 5.8 ms, and call characteristics do not differ between sexes (Keesom et al., 2015). Adult *P. campbelli* of both sexes produce USVs centered around 71 kHz during sexual behaviour (Pierce et al., 1989).

For pup USVs, there is only one study, for 3-d pup *P. sungorus*, emitting USVs and broadband audible calls during 5-min isolation tests at 15 °C (Hashimoto et al., 2001). These USVs had chevron and wave-like contours, the maximum f₀ of 45–50 kHz, the peak frequency of 42–45 kHz and duration of 130–150 ms (Hashimoto et al., 2001).

For *Phodopus* hamsters, there is no direct experimental evidence that adult or pup USVs are the product of whistle mechanism. However, indirect data suggest that *Phodopus* species use whistle mechanism for producing their USVs, similar to cricetids tested in experiments employing light gases (Pasch et al., 2017; Riede and Pasch, 2020; Riede et al., 2022). In addition to USVs, *Phodopus* species produce low-frequency audible calls by phonation-based mechanism (Hashimoto et al., 2001; Keesom et al., 2015). Furthermore, the minimum f₀ of USVs in *Phodopus* species is above 30 kHz (Pierce et al., 1989; Hashimoto et al., 2001; Keesom et al., 2015), whereas the maximum confirmed f₀ of the phonation-based calls in cricetids is 16–17 kHz, as in adult grasshopper mice (Pasch et al., 2017) and 19–22 kHz in pup deer mice (Riede et al., 2022). These frequencies fit to the upper limit above the expected for the very short (0.6–0.7 mm) vocal fold of small rodents (Titze et al., 2016; Riede et al., 2022).

The aim of this study was to compare the acoustic traits of pup ultrasonic isolation calls among two parental species of dwarf hamsters (*P. campbelli* and *P. sungorus*) and their hybrids. In addition, we estimate within-species acoustic variation, by comparing pup isolation-induced USVs between two populations of *P. campbelli*.

2. Material and methods

2.1. Study site, subjects and dates

Pup isolation experiments were carried out in the Department of Comparative Ethology and Biocommunication of Severtsov Institute of Ecology and Evolution (Moscow, Russia), from December 2020 to September 2021. Subjects were balanced samples of captive-born 4-, 5-, 6-, 7-, and 8-d pup hamsters, belonging to four Study Groups: *Phodopus campbelli* (Mongolian) pups, *P. campbelli* (Kosh-Agach) pups, *P. sungorus* pups and F1 interspecific hybrid pups of male *P. sungorus* and female *P. campbelli* (Kosh-Agach). The *P. campbelli* (Mongolian) Study Group (*P. campM*) belonged to a maintained laboratory population started in 1985 from animals captured in North-East Mongolia. The *P. campbelli* Kosh-Agach Study Group (*P. campK*) belonged to a maintained laboratory

population started in 1988 from animals captured in Kosh-Agach area of the Altai Republic, Russia. The *P. sungorus* Study Group (*P. sung*) belonged to a maintained laboratory population started in 1984 from animals captured in Karasuk area of Novosibirsk region, Russia. The F1 Hybrids of male *P. sung* and female *P. campK* were obtained experimentally. Each parental pair (pure-breeding or consisting of two species) was permanent; pure species pairs were not used to generate hybrid pups.

Parental pairs with litters were kept in plastic cages of 23 x 23 x 30 height cm on a 14 L:10D photoperiod (light onset 5:00) and temperature 22 ± 2 °C with 8–10 cm lay of sawdust bedding, one 10×10×10 cm shelter, 2–3 cardboard pipes of various diameters (4–5 cm) and lengths (10–15 cm) and toilet paper as nest material. Animals received laboratory rodent chow (22% protein), oats, vegetables and water ad libitum. Parental pairs were regularly checked for presence of litters. Parturition was considered as day zero of pup life.

2.2. Experimental design

Call-eliciting tests for recording pup isolation-induced USVs from the four Study Groups were conducted in a room without windows, where other animals were not present. This allowed recording USVs reliably assigned to the focal pup. Experiments were conducted during the daylight phase of the daily photoperiod at room temperature 20–25 °C; all electrical equipment with the exception of a single ceiling fluorescent lamp was turned off to decrease the level of background ultrasonic noise. Recording equipment worked in the same room, but on accusers, to avoid potential induced noise from the electric circuit.

Each pup was tested only in one single test trial, because uniform serial tests conducted for a few consecutive days with the same animal may result in habituation to the experimental procedure. Furthermore, consecutive pup isolation experiments (even just regular weighing) may dramatically slow the rate of pup growth, as, e.g., in yellow steppe lemming *Eolagurus luteus* (Yurlova et al., 2020).

Before the test trial, the focal pup was removed from the parental cage and transferred in a clean translucent plastic cup to the experimental area. The room with home cages of animals and the experimental room were on the same floor, and time from taking the focal pup to the start of the experiment did not exceed 60 s. Each test trial started when a focal pup was placed in the experimental plastic container 19 × 13×7 height cm. Each test trial lasted 4 min and included two stages, each 2 min: Isolation Stage (the focal pup isolated in the container) and Touch Stage (the isolated pup was prodded manually with a cotton bud roughly twice per second) (following Zaytseva et al., 2019; Klenova et al., 2021; Dymkaya et al., 2022).

After the end of test trial, the focal pup was removed from the experimental container by hand and sexed based on the size and position of the urogenital papilla. The focal pup was then measured with electronic calipers (Kraf Tool Co., Lenexa, Kansas, US) accurate to 0.01 mm. In each pup, we measured body length (from the tip of the muzzle to anus) and head length (from tip of muzzle to occiput). This cycle of two measurements was repeated thrice and the average value was calculated and used in statistical analysis. Subsequent to deriving these measurements, the focal pup was weighed on an electronic scale G&G TS-100 (G&G GmbH, Neuss, Germany) accurate to 0.01 g. Weighing occurred in the same plastic cup, in which the pup was transferred to the experimental room. Morphometric measurements and weight data were used for estimating potential pup body size differences among the four Study Groups.

Until completing all tests with a focal litter, all non-focal pup littermates were temporally placed outside of the experimental room in a cartoon box 7×7×9 (height) cm standing on a chair near the heater, providing the temperature in the box area of 30–33 °C, to avoid animal cooling and discomfort-related vocalizing. Upon completing of all test trials with the focal litter, all tested pups were simultaneously returned to their home cage. All tested pups were accepted by both parents in all cases, with no refusals or pup deaths detected as a result of our test trials.

Before each test trial, the plastic transport cup and the experimental container were cleaned with water, dried with rubbing by clean cotton napkin and then rubbed with cotton washed with 40% ethanol, because a higher concentration of ethanol may affect rodent behavior (Lopez-Salesansky et al., 2021).

2.3. Acoustic recording

During each test trial, we continuously recorded the focal pup USVs (384 kHz sampling frequency, 16-bit resolution) using a Pettersson D1000X recorder with built-in microphone (Pettersson Elektronik AB, Uppsala, Sweden). The microphone was mounted at 35 cm over the table in the focal pup area, providing a high signal-to-noise ratio during recording. Recording of each test trial was stored as a separate wav-file. In parallel with recording, we viewed real-time spectrograms of pup USVs an Echo Meter Touch 2 PRO (Wildlife Acoustics, Inc., Maynard, MA USA) attached to a smartphone.

2.4. Animal samples

Our acoustic analysis included data from 80 test trials where individual pups were highly vocal in the ultrasonic range of frequencies, one test trial per pup, 20 trials in total per Study Group. The 80 test trials were selected from the total set of 288 trials with 288 2–10-d pups: 63 trials with *P. campM*; 65 *P. campK*; 83 trials with *P. sung* and 77 trials with Hybrids. Acoustic analyses were limited to USVs derived from pups from 4 to 8 d of age, because they produced pup isolation calls primarily in the ultrasonic range of frequencies. Pups of 2–3-d old produced many audible calls but few USVs and pups beyond 8 d old were mostly silent.

Twenty *P. campM* subject pups originated from 17 litters delivered by 15 parental pairs; 20 *P. campK* pups originated from 18 litters delivered by 14 parental pairs; 20 *P. sung* pups originated from 17 litters delivered by 15 pairs and 20 Hybrid pups originated from 18 litters delivered by 14 parental pairs. For each Study Group we selected 20 pups, including one pup per litter (rarely two), 4 pups of each age (4, 5, 6, 7, 8 d) with balanced sex ratios 1:1. Thus, our analyses included 80 pups, 16 pups of each age (4, 5, 6, 7, 8 d).

2.5. Call samples

For each pup (80 pups in total, 20 pups per Study Group), we included in acoustic analyses the first 50 USVs from the start of each pup test trial, 1000 USVs per Study Group, 4000 USVs in total. Most (3900 of 4000) USVs were selected from the Isolation Stage of test trials, and remaining 100 (2.5%) USVs were taken from the Touch Stage of test trials in cases when the number of USVs from the first stage was less than 50. These 100 USVs from the Touch Stage belonged to four of the sixteen 8-d pups, one 8-d pup per Study Group: one *P. campM* pup (45 USVs), one *P. campK* pup (20 USVs), one *P. sung* pup (8 USVs) and one Hybrid pup (27 USVs). The 8-d pups vocalized less actively compared to other ages, probably because of acquiring own thermoregulation.

