

Cross-fostering effects on ultrasonic calls in two gerbil species

Ilya A. Volodin*, Julia D. Kozhevnikova, Olga G. Ilchenko,
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ABSTRACT. Mammals not experiencing vocal learning may slightly modify their voice calls (produced by vibration of the vocal folds) towards a higher similarity with conspecific groupmates. This pilot study is the first focused on interspecies social effects on whistle vocalizations (ultrasounds produced by turbulence at the vocal tract). Pup cross-fostering was applied between two related gerbil species *Meriones unguiculatus* and *M. vinogradovi*, producing acoustically different ultrasonic contact calls when adult (higher-frequency in *M. vinogradovi*). Calls of 3 survived foster individuals (2 *M. unguiculatus* and 1 *M. vinogradovi*) and of 22 control non-foster individuals raised by their own species (10 *M. unguiculatus* and 12 *M. vinogradovi*) were analysed bioacoustically. Call duration of non-fosters did not differ between species, whereas the fundamental and peak frequencies were lower in non-foster *M. unguiculatus*. Foster *M. unguiculatus* produced calls shorter and higher in the fundamental and peak frequencies than non-foster *M. unguiculatus*. Foster *M. vinogradovi* produced calls shorter and higher in the beginning and minimum fundamental frequencies than non-foster *M. vinogradovi*. We discuss that the observed trend, towards higher-frequency calls, was only expectable for foster *M. unguiculatus*, whereas the same trend observed in foster *M. vinogradovi* was opposed to the expected. These findings provide the possibility that the acoustic properties in foster *M. unguiculatus* are changed by social effect which apparently lacked on the calls of the foster individual *M. vinogradovi*. We discuss that these limited data on gerbils are consistent with published contradictory data on laboratory mice strains.

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Влияние перекрестного выращивания на ультразвуковые крики двух видов песчанок

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РЕЗЮМЕ. Млекопитающие без вокального научения могут проявлять вокальную пластичность, видоизменяя крики в сторону большего сходства с конспецификами своей социальной группы. Ранее модификация звуков под влиянием социального окружения была показана для голосовых криков, издаваемых с помощью вибрации голосовых связок. В этом пилотном исследовании мы оценили влияние перекрестного выращивания на свистовые ультразвуки, издаваемые в результате турбулентности при прохождении струи воздуха через вокальный тракт, для двух видов песча-

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нок (*Meriones unguiculatus* и *M. vinogradovi*) со значительными различиями основной частоты криков у взрослых особей (выше у *M. vinogradovi*). Проанализированы ультразвуки 25 взрослых особей, трех приемных, выращенных родителями другого вида (2 *M. unguiculatus* и 1 *M. vinogradovi*) и 22 контрольных, выращенных своим видом (10 *M. unguiculatus* и 12 *M. vinogradovi*). У контрольных *M. unguiculatus* длительность криков не отличалась от *M. vinogradovi*, тогда как основная и пиковая частоты криков *M. unguiculatus* были ниже, чем у *M. vinogradovi*. Крики *M. unguiculatus*, выращенных *M. vinogradovi*, были короче и выше по основной и пиковой частотам, чем у контрольных *M. unguiculatus*. Крики *M. vinogradovi*, выращенной *M. unguiculatus*, были короче и выше по начальной и минимальной основным частотам, чем у контрольных *M. vinogradovi*. Тренд изменений в сторону более высокочастотных криков был ожидаемым у *M. unguiculatus*, а у *M. vinogradovi* тот же тренд был противоположен ожидаемому. Противоречивые данные также прежде сообщались для разных линий лабораторных мышей.

КЛЮЧЕВЫЕ СЛОВА: акустическое поведение, *Meriones vinogradovi*, *Meriones unguiculatus*, грызуны, социальные эффекты, ультразвуковая вокализация.