2.6. Acoustic analysis

Spectrographic analysis of pup USVs was conducted with Avisoft SASLab Pro v. 5.3.00 (Avisoft Bioacoustics, Berlin, Germany). Using the semi-automatic option of Avisoft, we measured call duration and peak power of call fundamental frequency (peakf0) (sampling rate 384 kHz, Fast Fourier Transform FFT 1024, Hamming window, frame 50% and overlap 87.5%, providing time resolution 0.33 ms and frequency resolution 375 Hz) (Fig. 1). Based on visual inspection of spectrograms we found that in most (3899 of 4000) USVs, fpeak was located on call fundamental frequency band. In the remaining 101 USVs, where fpeak was either located on a harmonic of fundamental frequency (98 USVs) or on a subharmonic of fundamental frequency (3 USVs), we measured the peak frequency repeatedly after filtering out the energetically expressed

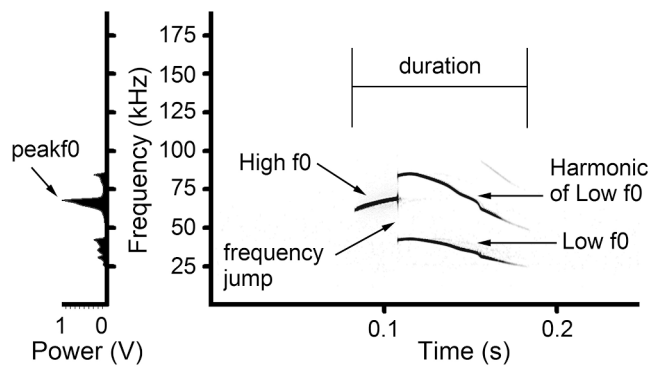


Fig. 1. Measured acoustic parameters in the ultrasonic call (USV) of 6-days old *Phodopus* hamster pup shown on spectrogram (right) and power spectrum (left). Example call contains frequency jump down. Designations: peakf0 – the peak power of call fundamental frequency; duration – call duration; High f0 – High-Frequency component; Low f0 – Low-Frequency component; Harmonic of Low f0 – harmonic of Low-Frequency component.

frequency bands, in order to shift the value of the peak frequency to call fundamental frequency band. Thus, in each of the 4000 USVs we measured the peak power of call fundamental frequency. To minimize error in measuring the peak power of call fundamental frequency, we automatically filtered out the lower 10 kHz in the spectrogram window.

Some USVs were broken with frequency jump(s) (Fig. 1). Presence of the frequency jump was identified when the jump of fundamental frequency was 10 kHz or more (Yurlova et al., 2020; Kozhevnikova et al., 2021) (Fig. 1). In each USV, we made only one measurement of peakf0 per call, independent of the number of notes in calls broken with frequency jump(s). In addition to frequency jumps, we examined each USV for the presence of three other kinds of nonlinear phenomena: subharmonics, biphonations and deterministic chaos (Yurlova et al., 2020; Klenova et al., 2021; Kozhevnikova et al., 2021; Riede et al., 2022).

2.7. Statistics

Statistical analyses were carried out with STATISTICA, v. 8.0 (StatSoft, Inc., Tulsa, OK, USA). If not indicated otherwise, means are given as mean \pm SD, all tests were two-tailed, and differences were considered significant where $p < 0.05$. To estimate the effect of Study Group on the acoustic parameters of USVs and to compare parameters of Low-Frequency USVs (LF USVs) and High-Frequency USVs (HF USVs), we used General Linear Mixed Model (GLMM) with Tukey post hoc, with Study Group and Call Category (LF USVs or HF USVs) included as fixed factors and animal individual identity (ID) as random factor. We added animal ID in GLMM, because we included in analysis 50 USVs per individual. For estimating the effect of Study Group and pup Age on peakf0 of USVs, we used GLMM with Tukey post hoc, with Study Group and pup Age included as fixed factors and animal ID as random factor. We combined the measurements of body length, head length and body weight to form an integrated body size index and, using Principal Component Analysis (PCA), we reduced the number of morphometric parameters and took the first axis of PCA as a proxy of body size. We used Fisher's exact test to compare percentages. For estimating correlations between body size and the acoustics of USVs, we used Pearson correlation test.

2.8. Ethical note

All procedures adhered to the 'Guidelines for the treatment of animals in behavioural research and teaching' (Anim. Behav., 2020, 159, I-XI) and the legal requirements of Russia pertaining to the protection of animal welfare. The experimental procedure was approved by the Committee of Bioethics of Lomonosov Moscow State University

(2011–36) and the Commission of Bioethics of Severtsov Institute of Ecology and Evolution RAS (2018–23).

3. Results

3.1. USV categories

Distribution of USVs peakf0 values was two-humped, indicating the presence of two categories, the Low-Frequency USVs (LF USVs) and the High-Frequency USVs (HF USVs) (Fig. 2). The peakf0 values of LF USVs were centered around 41 kHz and peakf0 values of HF USVs were centered around 60 kHz (Fig. 2).

Within individuals, the ranges of peakf0 did not overlap between LF USVs and HF USVs, displaying a hiatus. However, across the total sample of 4000 USVs from 80 individual pups, we observed the overlapping zone with margins from 44 kHz to 52 kHz (Fig. 2). The conditional demarcation line at about 49 kHz between LF USV and HF USV peakf0s was calculated as the crossing point of two normal distributions, created based on peakf0s of LF USVs and HF USVs.

In total for the four Study Groups, we found 1591 LF USVs and 2409 HF USVs (Fig. 3). Some ($n = 814$) LF USVs (without frequency jumps) contained only a LF component, and some ($n = 1947$) HF USVs (without frequency jumps) contained only a HF component. USVs containing both LF and HF components (i.e., had frequency jump), were classified to LF USVs or to HF USVs. If peakf0 fell on LF component, this call was assigned to LF USVs, if peakf0 fell on HF component, this call was assigned to HF USVs (Fig. 3). Thus, 777 USVs with both LF and HF components were assigned to LF USVs category, while 462 USVs with both LF and HF components were assigned to HF USVs category (Fig. 3).

3.2. Percentages of USV categories by study groups

Between populations of *P. campbelli* (*P. campM* and *P. campK*), USVs with both LF and HF components were more numerous in *P. campK* (Fisher's exact test, $p < 0.001$); USVs with LF component-only were equally common in *P. campM* and *P. campK* ($p = 0.99$), and USVs with HF component-only were more common in *P. campM* ($p < 0.001$) (Fig. 4). Between species (*P. camp* of either population and *P. sung*) USVs with LF component-only were more abundant in *P. camp* than in *P. sung* ($p < 0.001$); USVs with HF component-only were more abundant in *P. sung* than in *P. camp* ($p < 0.001$), and USVs with both LF and HF components were more abundant in *P. sung* than in *P. campK* ($p < 0.001$), but not in *P. campM* (Fig. 4). In Hybrids, USVs with both components were more abundant than in either parental species ($p = 0.023$ with *P. campK*; $p < 0.001$ with *P. sung*), USVs with LF component-only were less common than in *P. campK* ($p < 0.001$) and USVs with HF component-only were less common than in *P. sung* ($p < 0.001$) (Fig. 4).

In addition to frequency jumps (USVs with both LF and HF components) we also found two other kinds of nonlinear phenomena: subharmonics and biphonations. Subharmonics were more numerous in *P. campM* (98 of 1000 USVs) and in *P. campK* (71 of 1000 USVs) than in *P. sung* (42 of 1000 USVs) or Hybrids (32 of 1000 USVs) (Fisher's exact test, $p < 0.01$ for all comparisons). Biphonations were less common and were only found in 6 USVs of *P. campM*, 8 USVs of *P. campK*, 2 USVs of *P. sung* and in none of the USVs of Hybrids. Deterministic chaos was not found in any of the 4000 USVs.

3.3. Acoustic variables

The LF USVs (81.7 ± 35.9 ms) were longer than HF USVs (68.0 ± 31.4 ms) and lower in peakf0 (41.4 ± 5.53 kHz) than HF USVs (59.8 ± 6.96 kHz) (Table 1). Study Group did not affect call duration, but significantly affected peakf0 (Table 1). Significant interactions of factors Study Group and Call Category (LF USVs or HF USVs) on the acoustic parameters were detected (Table 1, Fig. 5).

The LF USVs differed between *P. campM* and *P. campK* populations in

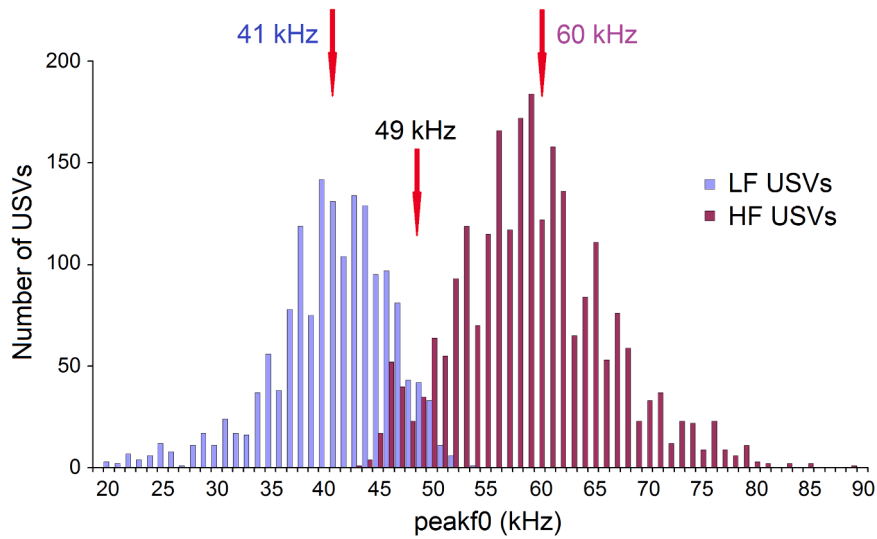


Fig. 2. Distribution of peakf0 values for Low-Frequency (LF USVs) and the High-Frequency (HF USVs) ultrasonic call categories. Designations: peakf0 – the peak frequency of call fundamental frequency. $n = 4000$ USVs from 80 individual pups of four Study Groups.