Introduction

In mammals, two sound producing mechanisms (phonation and turbulence) generate respectively two kinds of vocal output (voicing and whistling), potentially differing in their plasticity to social environment. Most mammalian vocalizations are voice calls produced with synchronous vibration of the vocal folds (Fitch & Hauser, 2002; Finck & Lejeune, 2010). **The whistle calls of mammals are products of turbulence in the vocal tract** (Mahrt *et al.*, 2016; Riede *et al.*, 2017; Azola *et al.*, 2018; Håkansson *et al.*, 2022). **Both voice and whistle calls can be produced in ranges of human-audible (below 20 kHz) or ultrasonic (over 20 kHz) frequencies.** Experimental studies indicate that rodent ultrasonic calls are turbulence-based whistles (Riede, 2011, 2013; Riede & Pasch, 2020; Håkansson *et al.*, 2022).

In rodents, the ultrasonic calls are innate and do not need in auditory feedback for their emergence and ontogenetic development (Kikusui *et al.*, 2011; Hammerschmidt *et al.*, 2012; Mahrt *et al.*, 2013). For mammalian whistle calls, research studying the social effects on the acoustics are only limited with studies of the ultrasonic courtship song of male mice *Mus musculus* Linnaeus, 1758. Social deprivation affects the duration and proportion of different call types during interactions with conspecifics (Chabout *et al.*, 2012). **Two individual male domestic mice housed together with one female displayed matching pitch characteristics of male ultrasonic courtship song** (Arriaga *et al.*, 2012).

For voice calls of mammals whose repertoires are stated at birth, broader evidence of acoustic plasticity in response to variation of social environment is available. Replacement of mates in marmosets *Callithrix* Erxleben, 1777 results in modifying the acoustic structure of their contact calls towards a stronger similarity with calls of a new mate (Snowdon & Elowson, 1999; Rukstalis *et al.*, 2003). Group-specific call traits were found in Japanese macaques *Macaca fuscata* (Blyth, 1875), Campbell monkeys *Cercopithecus campbelli* Waterhouse, 1838 and chimpanzee *Pan troglodytes* (Blumen-

bach, 1775) (Lemasson *et al.*, 2003, 2011; Crockford *et al.*, 2004; Tanaka *et al.*, 2006). Domestic cats *Felis catus* Linnaeus, 1758 preferably use meows whose structure provokes a stronger response in their owners (Nicastro, 2004; McComb *et al.*, 2009). Contact calls of unrelated young artiodactyls were more acoustically similar within than between groups (Briefer & McEligott, 2012; Volodin *et al.*, 2014).

Modifying the acoustics of voice and whistle calls according to call traits of groupmates may indicate vocal production learning (Janik & Slater, 2000; Janik & Knörnschild, 2021). This kind of vocal plasticity increases the complexity of communication systems (Janik & Slater, 2000) thus allowing to group-living animals better managing their social surrounding (Owings & Morton, 1998).

Cross-fostered rodents are a convenient model for studying the social effects on vocalizations. For example, in one of two cross-fostered groups of grasshopper mice *Onychomys* Baird, 1857, a shift of fundamental frequency of their high-frequency phonation-based calls was observed, but, against expectations, in the opposite direction (Pasch *et al.*, 2016). Fostered by unrelated colonies naked mole-rats *Heterocephalus glaber* Rüppell, 1842 modified the acoustics of their low-frequency faint contact chirps to match those typical for their adoptive colonies (Barker *et al.*, 2021). At the same time, in **laboratory mice, proportion of different syllables in male ultrasonic courtship songs did not change in individuals raised by foster strains** (Kikusui *et al.*, 2011).

For the Mongolian gerbil *Meriones unguiculatus* (Milne-Edwards, 1867) and Vinogradov's gerbil *M. vinogradovi* Heptner, 1931, data on maximum fundamental frequency of ultrasonic isolation calls are available for 6–10-day old pups (50–53 kHz in either species, Kozhevnikova *et al.*, 2021) and for adult Mongolian gerbil ultrasonic contact calls (27–38 kHz, Kobayasi & Riquimaroux, 2012; Ter-Mikaelian *et al.*, 2012). For adult *M. vinogradovi*, data have yet to be obtained. However, our preliminary unpublished data indicate that, in contrast to the lack of interspecies difference in pups, in adults, the maximum fundamental

frequency of the ultrasonic contact calls of *M. unguiculatus* and *M. vinogradovi* displays substantial interspecies differences (of about one and half times higher in *M. vinogradovi*).

The aim of this pilot study was to estimate the social effects of the ultrasonic contact calls on the acoustics of two gerbil species. We compare, by applying the unified for all individuals call-eliciting test procedure, the acoustic parameters of the ultrasonic contact calls produced by cross-fostered adult *M. unguiculatus* and *M. vinogradovi* with those of control *M. unguiculatus* and *M. vinogradovi* adults raised by their own species. We expected, that, if the social environment affects vocalization of foster pups, **this effect should result in increasing frequency parameters of ultrasonic calls in foster *M. unguiculatus* (raised by *M. vinogradovi*) but in decreasing frequency parameters of ultrasonic calls in foster *M. vinogradovi* (raised by *M. unguiculatus*).**

Materials and methods

Animals and dates

Study animals were 25 adult gerbils, 3 cross-fostered 240-day-old individuals raised by another species (2 female *M. unguiculatus* and 1 female *M. vinogradovi*, without breeding experience) and 22 control non-foster individuals (not littermates of foster animals) raised by their own parents (5 male and 5 female *M. unguiculatus* and 6 male and 6 female *M. vinogradovi*; all previously had litters). Two foster *M. unguiculatus* were raised by two pairs of *M. vinogradovi* together with their own pups and one foster *M. vinogradovi* was raised by a pair of *M. unguiculatus* together with their own pups. Study animals of both species originated from sustainable laboratory populations, kept in Moscow Zoo for many generations (Volodin *et al.*, 1996). Call-eliciting tests were conducted from 30 May 2018 to 30 November 2020 in the Experimental Department of Small Mammals of Moscow Zoo, Russia. The animals were kept in pairs with one or two subsequent litters in wire-mesh cages 40x50x40 cm. To avoid potential effects of parental species on the acoustics of foster pups, we controlled for those cages with foster pups were not in neighbourhood with the cages containing individuals of their parental species.

Cross-fostering procedure

For **detecting the litters, the authors conducted regular** (at least three times a week) inspections of animal pairs. Day of pup birth was considered the first day of pup life. In total, six pups (3 *M. unguiculatus* pups and 3 *M. vinogradovi* pups) were cross-fostered between species. At time of cross-fostering, the pups were 1–4 days old; age differences of own and foster pups were within 1–3 days. We did not remove any pups from **the parental litter. Only three of the 6 cross-fostered pups** (2 female *M. unguiculatus* and 1 female *M. vinogradovi*) survived to the adulthood (240 days

of age), other three cross-fostered pups died between 5 and 15 days of age. The precise reason of mortality of the fosters remains unknown, because after cross-fostering we did not disturb the litter with experimental animals up to 15 days of age. Three of the six cross-fostered animals were not found during this inspection, whereas all own pups were alive. The survived foster pups **were kept together with adoptive parents and littermates up to the age of 60 days old and then separated together with one littermate of the opposite sex (male) and kept in this interspecies pair up to the test audio recording occurred at 240 days of age.**

Call-eliciting tests

We conducted one call-eliciting test per animal, 25 tests in total. Tests were conducted in a room where other animals were absent. The focal animal was transferred from vivarium to the experimental room within a minute. Each test lasted 8 min and included four stages: 2-min isolation stage, 2-min touch stage, 2-min restrain stage and 2-min measurement stage (following Zaytseva *et al.*, 2019; Klenova *et al.*, 2021). Tests were unified for foster and non-foster animals and for both species.

Test started when the focal animal was placed on a clean unfamiliar table surface in a plastic cylinder 400 mm high with internal diameter 360 mm. During the isolation stage, the animal could move freely within the cylinder. During the touch stage, the animal was gently touched with a teeth brush approximately twice a second. During the restrain stage, the animal was grasped with a hand by experimenter (IAV) from the side of animal back, turned with belly up and kept in horizontal position. **During the measurement stage, the focal animal was measured still hand-held.** For measuring the lengths of animal head and body, we used electronic calipers (Kraf Tool Co., Lenexa, KS, USA), accurate to 0.01 mm. We measured body length of the hand-held animal from the tip of the snout to the anus, and head length from the tip of the snout to the occiput (following Yurlova *et al.*, 2020; Volodin *et al.*, 2021). These measurements were repeated three times and the mean value was taken for analysis. The end of measurements was the end of the test trial. After the trial, the focal animal was weighed on G&G TS-100 electronic scales (G&G GmbH, Neuss, Germany, accurate to 0.01 g). Before the start of a new test, the table surface and the plastic cylinder were cleaned with water and rubbed with cotton washed with 40% ethanol, because high concentration of ethanol affects rodent behaviour (Lopez-Salesansky *et al.*, 2021).