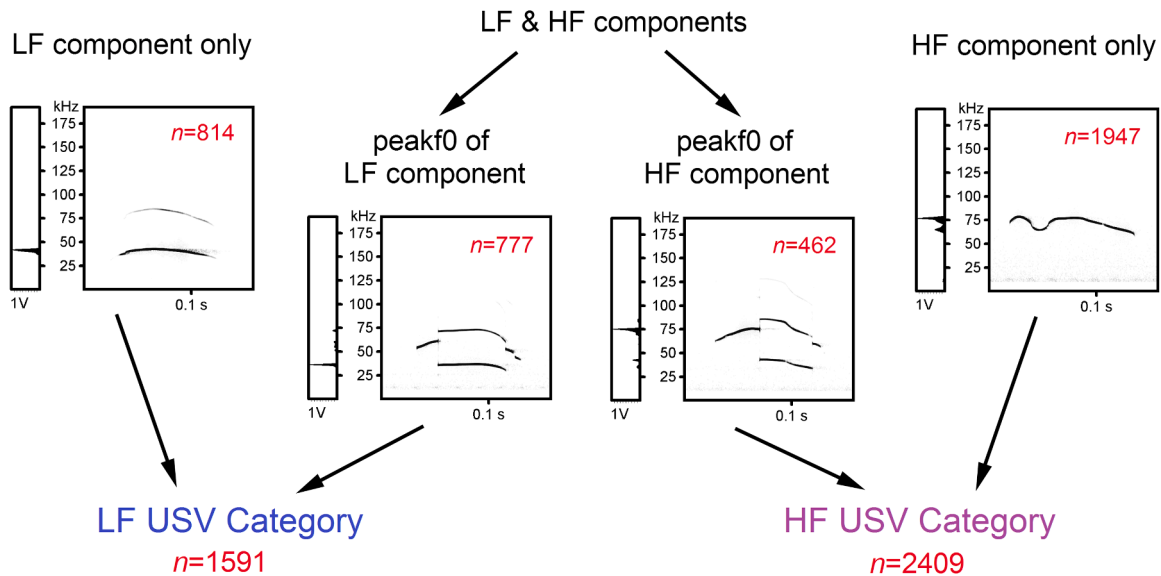


Fig. 3. Classifying pup ultrasonic isolation calls to Low-Frequency (LF USVs) and High-Frequency (HF USVs) Categories. For each of the four example calls, a narrow box on the left displays peakf0 value on the power spectrum of call shown on the spectrogram on the right. Calls with peakf0 falling on LF component were assigned to LF USVs, calls with peakf0 falling on HF component were assigned to HF USVs. Designations: peakf0 – the peak frequency of call fundamental frequency. $n = 4000$ USVs from 80 individual pups of four Study Groups.

duration and peakf0: LF USVs were shorter in duration and higher in peakf0 in *P.campM* than in *P.campK* (Fig. 5). Duration of LF USVs was higher in *P.sung* than in *P.campM* but did not differ from *P.campK*. The peakf0 of LF USVs was higher in *P.sung* than in *P.campK* but did not differ from *P.campM*. The LF USVs of Hybrids were shorter in duration and lower in peakf0 than in either parental species (Fig. 5).

The HF USVs did not differ in duration or peakf0 between *P.campM* and *P.campK* populations (Fig. 5). In *P.sung* pups, HF USVs were shorter and higher in peakf0 than in either *P. campbelli* population. In Hybrids, HF USVs did not differ in duration or peakf0 from *P.campK* but were longer and lower in peakf0 than in *P.sung* (Fig. 5).

Example call spectrograms illustrating LF USVs and HF USVs of pups from each Study Group were presented in Fig. 6. Example USVs were selected based on their close-to-average parameters values for the Study Groups (Table 1).

3.4. Age and body size effects on call frequency

For LF USVs, Study Group and pup Age affected peakf0 (Study Group: $F_{3,1515} = 88.57; p < 0.001$; Age: $F_{4,1515} = 26.01; p < 0.001$). For peakf0, a significant interaction between factors Study Group and Age was detected ($F_{12,1515} = 9.06; p < 0.001$). Across the four Study Groups, peakf0 of LF USVs decreased from the 4th to the 6th day of age and increased from the 6th to 8th day of age (Fig. 7). This trend was primarily based on changes in values of peakf0 in *P.campK* and Hybrid pups, whereas in *P.campM* and *P.sung* pups, peakf0 values changed only slightly with age (Fig. 7).

For HF USVs, Study Group and pup Age affected peakf0 (Study Group: $F_{3,2335} = 29.14; p < 0.001$; Age: $F_{4,2335} = 48.68; p < 0.001$). For peakf0, a significant interaction between factors Study Group and Age was detected ($F_{12,2335} = 12.32; p < 0.001$). Across the four Study Groups, peakf0 of HF USVs displayed a steady decrease from the 4th to

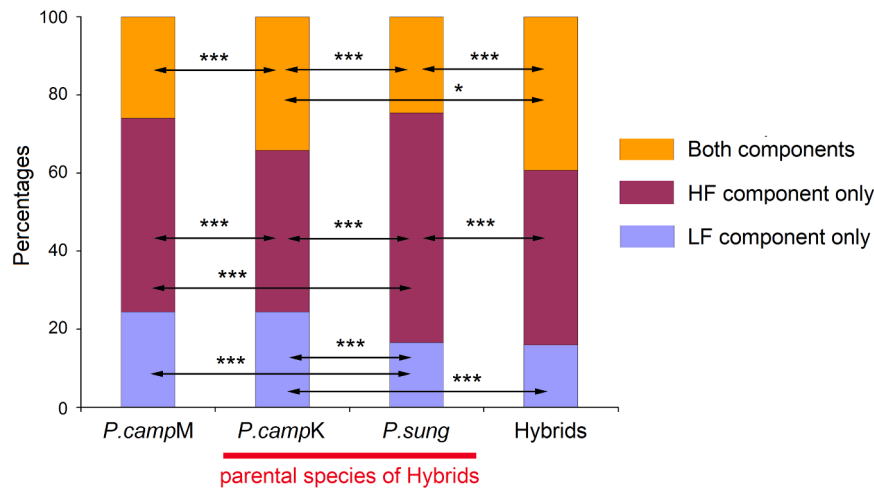


Fig. 4. Percentage of ultrasonic calls (USVs) with Low-Frequency (LF) component only, with High-Frequency (HF) component only and with both components, in pup hamsters of four Study Groups. Designations: *P.campM* – *P. campbelli* (Mongolian) pups; *P.campK* – *P. campbelli* (Kosh-Agach) pups; *P.sung* – *P. sungorus* pups; Hybrids – hybrids between male *P.sung* and female *P.campK*. *** – $p < 0.001$; * – $p < 0.05$ (Fisher’s exact test).

Table 1

Values (mean ± SD) for duration and peakf0 of 4–8-days-old hamster pup ultrasonic calls (USVs) and GLMM results for the effects of factors Study Group, Call Category (LF USVs or HF USVs) and their interaction effect on USV duration and peakf0. Designations: *P.campM* – *P. campbelli* (Mongolian) pups; *P.campK* – *P. campbelli* (Kosh-Agach) pups; *P.sung* – *P. sungorus* pups; Hybrids – hybrids between male *P.sung* and female *P.campK*; LF USVs – low-frequency USVs, HF USVs – high-frequency USVs, Duration – call duration; peakf0 – the peak frequency of call fundamental frequency; n – number of calls.

Study Group	<i>P.campM</i>		<i>P.campK</i>		<i>P.sung</i>		Hybrids	
Call Category	LF USVs, $n = 431$	HF USVs, $n = 569$	LF USVs, $n = 517$	HF USVs, $n = 483$	LF USVs, $n = 331$	HF USVs, $n = 669$	LF USVs, $n = 312$	HF USVs, $n = 688$
Duration (ms)	68.2 ± 36.4	70.3 ± 28.8	90.5 ± 28.0	69.8 ± 29.4	87.7 ± 41.3	60.6 ± 34.1	79.3 ± 35.2	72.1 ± 31.1
	Study Group: $F_{3,3916} = 1.49$; $p = 0.22$; Call Category: $F_{1,3916} = 32.93$; $p < 0.001$; Study Group & Call Category: $F_{3,3916} = 24.17$; $p < 0.001$							
Peakf0 (kHz)	43.6 ± 4.9	58.6 ± 5.7	40.6 ± 4.4	59.2 ± 5.9	42.6 ± 4.6	62.4 ± 6.5	38.4 ± 7.0	58.7 ± 8.2
	Study Group: $F_{3,3916} = 3.87$; $p = 0.012$; Call Category: $F_{1,3916} = 7837.11$; $p < 0.001$; Study Group & Call Category: $F_{3,3916} = 34.43$; $p < 0.001$							

the 8th day of life (Fig. 7). This trend appears to be attributable to changes in peakf0 in *P.campK*, *P.sung* and Hybrid pups, whereas in *P.campM* pups, the age-related changes in peak f0 were not evident (Fig. 7).

With Principal Component Analysis (PCA), we reduced the number of morphometric traits and took the first PCA axis, which accounted for 91.83% of the variation, as a proxy index of pup body size. Average values of peakf0 for LF USVs of individual pups were not correlated with pup body size index in any Study Group (Table 2). However, peakf0 of HF USVs were negatively correlated with pup body size index in *P.sung* and Hybrids (Table 2).

4. Discussion

4.1. Ultrasonic calls of hybrids

Our study showed that hybrids had calls unlike either of the parents. This was unexpected because vocalizations of rodents are genetically determined (Hammerschmidt et al., 2012; Mahrt et al., 2013). We investigated acoustic parameters of pup USVs of dwarf hamster interspecies hybrids and parental species and found that hybrid offspring produced USVs with new properties, out of range of frequencies of both parental species. This study on inheritance of USV acoustics and call type percentages by dwarf hamster pups (*Phodopus campbelli* and *P. sungorus*) is the first research on whistle calls of mammalian interspecific hybrids. As *P. campbelli* and *P. sungorus* are allopatric and do not hybridize in nature, our analyses, made on captive populations cannot be directly tested in the field on wild animals. However, they present a

model for mechanisms of inheritance of the whistle calls for future studies of USVs in interspecies hybrids of sympatric species in nature.

We found that in hamster hybrids, duration and peakf0 of HF USVs were closer to one of parental species, whereas for LF USVs, the values were lower in Hybrids than in either parental species. Consistently, in 2–12-d hybrid pups of four different laboratory strains of domestic mice, all fundamental frequency parameters of USVs were at the level of the lowest values of the parental strains (Hahn et al., 1997, 1998; Thornton et al., 2005). We can therefore propose that there are different patterns of inheritance of acoustic properties for the whistle versus voice calls in mammalian hybrids. Further research on mammals producing whistle calls is necessary to confirm or reject this hypothesis and for searching the background of such differences.