Call recording

For recording the ultrasonic calls (384 kHz, 16 bit) we used the ultrasonic recorder Pettersson D1000X with built-in microphone (Pettersson Elektronik AB, Uppsala, Sweden). The ultrasonic microphone was mounted at 30–40 cm over the experimental area, what provided a high signal-to-noise ratio during the recording. Audio recording made during each call-eliciting test (one per individual) was stored as a separate wav-file.

Call samples and analysis

We selected for acoustic analysis only contact ultrasonic calls (thereafter contact-USVs, Fig. 1), following (Ter-Mikaelian *et al.*, 2012); calls of other types whenever present in the recordings, were ignored. For acoustic analyses, the contact-USVs were selected from all stages of the call-eliciting tests. **For the three foster individuals, we included in acoustic analysis all measurable contact-USVs: 80 contact-USVs from two foster *M. unguiculatus* and 58 contact-USVs from one foster *M. vinogradovi*.** For the 22 non-foster control individuals, **we included in acoustic analysis from 7 to 20 contact-USVs per non-foster** for those individuals which provided not more than 20 contact-USVs per test. From non-fosters which provided more than 20 contact-USVs per test, we randomly selected 20 contact-USVs per individual. **In total, we included in analysis 530 contact-USVs: 138 from fosters and 392 from non-fosters (178 from 10 non-foster *M. unguiculatus* and 214 from 12 non-foster *M. vinogradovi*).**

Spectrographic analysis of contact-USVs was conducted using Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany); data of measurements were automatically exported to Microsoft Excel (Microsoft Corp., Redmond, WA, USA). As a preliminary visual inspection of call spectrograms showed that fundamental frequency of the contact-USVs always exceeded 10 kHz, we filtered out the lower 10 kHz in the spectrogram window, to remove the background noise. For each contact-USV, we manually measured in the spectrogram window of Avisoft (with sampling rate 384 kHz, Fast Fourier Transform (FFT) length 1024 points, Hamming window, frame 50%, overlap 87.5%), the duration and the four variables of the fundamental frequency: the beginning ($f0_{\text{beg}}$), the end ($f0_{\text{end}}$), the maximum ($f0_{\text{max}}$) and the minimum ($f0_{\text{min}}$), using the standard marker and the reticular cursors (Fig. 1). For each contact-USV, **we automatically measured the peak frequency of the entire call (f_{peak}) in the power spectrum window of Avisoft (Fig. 1).**

Statistical analyses

All statistical analyses were made with STATISTICA 8.0 (StatSoft Inc., Tulsa, OK, USA). Means are given as mean \pm SD, all tests were two-tailed, the differences were considered significant whenever $p < 0.05$. We used a one-way ANOVA to compare body mass and body dimensions between species. We used GLMM for **estimating the effects of cross-fostering** on the acoustics of contact-USVs, with the way of raising (foster vs non-foster) included as fixed factor and animal identity (ID) nested in the way of raising, included as random factor.

Results

Male and female *M. unguiculatus* did not differ in body mass, body length and head length, whereas male *M. vinogradovi* were larger in body mass, body length and head length than female *M. vinogradovi* (Table 1). Foster and non-foster female *M. unguiculatus* did not

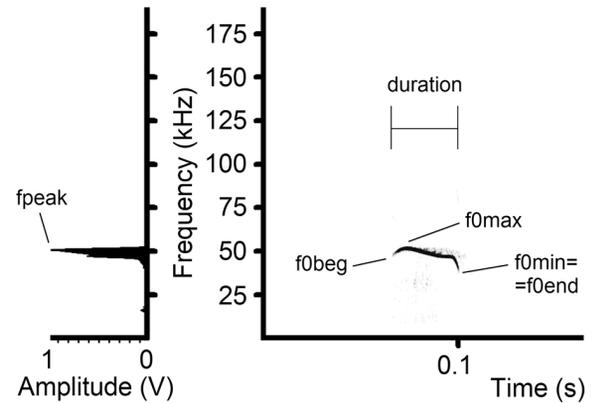


Fig. 1. Measured acoustic parameters on spectrogram (right) and power spectrum (left) illustrated by example contact ultrasonic call (contact-USV) of an adult female *Meriones vinogradovi*. Designations: duration — call duration; $f0_{\text{max}}$ — the maximum fundamental frequency; $f0_{\text{min}}$ — the minimum fundamental frequency; $f0_{\text{beg}}$ — the beginning fundamental frequency; $f0_{\text{end}}$ — the end fundamental frequency; f_{peak} — the peak frequency. Spectrogram was created with the following settings: sampling frequency 384 kHz, Hamming window, FFT 1024 points, frame 50%, overlap 87.5%.

differ by body mass, body length and head length. Similarly, foster female *M. vinogradovi* did not differ by body mass, body length and head length from non-foster female *M. vinogradovi* (Table 1).

Spectrograms of contact-USVs for non-foster and foster gerbils of both species are presented on Fig. 2. In non-foster control animals, duration of the contact-USVs did not differ between species, whereas the peak frequency and all parameters of fundamental frequency were lower in *M. unguiculatus* (Table 2; Fig. 3). Contact-USVs of foster *M. unguiculatus* were shorter and higher in fundamental and peak frequency than in non-foster *M. unguiculatus* (Table 2; Fig. 3). Contact-USVs of foster *M. vinogradovi* were shorter and higher in the beginning and minimum fundamental frequencies compared to non-foster *M. vinogradovi*. The values of

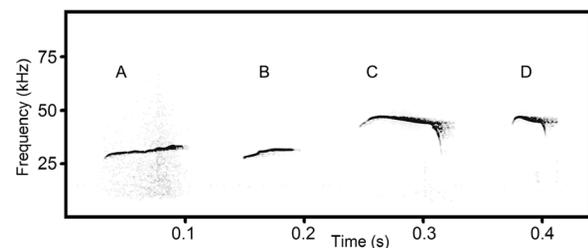


Fig. 2. Spectrogram illustrating example contact-USV calls of adult gerbils: A – *Meriones unguiculatus*, raised by own species, B – *M. unguiculatus*, raised by foster species, C – *M. vinogradovi*, raised by own species, D – *M. vinogradovi*, raised by foster species. Spectrogram was created with the following settings: sampling frequency 192 kHz, Hamming window, FFT 1024 points, frame 50%, overlap 93.75%.

Table 1. Values (mean \pm SD) for body size parameters of male and female adult *Meriones unguiculatus* and *Meriones vinogradovi* raised by own species (non-foster) or raised by foster species (foster) and one-way ANOVA results for comparison between species. Each table line indicates one ANOVA analysis. Designation: N — number of individuals. Different letters indicate significant differences between groups, the same letters indicate no significant differences between groups based on Tukey post hoc pairwise comparisons.

Body parameter	<i>Meriones unguiculatus</i>			<i>Meriones vinogradovi</i>			ANOVA
	non-foster, males, N=5	non-foster, females, N=5	foster, females, N=2	non-foster, males, N=6	non-foster, females, N=6	foster, females, N=1	
Body mass (g)	73.8 \pm 12.4 ^a	72.8 \pm 15.2 ^a	62.0 \pm 8.5 ^a	195.0 \pm 21.6 ^b	134.3 \pm 22.6 ^c	120 ^{a,c}	$F_{5,19}=37.15$; $p<0.001$
Body length (mm)	104.5 \pm 8.7 ^a	99.9 \pm 6.1 ^a	105.0 \pm 7.1 ^{a,d}	156.8 \pm 6.3 ^b	134.8 \pm 6.6 ^c	130 ^{c,d}	$F_{5,19}=52.77$; $p<0.001$
Head length (mm)	37.4 \pm 1.7 ^a	38.5 \pm 0.8 ^a	39.2 \pm 0.1 ^{a,d}	47.2 \pm 1.3 ^b	45.8 \pm 1.4 ^b	43.9 ^{b,d}	$F_{5,19}=52.21$; $p<0.001$