We found that hamster pup hybrids were intermediate between parental species in percentages of all different combinations of LF and HF call components. Consistent with our data, hybrids of two subspecies of domestic mice, *Mus musculus musculus* and *M. m. domesticus* were intermediate between their parental subspecies in percentages of different USV types in male courtship song (Musolf et al., 2015).

4.2. Differences of ultrasonic calls of between species and between populations within species

We found substantial interspecific differences in characteristics of USVs, expectable because these species, although closely related, are allopatric in nature (Ross, 1995, 1998). We compared percentages of different combinations of LF and HF call components and USV acoustics between *P. sungorus* and *P. campbelli* and between two populations

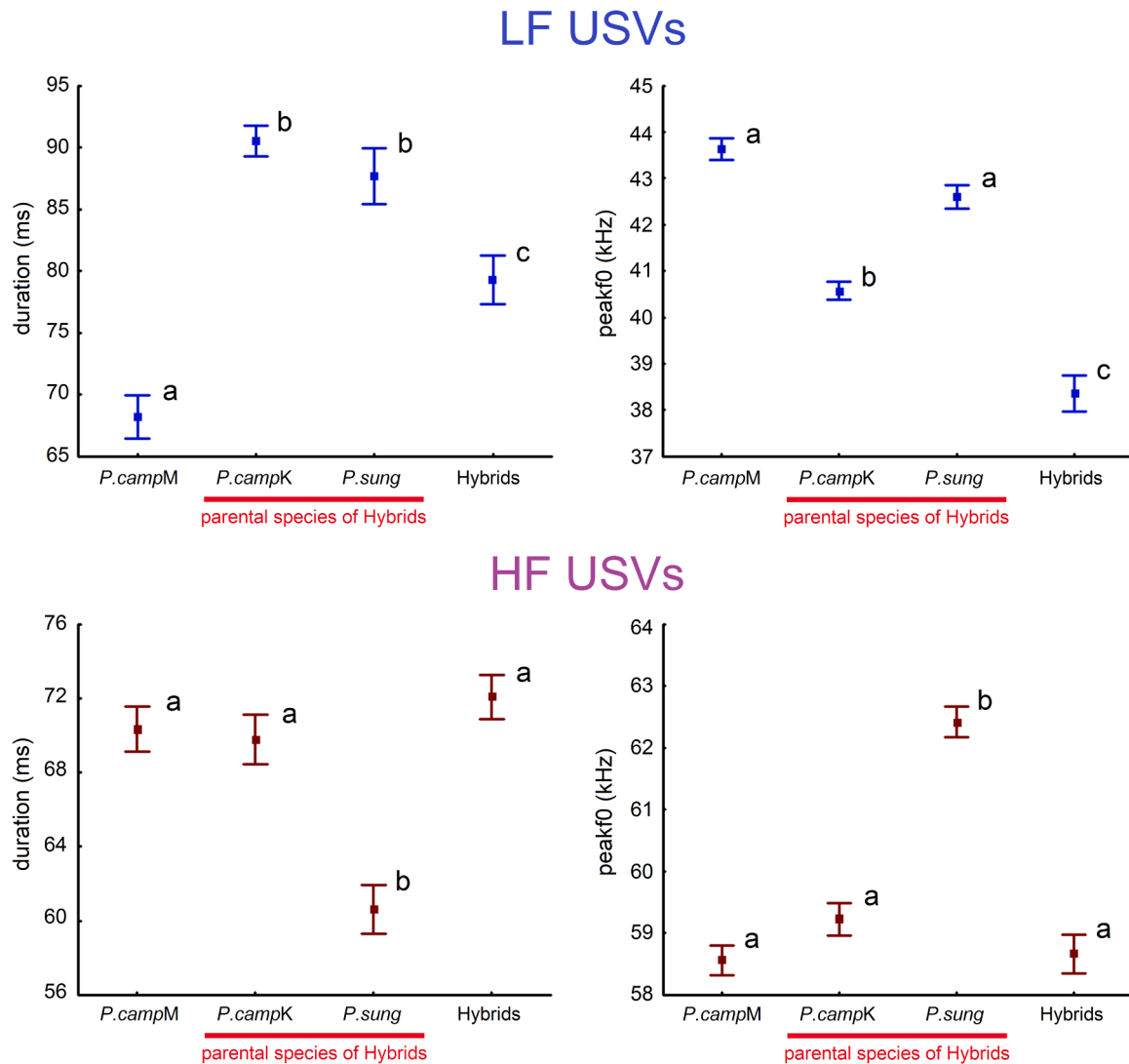


Fig. 5. Comparison of duration and peakf0 of Low-Frequency ultrasonic calls (LF USVs) and High-Frequency ultrasonic calls (HF USVs) among four Study Groups. Central points indicate means, whiskers indicate SE. Designations: peakf0 – the peak power of call fundamental frequency; *P.campM* – *P. campbelli* (Mongolian) pups; *P.campK* – *P. campbelli* (Kosh-Agach) pups; *P.sung* – *P. sungorus* pups; Hybrids – hybrids between male *P.sung* and female *P.campK*. The same superscripts indicate the lack of significant differences between the values ($p > 0.05$, Tukey post hoc).

within *P. campbelli*. Percentages of USVs with LF, HF or both components differed to a greater degree between species than between populations of *P. campbelli*, thus reflecting closer relationship between populations than between species. Unexpectedly, acoustic parameters of LF USVs differed between populations but not between species, whereas parameters of HF USVs differed between species but not between populations. Similar results were previously obtained in comparing USV percentages and acoustic characteristics between four populations, two subspecies and two species of the genus *Mus* (Musolf et al., 2015). In the study by Musolf et al. (2015), percentages of different types of adult male USV courtship songs could differ to a greater degree between populations within species than between subspecies within species. Between populations and subspecies, USVs primarily differed in terms of frequency and temporal parameters, whereas between species, differences in amplitude and frequency parameters were detected (Musolf et al., 2015). Further, even different strains of laboratory mice may be distinctive in their usage of different USV types (Kikusui et al., 2011) or in terms of the acoustic properties of matched call types of USVs (Arriaga et al., 2012; Klenova et al., 2021). Overall, our findings are consistent with those from previous studies suggesting that the percentages and acoustic characteristics of USVs in rodents are inherited genetically

(Kikusui et al., 2011; Hammerschmidt et al., 2012; Mahrt et al., 2013; Musolf et al., 2015).

4.3. USV parameters of hamster pups

The 42.6-kHz peak frequency of 4–8d *P. sungorus* LF USVs in this study coincides with the 42–45-kHz peak frequency of 3d *P. sungorus* pup isolation USVs (Hashimoto et al., 2001). However, call duration in our study (87.7 ms) was much shorter than in the previous study (130–150 ms) (Hashimoto et al., 2001), what could be due to different principles of selecting USVs for analysis. Limited numbers of animals and calls probably did not allow detecting HF USVs in *P. sungorus* pups in the study by Hashimoto with coauthors (2001). The peakf0 values of *P. sungorus* and *P. campbelli* pups in our study were similar with peak frequencies reported for pup isolation USVs in golden (*Mesocricetus auratus*) and Chinese (*Cricetulus griseus*) hamsters (Hashimoto et al., 2001; Schneider and Fritzsche, 2011), but were substantially higher than in California deer mice (*Peromyscus californicus*) pups (Riede et al., 2022).

The 71-kHz frequency of adult male *P. campbelli* USVs, emitted in the context of sexual behavior (Pierce et al., 1989) and the 59.8-kHz

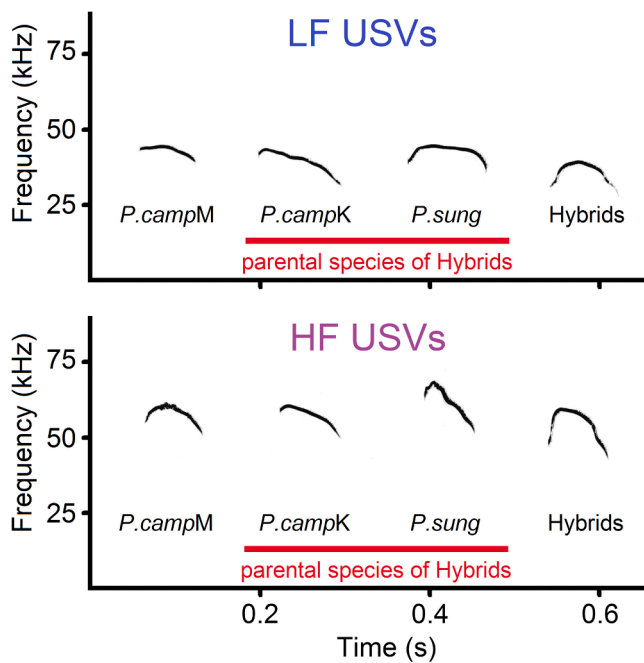


Fig. 6. Spectrogram illustrating Low-Frequency ultrasonic calls (LF USVs) and High-Frequency ultrasonic calls (HF USVs) of pups from four Study Groups. Example USVs were selected based on their close-to-average parameters values for the Study Groups: *P.campM* – *P. campbelli* (Mongolian) pups; *P.campK* – *P. campbelli* (Kosh-Agach) pups; *P.sung* – *P. sungorus* pups; Hybrids – hybrids between male *P.sung* and female *P.campK*.

frequency of adult male and female *P. sungorus* USVs associated with aggression (Keesom et al., 2015), are similar to peakf0 values of pup isolation HF USVs in our study. In rodents, the fundamental frequency of USVs may either increase from pups to adults, as in fat-tailed gerbils *Pachyromys duprasi* (Zaytseva et al., 2019), or decrease, as in domestic mice (Riede et al., 2020), yellow steppe lemmings (Yurlova et al., 2020) and Mongolian gerbils *Meriones unguiculatus* (Kozhevnikova et al., 2021; Volodin et al., 2023) or even remain practically unchanged, as in California deer mice (Johnson et al., 2017) and in Vinogradovi gerbils *Meriones vinogradovi* (Kozhevnikova et al., 2021; Volodin et al., 2023). Probably, pup LF USVs disappear in *Phodopus* hamsters with age, which results in an ontogenetic increase of USV average fundamental frequency in adults. However, further research is necessary to confirm this possibility.

Average USV duration of adult *P. sungorus* engaged in aggressive interactions (92.9 ms, Keesom et al., 2015) was longer than those of pup LF USVs (87.7 ms) and HF USVs (60.6 ms) in our study. In all other studied rodent species, USV duration decreased from pups to adults (Liu et al., 2003; Johnson et al., 2017; Zaytseva et al., 2019; Yurlova et al., 2020; Kozhevnikova et al., 2021; Dymkaya et al., 2022; Volodin et al., 2023). Further research of vocal ontogeny is necessary to reveal whether the changes of USV duration in *Phodopus* hamsters correspond to this trend or not.

We found that frequency jumps of 10 or more kHz were common in *Phodopus* pup USVs: from 24.6% of USVs in *P. sungorus* pups to 39.2% of USVs hybrid pups (Fig. 4). Comparative data for hamster pups are unavailable, but there are some comparative data on adult hamsters. For example, 34.6% (56 of 162) of USVs of adult *P. sungorus* had frequency jumps (Keesom et al., 2015). In adult golden hamsters, frequency jumps of 5 or more kHz were detected in 70% female USVs and 18% male USVs (Floody and Pfaff, 1977). Another study on golden hamsters showed that frequency jumps of 10 or more kHz were present in 12% of female USVs and 26% of male USVs (Fernández-Vargas and Johnston, 2015). In addition, published spectrograms of USVs of adult golden hamsters display subharmonics and deterministic chaos (Floody and Pfaff, 1977;

Fernández-Vargas and Johnston, 2015), however, the authors do not provide the percentage of USVs with these nonlinear phenomena. Among 5–10-d rodent pups of different species, percentages of USVs with nonlinear phenomena vary extensively, from nearly zero, as in some species of gerbils (Kozhevnikova et al., 2021) to 30–40% of all USVs in mice and voles (Grimsley et al., 2011; Yurlova et al., 2020). Pup USVs of *Phodopus* hamsters evidently belong to the second group.

4.4. Low and high-frequency USVs in rodents

We found that USVs of 4–8-d *P. sungorus*, *P. campbelli* and hybrid pups contain two components, one centered around 41.4 kHz (LF) and another centered around 59.8 kHz (HF). Similarly, laboratory mouse and rat pups also produce USVs which fall into two frequency ranges (Liu et al., 2003; Boulanger-Bertolus et al., 2017). Further, as in *Phodopus* hamster pups, mice and rat pups produced USVs in which the low and high-frequency components occur both separately and together, and can display frequency jumps (Grimsley et al., 2011; Boulanger-Bertolus et al., 2017).

In 12–15-d laboratory rat pups, the isolation-induced LF USVs had the fundamental frequency centered around 40.5 kHz (from 35 to 45 kHz) with a duration of about 140 ms, and HF USVs had fundamental frequency centered around 66.4 kHz (from 60 kHz to 80 kHz), at very short duration of 21 ms (Boulanger-Bertolus et al., 2017). In 5–12-d laboratory pup mice, the isolation-induced LF USVs were centered around 67 kHz, at duration of 59 ms, and HF USVs were centered around 94 kHz, at duration of 30 ms (Liu et al., 2003). With increasing age, mice USVs became less variable and more stereotyped. Compared to pup isolation USVs, adult mice encounter-related USVs were centered around a single frequency of 80 kHz (Liu et al., 2003; Grimsley et al., 2011).

In 6–8- pup prairie voles *Microtus ochrogaster*, USVs had two widely spaced LF and HF components within calls (Warren et al., 2022). Although the authors did not provide the measurements for each component, their spectrogram displays frequency ranges of 20–35 kHz for the LF component and 35–70 kHz for the HF component. As in laboratory mice, with increasing pup age, variability of USVs decreased, USVs of prairie voles became more stereotyped, and at 8–16 d of age, most vole USVs contain only a LF component (Warren et al., 2022).

Contextual use of LF and HF components of USVs has been investigated only for laboratory rat pups (Boulanger-Bertolus et al., 2017). In pup isolation experiments, 12–15-d rats produced their 40-kHz and 66-kHz USVs equally often. However, after returning a mother to a pup, the number of 40-kHz USVs doubled but after removal of the mother, emission of 40-kHz USVs did not change, remaining at the same high level. Emission of 66-kHz USVs remained at the same level both with and without the mother present (Boulanger-Bertolus et al., 2017).

4.5. Pup age effect on USVs

Available data on the effects of pup age on USV acoustic properties do not reveal any common rule. In this study, LF and HF components of USVs changed inconsistently as *Phodopus* hamster pups developed: between 4 and 8 d of age, peakf0 decreased in the HF component, whereas LF component did not show a steady trend of changes. By contrast, in yellow steppe lemmings, the maximum fundamental frequency of USVs decreased rapidly from 1 to 4 d to 5–8 d of age, then increased in 9–12-d pups and then decreases again in 13–16-d and older pups, becoming indistinguishable in frequency from adult USVs (Yurlova et al., 2020). For a pooled sample of LF and HF components in laboratory pup mice, USV frequency was unchanged from 5 to 12 d of age (Liu et al., 2003) or slightly decreased from 5 to 11 d of age and then increased at 13 d of age (Grimsley et al., 2011). In California deer mice, USVs increased in frequency from 2 to 4–7 d of age and then decreased back to previous values at 21 d of age (Johnson et al., 2017). In Northern collared lemmings *Dicrostonyx groenlandicus*, USV fundamental frequency slightly

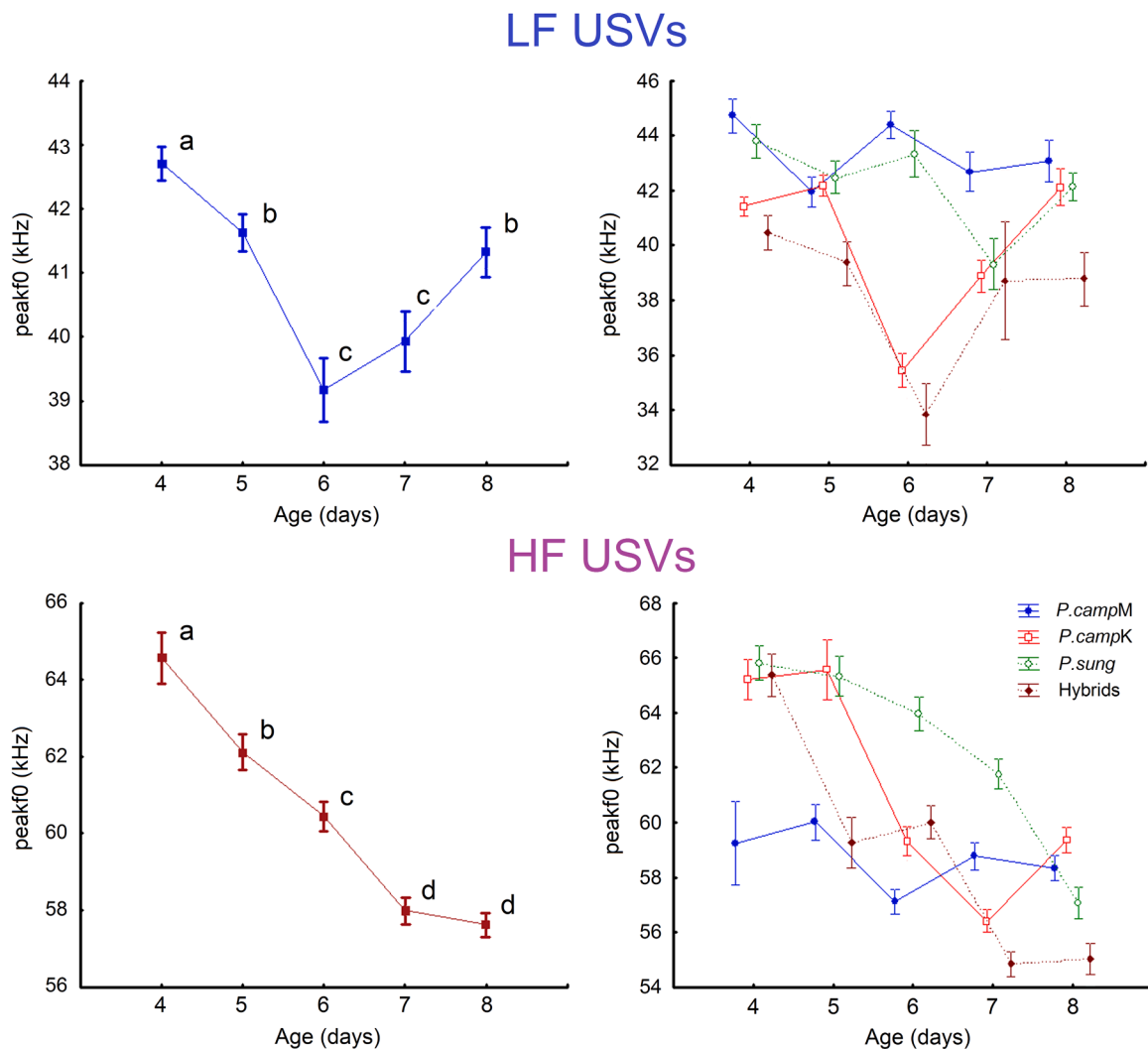


Fig. 7. Age-related changes of peakf0 in Low-Frequency ultrasonic calls (LF USVs) and High-Frequency ultrasonic calls (HF USVs) between 4th and 8th days-old pups. Left: results for the four Study Groups in total, Right: results for each Study Group separately. Central points indicate means, whiskers indicate SE. Designations: peakf0 – the peak frequency of call fundamental frequency; *P.campM* – *P. campbelli* (Mongolian) pups; *P.campK* – *P. campbelli* (Kosh-Agach) pups; *P.sung* – *P. sungorus* pups; Hybrids – hybrids between male *P.sung* and female *P.campK*. The same superscripts indicate the lack of significant differences between the values ($p > 0.05$, Tukey post hoc). Please pay attention to different scale dimensions of ordinate axis for results of the four Study Groups in total and for results of each Study Group separately.