Table 2. Values (mean \pm SD) for the contact ultrasonic calls (contact-USVs) acoustic parameters of adult *Meriones unguiculatus* and *M. vinogradovi* raised by own species (non-fosters) or by another species (fosters) and GLMM results for comparison between species. Each table line indicates one ANOVA analysis. Designations: non-foster — control individuals raised by own species; foster — individuals raised by another species; duration — call duration; f0max — the maximum fundamental frequency; f0min — the minimum fundamental frequency; f0beg — the beginning fundamental frequency; f0end — the end fundamental frequency; fpeak — the peak frequency; N — number of individuals; n — number of calls. Different letters indicate significant differences between groups, the same letters indicate no significant differences between groups based on Tukey *post hoc* pairwise comparisons.

Acoustic parameter	<i>Meriones unguiculatus</i>		<i>Meriones vinogradovi</i>		GLMM
	non-foster, N=10, n=178	foster, N=2, n=80	non-foster, N=12, n=214	foster, N=1, n=58	
Duration (ms)	57 \pm 41 ^a	45 \pm 50 ^b	49 \pm 35 ^{a,b}	27 \pm 11 ^c	$F_{3,505}=1.05$; $p=0.39$
f0max (kHz)	34.42 \pm 3.85 ^a	35.87 \pm 3.99 ^b	48.46 \pm 4.79 ^c	49.24 \pm 4.18 ^c	$F_{3,505}=49.46$; $p<0.001$
f0min (kHz)	30.12 \pm 3.55 ^a	32.69 \pm 3.62 ^b	39.91 \pm 6.42 ^c	41.86 \pm 3.98 ^d	$F_{3,505}=15.11$; $p<0.001$
f0beg (kHz)	30.87 \pm 3.72 ^a	33.31 \pm 4.07 ^b	43.81 \pm 5.39 ^c	45.65 \pm 3.66 ^d	$F_{3,505}=43.19$; $p<0.001$
f0end (kHz)	32.93 \pm 3.95 ^a	34.80 \pm 4.09 ^b	42.90 \pm 7.66 ^c	43.70 \pm 5.89 ^c	$F_{3,505}=12.14$; $p<0.001$
fpeak (kHz)	32.74 \pm 3.92 ^a	34.61 \pm 3.69 ^b	45.91 \pm 4.28 ^c	46.86 \pm 3.47 ^c	$F_{3,505}=36.66$; $p<0.001$

the peak frequency and of the maximum and end fundamental frequencies did not differ between foster and non-foster *M. vinogradovi* (Table 2; Fig. 3).

Discussion

This is the first study of interspecies cross-fostering effects on the acoustics of ultrasonic calls in mammals, which are produced with whistle mechanism (Mahrt *et al.*, 2016; Riede *et al.*, 2017; Håkansson *et al.*, 2022). Previous studies on cross-fostering wild-type grasshopper mice (Pasch *et al.*, 2016) and naked mole-rats (Barker *et al.*, 2021) were made on human-audible vocalizations which rodents produce with phonation mechanism (Riede *et al.*, 2011; Pasch *et al.*, 2017).

We showed that the contact ultrasonic calls of non-foster (control) animals are substantially lower-frequency in adult *M. unguiculatus* than in adult *M. vinogradovi*. In adult *M. vinogradovi*, the maximum fundamental and peak frequencies of contact ultrasonic calls (48.5 kHz and 45.9 kHz, respectively) were very similar with those of 6–10-day-old pup *M. vinogradovi* (52.7 kHz and 49.2 kHz, respectively) and pup *M. unguiculatus* (50.0 kHz and 44.5 kHz) (Ko-