Table 2

Pearson correlation between pup body size index and average values of peakf0 for Low-Frequency (LF USVs) and High-Frequency (HF USVs) ultrasonic calls. Designations: peakf0 – the peak frequency of call fundamental frequency; *P.campM* – *P. campbelli* (Mongolian) pups; *P.campK* – *P. campbelli* (Kosh-Agach) pups; *P.sung* – *P. sungorus* pups; Hybrids – hybrids between male *P.sung* and female *P.campK*. *N* = number of individual pups. Significant correlations are highlighted in bold.

Study Group	<i>P.campM</i> , <i>N</i> = 20	<i>P. campK</i> , <i>N</i> = 20	<i>P.sung</i> , <i>N</i> = 20	Hybrids, <i>N</i> = 20
LF USVs	$r = -0.29$; $p = 0.33$	$r = -0.15$; $p = 0.53$	$r = -0.11$; $p = 0.65$	$r = -0.27$; $p = 0.29$
HF USVs	$r = -0.15$; $p = 0.52$	$r = -0.20$; $p = 0.47$	$r = -0.79$; $p < 0.001$	$r = -0.54$; $p = 0.018$

decreases from 3 d to 8 d of age (Brooks and Banks, 1973). In prairie voles, the median frequency of USVs does not change between 6 d and 16 d of age (Warren et al., 2022).

4.6. Potential impacts of captivity on vocalization of dwarf hamsters

Keeping dwarf hamsters of two species for generations in the same vivarium under the same captive conditions might result in convergence of call traits rather than dissimilarity. Nevertheless, we found prominent differences in the acoustics between two populations of the same species, between two species and between parental species and hybrids.

Keeping mammals with innate vocalization in captivity per se does not change acoustic traits of vocalizations. For example, captive population of tame Belyaev foxes maintained for over 60 years retained intact all species-specific vocalizations (Gogoleva et al., 2008) occurring in wild foxes (Newton-Fisher et al., 1993). Subtle differences, detected in the acoustic structure of USVs between wild and laboratory California deer mice (Kalcounis-Rueppell et al., 2010) could be due to interpopulation differences (for instance, Campbell et al., 2010; Matrosova et al., 2016), rather than represented the effects of captivity.

For animal samples in our study, we used the neutral term “Study Groups”, not the terms “Lines” or “Strains” used in literature for some lab-maintained populations. The terms “Lines” or “Strains” would be incorrect here, as they are only applicable to either animals intentionally

selected for behavior (as e.g., rats selected for high or low calling rates, Lesch et al., 2020) or those genetically manipulated (as e.g., mice with artificially knocked out genes, Klenova et al., 2021). While dwarf hamsters were not selected for any kind of behavior and were not genetically modified, they were therefore representative proxies of their wild ancestors.

4.7. Analysed parameters of USVs

Our semi-automatic acoustic measurements took into account temporal, power and frequency characteristics of the entire calls. We measured and compared duration and peak frequency and, as in most (3899 of 4000) USVs the peak frequency was located on a call fundamental frequency band, the measurement of peak frequency also involved call fundamental frequency. In addition, we checked each call for presence of nonlinear phenomena (frequency jumps, biphonations, subharmonics and deterministic chaos). The used set of acoustic variables was sufficient to support our conclusions regarding the acoustic differences between parental species and hybrids. Inclusion additional frequency parameters (e.g., the beginning or end fundamental frequencies taken over the call contour) would be redundant here, because these parameters are highly correlated to peakf0 and thus would not increase the found differences. Measuring additional parameters of f0 manually would be useful however for further describing the acoustics of calls in dwarf hamsters in depth, e.g., regarding frequency ranges and frequency modulation.

CRedit authorship contribution statement

Ilya A. Volodin, Elena V. Volodina: Conceptualization. **Ilya A. Volodin, Nina Yu. Vasilieva:** Methodology. **Semen V. Piastolov, Ilya A. Volodin:** Software, Validation, Formal analysis, Visualization. **Semen V. Piastolov, Ilya A. Volodin, Elena V. Volodina:** Investigation, Writing – original draft. **Ilya A. Volodin, Nina Yu. Vasilieva, Anastasia M. Khrushchova, Olga N. Shekarova, Elena V. Volodina:** Resources. **Semen V. Piastolov, Ilya A. Volodin, Nina Yu. Vasilieva, Anastasia M. Khrushchova, Olga N. Shekarova, Elena V. Volodina:** Data curation, Writing – review & editing. **Ilya A. Volodin:** Supervision. **Ilya A. Volodin, Nina Yu. Vasilieva, Anastasia M. Khrushchova:** Project administration.

Declaration of Competing Interest

The authors declare no competing or financial interests.

Data availability

Data will be made available on request.

Acknowledgements

We thank Andrey Tchabovsky for providing the room for conducting experiments. We thank Polina Semenova for help with animal management. We thank Stephen Pollard for consulting regarding language and style. This study was not supported by any foundation.

References

- Arriaga, G., Zhou, E.P., Jarvis, E.D., 2012. Of mice, birds, and men: the mouse ultrasonic song system has some features similar to humans and song-learning birds. *PLoS ONE* 7, e46610. <https://doi.org/10.1371/journal.pone.0046610>.
- Azola, A., Palmer, J., Mulheren, R., Hofer, R., Fischmeister, F., Fitch, W.T., 2018. The physiology of oral whistling: a combined radiographic and MRI analysis. *J. Appl. Physiol.* 124, 34–39. <https://doi.org/10.1152/jappphysiol.00902.2016>.
- Beeck, V.C., Heilmann, G., Kerscher, M., Stoeger, A.S., 2021. A novel theory of Asian elephant high-frequency squeak production. *BMC Biol.* 19, 121. <https://doi.org/10.1186/s12915-021-01026-z>.

- Bikchurina, T.I., Tishakova, K.V., Kizilova, E.A., Romanenko, S.A., Serdyukova, N.A., Torgasheva, A.A., Borodin, P.M., 2018. Chromosome synapsis and recombination in male-sterile and female-fertile interspecies hybrids of the dwarf hamsters (*Phodopus*, Cricetidae). *Genes* 9, 227. <https://doi.org/10.3390/genes9050227>.
- Boulanger-Bertolus, J., Rincón-Cortés, M., Sullivan, R.M., Mouly, A.M., 2017. Understanding pup affective state through ethologically significant ultrasonic vocalization frequency. *Sci. Rep.* 7, 13483. <https://doi.org/10.1038/s41598-017-13518-6>.
- Brekke, T.D., Good, J.M., 2014. Parent-of-origin growth effects and the evolution of hybrid inviability in dwarf hamsters. *Evolution* 68, 3134–3148. <https://doi.org/10.1111/evo.12500>.
- Brooks, R.J., Banks, E.M., 1973. Behavioural biology of the collared lemming (*Dicrostonyx groenlandicus* Trail): An analysis of acoustic communication. *Anim. Behav. Monogr.* 6, 1–83. [https://doi.org/10.1016/0003-3472\(73\)90003-1](https://doi.org/10.1016/0003-3472(73)90003-1).
- Campbell, P., Pasch, B., Pino, J.L., Crino, O.L., Phillips, M., Phelps, S.M., 2010. Geographic variation in the songs of neotropical singing mice: testing the relative importance of drift and local adaptation. *Evolution* 64, 1955–1972. <https://doi.org/10.1111/j.1558-5646.2010.00962.x>.
- Dymskaya, M.M., Volodin, I.A., Smorkatcheva, A.V., Vasilieva, N.A., Volodina, E.V., 2022. Audible, but not ultrasonic, calls reflect surface-dwelling or subterranean specialization in pup and adult Brandt's and mandarin voles. *Behav. Ecol. Sociobiol.* 76, 106. <https://doi.org/10.1007/s00265-022-03213-6>.
- Fernández-Vargas, M., Johnston, R.E., 2015. Ultrasonic vocalizations in golden hamsters (*Mesocricetus auratus*) reveal modest sex differences and nonlinear signals of sexual motivation. *PLoS ONE* 10, e0116789. <https://doi.org/10.1371/journal.pone.0116789>.
- Fernández-Vargas, M., Riede, T., Pasch, B., 2022. Mechanisms and constraints underlying acoustic variation in rodents. *Anim. Behav.* 184, 135–147. <https://doi.org/10.1016/j.anbehav.2021.07.011>.
- Finck, C., Lejeune, L., 2010. Structure and oscillatory function of the vocal folds. In: *Handbook of Mammalian Vocalization: An Integrative Neuroscience Approach* (ed. S.M. Brudzynski), pp. 427–438. Amsterdam: Academic/Elsevier. doi: 10.1016/B978-0-12-374593-4.00039-5.
- Fitch, W.T., Hauser, M.D., 2002. Unpacking "Honesty": Vertebrate vocal production and the evolution of acoustic signals. In: Simmons, A., Fay, R.R., Popper, A.N. (Eds.), *Acoustic Communication, Springer Handbook of Auditory Research*. Springer, New York, pp. 65–137.
- Floody, O.R., Pfaff, D.W., 1977. Communication among hamsters by high-frequency acoustic signals: I. Physical characteristics of hamster calls. *J. Comp. Physiol. Psychol.* 91, 794–806. <https://doi.org/10.1037/h0077359>.
- Frey, R., Volodin, I.A., Fritsch, G., Volodina, E.V., 2016. Potential sources of high frequency and biphonic vocalization in the dhole (*Cuon alpinus*). *PLoS ONE* 11, e0146330. <https://doi.org/10.1371/journal.pone.0146330>.
- Gogoleva, S.S., Volodin, I.A., Volodina, E.V., Trut, L.N., 2008. To bark or not to bark: Vocalization in red foxes selected for tameness or aggressiveness toward humans. *Bioacoustics* 18, 99–132. <https://doi.org/10.1080/09524622.2008.9753595>.
- Grimsley, J.M.S., Monaghan, J.J.M., Wenstrup, J.J., 2011. Development of social vocalizations in mice. *PLoS ONE* 6, e17460. <https://doi.org/10.1371/journal.pone.0017460>.
- Hahn, M.E., Hewitt, J.K., Schanz, N., Weinreb, L., Henry, A., 1997. Genetic and developmental influences on infant mouse ultrasonic calling. I. A diallel analysis of the calls of 3-day olds. *Behav. Gen.* 27, 133–143. <https://doi.org/10.1023/a:1025637408900>.
- Hahn, M.E., Karkowski, L., Weinreb, L., Henry, A., Schanz, N., Hahn, E.M., 1998. Genetic and developmental influences on infant mouse ultrasonic calling. II. Developmental patterns in the calls of mice 2–12 days of age. *Behav. Gen.* 28, 315–325. <https://doi.org/10.1023/a:1021679615792>.
- Håkansson, J., Jiang, W., Xue, Q., Zheng, X., Ding, M., Agarwal, A.A., Elemans, C.P.H., 2022a. Aerodynamics and motor control of ultrasonic vocalizations for social communication in mice and rats. *BMC Biol.* 20, 3. <https://doi.org/10.1186/s12915-021-01185-z>.
- Håkansson, J., Mikkelsen, C., Jakobsen, L., Elemans, C.P.H., 2022b. Bats expand their vocal range by recruiting different laryngeal structures for echolocation and social communication. *PLoS Biol.* 20, e3001881. <https://doi.org/10.1371/journal.pbio.3001881>.
- Hammerschmidt, K., Reisinger, E., Westekemper, K., Ehrenreich, L., Strenzke, N., Fischer, J., 2012. Mice do not require auditory input for the normal development of their ultrasonic vocalizations. *BMC Neurosci.* 13, 40. <https://doi.org/10.1186/1471-2202-13-40>.
- Hashimoto, H., Saito, T.R., Moritani, N., Komeda, K., Takahashi, K.W., 2001. Comparative study on isolation calls emitted from hamster pups. *Exp. Anim.* 50, 313–318. <https://doi.org/10.1538/expanim.50.313>.
- Ishishita, S., Matsuda, Y., 2016. Interspecific hybrids of dwarf hamsters and Phasianidae birds as animal models for studying the genetic and developmental basis of hybrid incompatibility. *Genes Genet. Syst.* 91, 63–75. <https://doi.org/10.1266/ggs.16-00022>.
- Ishishita, S., Tsuboi, K., Ohishi, N., Tsuchiya, K., Matsuda, Y., 2015. Abnormal pairing of X and Y sex chromosomes during meiosis: I in interspecific hybrids of *Phodopus campbelli* and *P. sungorus*. *Sci. Rep.* 5, 9435. <https://doi.org/10.1038/srep09435>.
- Janik, V.M., Knörnschild, M., 2021. Vocal production learning in mammals revisited. *Philos. Trans. Roy. Soc. B* 376, 20200244. <https://doi.org/10.1098/rstb.2020.0244>.
- Janik, V.M., Slater, P.J.B., 2000. The different roles of social learning in vocal communication. *Anim. Behav.* 60, 1–11. <https://doi.org/10.1006/anie.2000.1410>.
- Johnson, S.A., Painter, M.S., Javurek, A.B., Murphy, C.R., Howald, E.C., Khan, Z.Z., Conard, C.M., Gant, K.L., Ellersieck, M.R., Hoffmann, F., Schenk, A.K., Rosenfeld, C.S., 2017. Characterization of vocalizations emitted in isolation by California mouse