zhevnikova *et al.*, 2021). Thus, we may conclude that during maturation from pups to adults, the fundamental and peak frequencies of the ultrasonic calls substantially decrease in *M. unguiculatus*, but remain practically unchanged in *M. vinogradovi*. So, we expected that the effect of social surrounding on ultrasonic calls might result in increase of frequency parameters in foster *M. unguiculatus* but in decrease in foster *M. vinogradovi*. However, we only observed the expected trend of changes in foster *M. unguiculatus* but not in foster *M. vinogradovi*, in which the trend towards higher-frequency calls was opposite to the expected. So far, cross-fostering effects on the acoustics of ultrasonic calls were only investigated between strains of laboratory mice. Male domestic mice produce complex ultrasonic courtship songs when courting a receptive female; these songs are substantially different by sets of syllables among different strains (Holy & Guo, 2005; Kikusui *et al.*, 2011; Arriaga & Jarvis, 2013). Cross-fostered male mice of B6 and BALB strains retained the sets of syllables in their courtship songs as in their parental strains (Kikusui *et al.*, 2011). Although peak frequency of the ultrasonic syllables of male mice songs differs between B6 and BxD strains for 6–9 kHz, group-housing of two males of different strains with

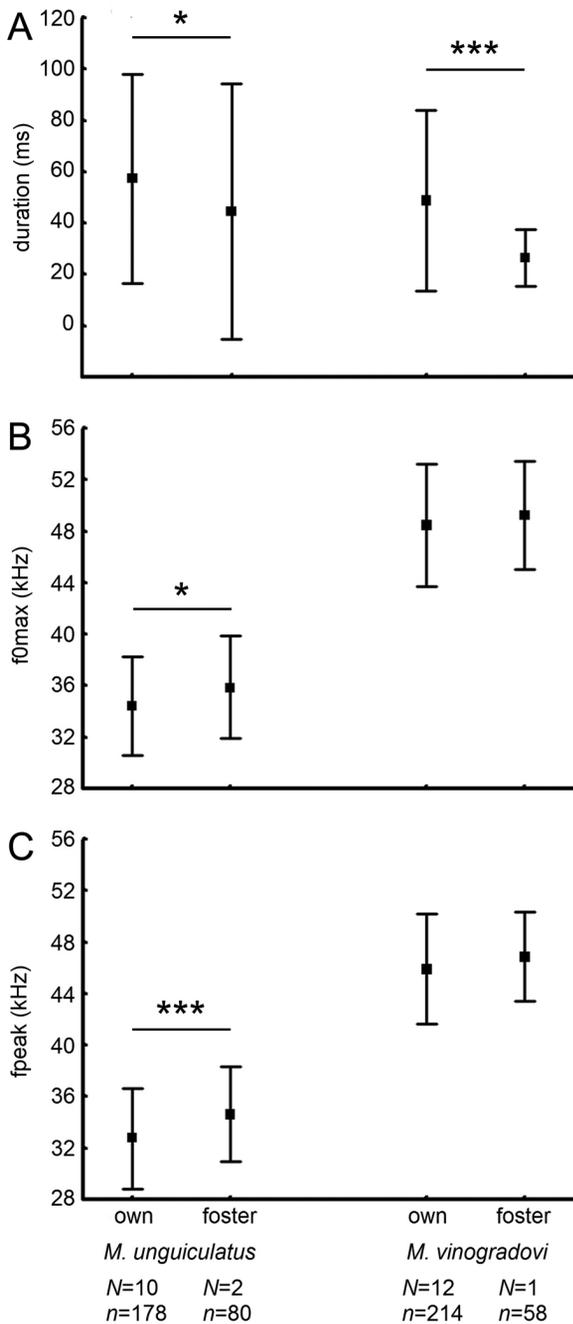


Fig. 3. The values of (A) duration, (B) maximum fundamental frequency (f0max) and (C) peak frequency (fpeak) of the ultrasonic contact calls (contact-USVs) of adult *Meriones unguiculatus* and *M. vinogradovi*, raised by own species or foster species. Designations: own — control non-foster individuals raised by own species; foster — cross-foster individuals raised by foster species; *N* — number of individuals; *n* — number of calls. Points indicate averages, whiskers indicate SD. * — $p < 0.05$, *** — $p < 0.001$, Tukey *post hoc*.