- (*Peromyscus californicus*) pups throughout the postnatal period. *J. Comp. Psychol.* 131, 30–39. <https://doi.org/10.1037/com0000057>.
- Kalounis-Rueppell, M.C., Petric, R., Briggs, J.R., Carney, C., Marshall, M.M., Willse, J.T., Rueppell, O., Ribble, D.O., Crossland, J.P., 2010. Differences in ultrasonic vocalizations between wild and laboratory California mice (*Peromyscus californicus*). *PLoS ONE* 5, e9705. <https://doi.org/10.1371/journal.pone.0009705>.
- Keesom, S.M., Rendon, N.M., Demas, G.E., Hurley, L.M., 2015. Vocal behaviour during aggressive encounters between Siberian hamsters, *Phodopus sungorus*. *Anim. Behav.* 102, 85–92. <https://doi.org/10.1016/j.anbehav.2015.01.014>.
- Kikusui, T., Nakanishi, K., Nakagawa, R., Nagasawa, M., Mogi, K., Okanoya, K., 2011. Cross fostering experiments suggest that mice songs are innate. *PLoS ONE* 6, e17721. <https://doi.org/10.1371/journal.pone.0017721>.
- Kitchen, D.M., Bergman, T.J., Dias, P.A.D., Ho, L., Canales-Espinosa, D., Cortés-Ortiz, L., 2019. Temporal but not acoustic plasticity in hybrid howler monkey (*Alouatta palliata* × *A. pigra*) loud calls. *Int. J. Primatol.* 40, 132–152. [org/10.1007/s10764-017-0004-8](https://doi.org/10.1007/s10764-017-0004-8).
- Klenova, A.V., Volodin, I.A., Volodina, E.V., Ranneva, S.V., Amstislavskaya, T.G., Lipina, T.V., 2021. Vocal and physical phenotypes of calyntenin2 knockout mouse pups model early-life symptoms of the autism spectrum disorder. *Behav. Brain Res.* 412, 113430. <https://doi.org/10.1016/j.bbr.2021.113430>.
- Kozhevnikova, J.D., Volodin, I.A., Zaytseva, A.S., Ilchenko, O.G., Volodina, E.V., 2021. Pup ultrasonic isolation calls of six gerbil species and the relationship between acoustic traits and body size. *R. Soc. Open Sci.* 8, 201558. <https://doi.org/10.1098/rsos.201558>.
- Lattenkamp, E.Z., Hörpel, S.G., Mengede, J., Firzlauff, U., 2021. A researcher's guide to the comparative assessment of vocal production learning. *Philos. Trans. Roy. Soc. B* 376, 20200237. <https://doi.org/10.1098/rstb.2020.0237>.
- Lesch, R., Orozco, A., Shilling, M., Zimmerberg, B., Fitch, W.T., 2020. Selection on ultrasonic call rate in neonatal rats affects low frequency, but not ultrasonic, vocalizations in adults. *Ethology* 126, 1007–1018. <https://doi.org/10.1111/eth.13075>.
- Liu, R.C., Miller, K.D., Merzenich, M.M., Schreiner, C.E., 2003. Acoustic variability and distinguishability among mouse ultrasound vocalizations. *J. Acoust. Soc. Am.* 114, 3412–3422. <https://doi.org/10.1121/1.1623787>.
- Long, A.M., Moore, N.P., Hayden, T.J., 1998. Vocalizations in red deer (*Cervus elaphus*), sika deer (*Cervus nippon*), and red × sika hybrids. *J. Zool.* 244, 123–134. <https://doi.org/10.1111/j.1469-7998.1998.tb00014.x>.
- Lopez-Salesansky, N., Wells, D.J., Chancellor, N., Whitfield, L., Burn, C.C., 2021. Handling mice using gloves sprayed with alcohol-based hand sanitiser: acute effects on mouse behaviour. *Anim. Technol. Welf.* 20, 11–20.
- Mahrt, E., Agarwal, A., Perkel, D., Portfors, C., Elemans, C.P.H., 2016. Mice produce ultrasonic vocalizations by intra-laryngeal planar impinging jets. *Curr. Biol.* 26, R880–R881. <https://doi.org/10.1016/j.cub.2016.08.032>.
- Mahrt, E.J., Perkel, D.J., Tong, L., Rubel, E.W., Portfors, C.V., 2013. Engineered deafness reveals that mouse courtship vocalizations do not require auditory experience. *J. Neurosci.* 33, 5573–5583. <https://doi.org/10.1523/JNEUROSCI.5054-12.2013>.
- Matrosova, V.A., Rusin, M.Y., Volodina, E.V., Proyavka, S.V., Savinetsky, L.E., Shekarova, O.N., Rashevskaya, H.V., Volodin, I.A., 2016. Genetic and alarm call diversity across scattered populations of speckled ground squirrels (*Spermophilus suslicus*). *Mammal. Biol.* 81, 255–265. <https://doi.org/10.1016/j.mambio.2016.01.001>.
- Matrosova, V.A., Ivanova, A.D., Volodina, E.V., Volodin, I.A., Alexandrov, D.Y., Sibiriyakova, O.V., Ermakov, O.A., 2019. Phylogenetic relationship and variation of alarm call traits of populations of red-cheeked ground squirrels (*Spermophilus erythrognus* sensu lato) suggest taxonomic delineation. *Integr. Zool.* 14, 341–353. <https://doi.org/10.1111/1749-4877.12383>.
- Musolf, K., Meindl, S., Larsen, A.L., Kalounis-Rueppell, M.C., Penn, D.J., 2015. Ultrasonic vocalizations of male mice differ among species and females show assortative preferences for male calls. *PLoS ONE* 10, e0134123. <https://doi.org/10.1371/journal.pone.0134123>.
- Newton-Fisher, N., Harris, S., White, P., Jones, G., 1993. Structure and function of red fox (*Vulpes vulpes*) vocalizations. *Bioacoustics* 5, 1–31. <https://doi.org/10.1080/09524622.1993.9753228>.
- Nikol'skiy, A.A., Denisov, V.P., Stoiko, T.G., Formosov, N.A., 1984. The alarm call in FI hybrids *Citellus pygmaeus* X *C. suslicus* (Sciuridae, Rodentia). *Zool. Zh.* 63, 1216–1225.
- Page, B., Goldsworthy, S.D., Hindell, M.A., 2001. Vocal traits of hybrid fur seals: intermediate to their parental species. *Anim. Behav.* 61, 959–967. <https://doi.org/10.1006/anbe.2000.1663>.
- Pasch, B., Tokuda, I.T., Riede, T., 2017. Grasshopper mice employ distinct vocal production mechanisms in different social contexts. *Proc. R. Soc. B* 284, 20171158. <https://doi.org/10.1098/rspb.2017.1158>.
- Pierce, J., Sawrey, D.K., Dewsbury, D.A., 1989. A comparative study of rodent ultrasonic vocalizations during copulation. *Behav. Neural Biol.* 51, 211–221. [org/10.1016/S0163-1047\(89\)90842-X](https://doi.org/10.1016/S0163-1047(89)90842-X).
- Reby, D., Wyman, M.T., Frey, R., Passilongo, D., Gilbert, J., Locatelli, Y., Charlton, B.D., 2016. Evidence of biphonation and source-filter interactions in the bugles of male North American wapiti (*Cervus canadensis*). *J. Exp. Biol.* 219, 1224–1236. [org/10.1242/jeb.131219](https://doi.org/10.1242/jeb.131219).
- Rendon, N.M., Keesom, S.M., Amadi, C., Hurley, L.M., Demas, G.E., 2015. Vocalizations convey sex, seasonal phenotype, and aggression in a seasonal mammal. *Physiol. Behav.* 152, 143–150. <https://doi.org/10.1016/j.physbeh.2015.09.014>.
- Riede, T., 2011. Subglottal pressure, tracheal airflow, and intrinsic laryngeal muscle activity during rat ultrasound vocalization. *J. Neurophysiol.* 106, 2580–2592. <https://doi.org/10.1152/jn.00478.2011>.
- Riede, T., Pasch, B., 2020. Pygmy mouse songs reveal anatomical innovations underlying acoustic signal elaboration in rodents. *J. Exp. Biol.* 223, jeb.223925. <https://doi.org/10.1242/jeb.223925>.
- Riede, T., Borgard, H.L., Pasch, B., 2017. Laryngeal airway reconstruction indicates that rodent ultrasonic vocalizations are produced by an edge-tone mechanism. *R. Soc. Open Sci.* 4, 170976. <https://doi.org/10.1098/rsos.170976>.
- Riede, T., Coyne, M., Tafoya, B., Baab, K.L., 2020. Postnatal development of the mouse larynx: negative allometry, age-dependent shape changes, morphological integration, and a size-dependent spectral feature. *J. Speech Lang. Hear. Res.* 63, 2680–2694. <https://doi.org/10.1044/2020.JSLHR-20-00070>.
- Riede, T., Kobrina, A., Bone, L., Darwaiz, T., Pasch, B., 2022. Mechanisms of sound production in deer mice (*Peromyscus spp.*). *J. Exp. Biol.* 225, jeb243695. <https://doi.org/10.1242/jeb.243695>.
- Ross, P.D., 1995. *Phodopus campbelli*. *Mammal. Species* 503, 1–7.
- Ross, P.D., 1998. *Phodopus sungorus*. *Mammal. Species* 595, 1–9.
- Rutovskaya, M.V., 2019. Inheritance of the acoustic signal parameters in interspecific hybrids of the bank (*Myodes glareolus*) and the Tien Shan (*M. centralis*) voles. *BMC Evol. Biol.* 19, 44. <https://doi.org/10.1186/s12862-019-1374-7>.
- Safronova, L.D., Vasil'eva, N.Yu., 1996. Meiotic abnormalities in interspecies hybrids between *Phodopus sungorus* (Pallas, 1773) and *Ph. campbelli* (Thomas, 1905). *Genetica* 32, 560–569.
- Safronova, L.D., Malygin, V.M., Levenkova, E.S., Orlov, V.N., 1992. Cytogenetic sequelae of hybridization of hamsters *Phodopus sungorus* and *Phodopus campbelli*. *Dokl. Akad. Nauk* 327, 266–271.
- Safronova, L.D., Cherepanova, E.V., Vasil'eva, N.Yu., 1999. Specific features of the first meiotic division in hamster hybrids obtained by backcrossing *Phodopus sungorus* and *Phodopus campbelli*. *Rus. J. Gen.* 35, 184–188.
- Schneider, N., Fritzsche, P., 2011. Isolation calls and retrieving behavior in laboratory and wild-derived golden hamsters - No sign for inbreeding depression. *Mammal. Biol.* 76, 549–554. <https://doi.org/10.1016/j.mambio.2011.03.002>.
- Scribner, S.J., Wynne-Edwards, K.E., 1994. Moderate water restriction differentially constrains reproduction in two species of dwarf hamster (*Phodopus*). *Can. J. Zool.* 72, 1589–1596. <https://doi.org/10.1139/z94-211>.
- Shmyrov, A.A., Kuzmin, A.A., Kuzmin, A.A., Titov, S.V., 2012. Characterization of hybrids between the russet (*Spermophilus major*) and the yellow (*Spermophilus fulvus*) ground squirrels according to morphological and acoustic attributes. *Zool. Zh.* 91, 119–126.
- Sibiriyakova, O.V., Volodin, I.A., Volodina, E.V., 2021. Polyphony of domestic dog whines and vocal cues to body size. *Curr. Zool.* 67, 165–176. <https://doi.org/10.1093/cz/zoaa042>.
- Sokolov, V.E., Vasil'eva, N.Yu., 1993a. Hybridologic analysis confirms the species specificity of *Phodopus sungorus* (Pallas, 1773) and *Phodopus campbelli* (Thomas, 1905). *Dokl. Akad. Nauk* 332, 120–123.
- Sokolov, V.E., Vasil'eva, N.Yu., 1993b. Behavior of the Campbell hamster (*Phodopus campbelli* Thomas, 1905) in nature: confirmation of the biological signal field theory. *Dokl. Akad. Nauk* 332, 667–670.
- Suthers, R.A., Fattu, J.M., 1973. Mechanisms of sound production by echolocating bats. *Am. Zool.* 13, 1215–1226. <https://doi.org/10.1093/icb/13.4.1215>.
- Suthers, R.A., Fattu, J.M., 1982. Selective laryngeal neurotomy and the control of phonation by the echolocating bat, *Eptesicus*. *J. Comp. Physiol. A* 145, 529–537. <https://doi.org/10.1007/BF00612818>.
- Thornton, L.M., Hahn, M.E., Schanz, N., 2005. Genetic and developmental influences on infant mouse ultrasonic calling. III. Patterns of inheritance in the calls of mice 3–9 days of age. *Behav. Gen.* 35, 73–83. <https://doi.org/10.1007/s10519-004-0857-4>.
- Titze, I., Riede, T., Mau, T., 2016. Predicting achievable fundamental frequency ranges in vocalization across species. *PLoS Comput. Biol.* 12, e1004907. <https://doi.org/10.1371/journal.pcbi.1004907>.
- Vasilieva, N.Yu., Khrushchova, A.M., 2010. Nursing father - myth or reality? The role of secretions of father-male specific skin glands in survival and development of Campbell's hamsters juveniles (*Phodopus campbelli* Thomas, 1905; Cricetidae, Rodentia). *Zh. Obshch. Biol.* 71, 195–204.
- Volodin, I.A., Sibiriyakova, O.V., Volodina, E.V., 2016. Sex and age-class differences in calls of Siberian wapiti *Cervus elaphus sibiricus*. *Mammal. Biol.* 81, 10–20. <https://doi.org/10.1016/j.mambio.2015.09.002>.
- Volodin, I.A., Volodina, E.V., Frey, R., 2017. Bull bellows and bugles: a remarkable convergence of low and high-frequency vocalizations between male domestic cattle *Bos taurus* and the rutting calls of Siberian and North American wapiti. *Bioacoustics* 26, 271–284. <https://doi.org/10.1080/09524622.2016.1275805>.
- Volodin, I.A., Volodina, E.V., Rutovskaya, M.V., 2022. Camel whistling vocalisations: male and female call structure and context in *Camelus bactrianus* and *Camelus dromedarius*. *Bioacoustics* 31, 132–147. <https://doi.org/10.1080/09524622.2021.1889403>.
- Volodin, I.A., Kozhevnikova, J.D., Ilchenko, O.G., Sapozhnikova, S.R., Volodina, E.V., 2023. Cross-fostering effects on ultrasonic calls in two gerbil species. *Rus. J. Theriol.* 22, 3–10. <https://doi.org/10.15298/rusjtheriol.22.1.01>.
- Warren, M.R., Campbell, D., Borie, A.M., Ford, C.L., Dharani, A.M., Young, L.J., Liu, R.C., 2022. Maturation of social-vocal communication in prairie vole (*Microtus ochrogaster*) pups. *Front. Behav. Neurosci.* 15, 814200. <https://doi.org/10.3389/fnbeh.2021.814200>.
- Wyman, M.T., Locatelli, Y., Charlton, B.D., Reby, D., 2016. Female sexual preferences toward conspecific and hybrid male mating calls in two species of polygynous deer, *Cervus elaphus* and *C. nippon*. *Evol. Biol.* 43, 227–241. <https://doi.org/10.1007/s11692-015-9357-0>.
- Wynne-Edwards, K.E., 1987. Evidence for obligate monogamy in the Djungarian hamster, *Phodopus campbelli*: pup survival under different parenting conditions. *Behav. Ecol. Sociobiol.* 20, 427–437. <https://doi.org/10.1007/BF00302986>.