one female for 8 weeks resulted in matched peak frequencies of male song ultrasonic syllables, decreasing in one male and increasing in another one (Arriaga *et*

al., 2012). Male mice kept singly for long time (socially deprived) produced at interaction with unfamiliar conspecific longer ultrasonic calls and changed substantially the proportion of different types of ultrasonic calls compared to males kept in groups (Chabout *et al.*, 2012). Raising genetically deaf and normally hearing pup laboratory mice by deaf mothers revealed lack of differences in the acoustic development in terms of the number, usage and structure of pup vocalizations (Hammerschmidt *et al.*, 2012). Similarly, there were no differences in adult male courtship songs in relation to hearing ability (Hammerschmidt *et al.*, 2012). Experimental deafening pup mice at 2 days of age also did not result in changes of the temporal structure of vocalization bouts, the types of vocalizations, the patterns of syllables, and the acoustic features of each syllable type emitted by deaf males in the presence of a female compared to hearing males (Mahrt *et al.*, 2013). These two last studies suggest that development of adult ultrasonic calls of laboratory mice does not demand the auditory feedback along ontogeny (Hammerschmidt *et al.*, 2012; Mahrt *et al.*, 2013), what is necessary for the vocal production learning (Janik & Knörnschild, 2021; Lattenkamp *et al.*, 2021).

The applied recording procedure, including isolation and handling the animal, was appropriate for promoting emission the contact-USVs. Ultrasonic calls recorded during the experimental procedure were similar in the acoustic structure with contact-USVs described earlier in captive groups of *M. unguiculatus*: mean duration 26 ms and mean f0 30 kHz (Ter-Mikaelian *et al.*, 2012) and mean duration 34 ms and f0 from 29 to 35 kHz (Kobayasi & Riquimaroux, 2012). The contact-USVs of *M. unguiculatus* occurred not only during peaceful interactions in family groups (Kobayasi & Riquimaroux, 2012), but also when two unfamiliar animals were released to novel territory and at the beginning stages of aggressive interactions (Ter-Mikaelian *et al.*, 2012). For *M. vinogradovi*, contact-USVs produced by animals in captive groups have yet to be studied.

Acoustic parameters of voice calls depend on body size: the fundamental and peak frequencies are commonly lower in larger-sized animals, because they have larger sound-producing structures (vocal folds in the larynx) and longer vocal tract (Charlton & Reby, 2016; Bowling *et al.*, 2017; Garcia *et al.*, 2017). For the whistle calls, such inverse relationship with body size is lacking. In rodents, from pups to adults, the fundamental frequency of whistle ultrasonic calls may increase (Zaytseva *et al.*, 2019), remain unchanged (Johnson *et al.*, 2017; Dymkaya *et al.*, 2022) or decrease (Yurlova *et al.*, 2020; this study). The fundamental frequency of rodent ultrasonic calls does not depend on body size in adults of four species (Riede & Pasch, 2020) and in pups of six species (Kozhevnikova *et al.*, 2021).

Adult individual *M. unguiculatus* and *M. vinogradovi* are strongly different in body size: *M. vinogradovi* is larger and twice heavier than *M. unguiculatus*. However, the whistle ultrasonic calls of *M. vinogra-*

dovi (mean f_{0max} 48.46 kHz) are substantially higher-frequency than in *M. unguiculatus* (mean f_{0max} 34.42 kHz). In our study, these differences in body size did not affect body size of fosters: foster females of both species **did not differ in body size from the non-foster control females of own species**. In contrast, in the cross-fostering study of grasshopper mice, the effect of malnutrition of foster pups was found, **which, by opinion of the authors, could affect the acoustics of the fosters** (Pasch *et al.*, 2016).

Overall, our preliminary data indicate subtle modifications of acoustic traits under **social influences on the ultrasonic whistle calls** of one of the study gerbil species. Similarly slight social effects on vocalizations were shown for audible calls produced with phonation mechanism in different mammalian taxa not experiencing vocal production learning. Such studies of social effects on vocalizations are important for understanding **the limits of vocal plasticity** in mammalian species with innate vocal repertoires incapable to vocal production learning (Janik & Slater, 2000; Janik & Knörnschild, 2021; Vernes *et al.*, 2021).

With small number of individuals, potential effect of acoustic individuality on the obtained results can be very high. However, even such pilot study with a small number of individuals is very valuable because of the critically scarce number of studies of social effects on the acoustics of ultrasonic calls. Cross-fostering experiments are extremely time, resources and labor-consuming, so animal samples are commonly small and published research is scarce (Kikusui *et al.*, 2011; Pasch *et al.*, 2016; Barker *et al.*, 2021).

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