- Wynne-Edwards, K.E., 1995. Biparental care in Djungarian but not Siberian dwarf hamsters (*Phodopus*). *Anim. Behav.* 50, 1571–1585. [https://doi.org/10.1016/0003-3472\(95\)80012-3](https://doi.org/10.1016/0003-3472(95)80012-3).
- Wynne-Edwards, K.E., 1998. Evolution of parental care in *Phodopus*: Conflict between adaptations for survival and adaptations for rapid reproduction. *Am. Zool.* 38, 238–250. <https://doi.org/10.1093/icb/38.1.238>.
- Wynne-Edwards, K.E., Lisk, R.D., 1989. Differential effects of paternal presence on pup survival in two species of dwarf hamster (*Phodopus sungorus* and *Phodopus campbelli*). *Physiol. Behav.* 45, 465–469. [https://doi.org/10.1016/0031-9384\(89\)90059-0](https://doi.org/10.1016/0031-9384(89)90059-0).
- Yurlova, D.D., Volodin, I.A., Ilchenko, O.G., Volodina, E.V., 2020. Rapid development of mature vocal patterns of ultrasonic calls in a fast-growing rodent, the yellow steppe lemming (*Eolagurus luteus*). *PLoS ONE* 15, e0228892. <https://doi.org/10.1371/journal.pone.0228892>.
- Zaytseva, A.S., Volodin, I.A., Ilchenko, O.G., Volodina, E.V., 2019. Ultrasonic vocalization of pup and adult fat-tailed gerbils (*Pachyuromys duprasi*). *PLoS ONE* 14, e0219749. <https://doi.org/10.1371/journal.pone.0219749>.