BRILL

Behaviour 161 (2024) 587–611

Behaviour
brill.com/beh

Startle together, shout in chorus: collective bursts of alarm calls in a social rodent, the Harting's vole (*Microtus hartingi*)

Ilya A. Volodin [a,*], **Marina V. Rutovskaya** [b], **Fedor N. Golenishchev** [c] and **Elena V. Volodina** [b]

[a] Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Vorobievy Gory 1/12, Moscow 119234, Russia
[b] Department of Behaviour and Behavioural Ecology of Mammals, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky Prospect 33, Moscow 119071, Russia
[c] Zoological Institute, Russian Academy of Sciences, Universitetkaya Emb. 1, Saint Petersburg 199034, Russia
[*]Corresponding author's e-mail address: volodinsvoc@gmail.com
ORCID iDs: Volodin: 0000-0001-6278-0354; Rutovskaya: 0000-0003-3964-1529; Golenishchev: 0000-0003-2889-4774; Volodina: 0000-0001-9755-4576

Received 28 February 2024; initial decision 3 June 2024; revised 11 June 2024; accepted 28 June 2024; published online 2 August 2024

Abstract

We investigate the acoustic structure of alarm calls in a highly social rodent, the Harting's vole (*Microtus hartingi*) and describe the phenomenon of collective shouting of bursts of alarm calls which could be produced in synchronized series. The alarm calls of Harting's voles were recorded using an automatic device from 10 different family groups, containing from 4 to 15 potential callers, released to outdoor enclosures. Natural predators and humans served as call-eliciting stimuli. We reveal acoustic differences between urgent alarm calls, evoked by close-vicinity predators and identified from recordings by their calls and by rustle noise from the caller's escape to burrow, and other alarm calls. We also reveal acoustic parameters between alarm calls produced in bursts and other alarm calls (produced in individual series or by a few non-synchronized callers). We discuss why the alarm calls of Harting's voles are unusually high-frequency (about 17 kHz on average in the maximum fundamental frequency) among other vole species producing high-frequency alarms. Adaptive significance of producing the collective synchronized bursts of alarm calls by Harting's voles remains unclear without direct observations of vocal vigilance in this species under natural conditions.

Published with license by Koninklijke Brill BV | DOI: 10.1163/1568539X-bja10274
 | ISSN: 0005-7959 (print) 1568-539X (online)

Keywords
alert behaviour, anti-predator response, Arvicolinae, rodent, vigilance, vocalization.

1. Introduction

Mobbing potential predators in the context of anti-predatory vigilance behaviour was described for many mammals (Seyfarth et al., 1980; Manser, 2001; Zuberbühler, 2009; Volodina et al., 2018; Volodin et al., 2021). In rodents, the anti-predatory alarm calling is especially well-developed (Shelley & Blumstein, 2005; Garcia-Navas & Blumstein, 2016; McRae, 2020). The alarm calls are known for marmots (Blumstein, 2007a), squirrels (McRae & Green, 2017), ground squirrels (Nikolskii, 1979; Matrosova et al., 2012), rats (le Roux et al., 2002; Brudzynski & Holland, 2005; Litvin et al., 2007; Chen et al., 2023), gerbils (Randall & Rogovin, 2002; Ter-Mikaelian et al., 2012) and voles (Pandourski, 2011; Rutovskaya, 2012). In most rodent species, the alarm calls are intense sounds emitted in series with quasi-regular inter-call intervals in the audible range of frequencies (below 20 kHz), although some rodent species produce ultrasonic alarms (Brudzynski & Holland, 2005; Ter-Mikaelian et al., 2012; Volodin et al., 2024).

The alarm calls promote conspecifics to interrupt their current activity, to look around and to modify behaviour accordingly to threat urgency (Fichtel & Kappeler, 2002; Blumstein, 2007b). As a rule, only one individual is calling, however, for ground squirrels, a few colony members can produce the alarm calls together (Sloan & Hare, 2008).

For the voles of Arvicolinae subfamily, the alarm calls are only known for the four species: the Brandt's vole *Lasiopodomys brandtii* (Nikolskii & Sukhanova, 1992; Rutovskaya, 2012), the narrow-headed vole *L. gregalis* (Rutovskaya & Nikolskii, 2014), the closely related to *L. gregalis* recently identified cryptic species the Raddey's vole *L. raddey* (Rutovskaya & Nikolskii, 2014) and the Harting's vole *Microtus hartingi* (Pandourski, 2011). All these four species are highly social and live in extended family colonies consisting of a parental pair and a few generations of their offspring (Çolak et al., 1998; Kislyi et al., 2021; Kryštufek & Shenbrot, 2022; Gromov, 2023).

The Harting's vole belongs to the "guentheri" group among the social voles subgenus *Sumeriomys* of the Arvicolinae subfamily (Golenishchev et al., 2002, 2003; Kryštufek et al., 2012; Abramson et al., 2021; Kryštufek & Shenbrot, 2022). The Harting's vole is a middle-sized vole, with body mass

40–50 g in both sexes (Çolak et al., 1998; Kryštufek & Shenbrot, 2022). Taxonomic position of *Microtus hartingi* and its subspecies is currently under permanent revision, on the basis of *Cytb* gene analysis (Golenishchev & Malikov, 2011; Kryštufek et al., 2012; Yiğit et al., 2017; Thanou et al., 2020; Golenishchev et al., 2022), comparative skull and brain morphometrics (Markov et al., 2014; Zorenko et al., 2020, 2023), baculum and sperm morphometrics (Golenishchev et al., 2002; Yiğit et al., 2012; Zorenko & Golenishchev, 2015; Zorenko & Kagainis, 2021) and experimental interspecies hybridization (Zorenko et al., 2016; Golenishchev et al., 2022; Zorenko, 2023). Earlier, the Harting's vole was considered within Guenter's vole *Microtus guentheri*, but currently these two species are recognized as sister species, the Harting's vole as more western species (the Balkans and the Anatolia peninsula) and the Guenter's vole as more south-eastern species (Syria and Israel) (Thanou et al., 2020; Kryštufek & Shenbrot, 2022).

For the Harting's vole, the alarm call was previously described by one single call, recorded as a single event only once in the wild in Bulgarian Rodopes on a bat detector (Pandourski, 2011). The spectrogram shows that this call was high-frequency, expanding up to 17.2 kHz reminiscent by sounding a call of some bird (Pandourski, 2011). To prove the belonging this call to Harting's vole, five individual Harting's voles were then captured in this place (Pandourski, 2011). In the current study, we tested a hypothesis that Harting's voles indeed produce the alarm calls at such high frequencies as were reported by Pandourski (2011).

During dyad interactions on a neutral territory, male and female Harting's voles produced the squeaks (Rutovskaya, 2019a). The duration of the squeaks varied from 30 to 180 ms; the maximum fundamental frequency ranged from 4 to 13 kHz. The squeaks had different contours of the fundamental frequency, downward, upward or, most often, the-rise-and-fall contour (Rutovskaya, 2019a).

Although Harting's voles were bred for research in captivity for many years (Golenishchev et al., 2022; Zorenko, 2023), the alarm calls have never been recorded from captive populations of this species (Rutovskaya, 2019a). The aim of this study was to describe in detail the acoustic variation of alarm calls of Harting's voles. We design an experimental situation eliciting the alarm calls in outdoor semi-captive groups of Harting's voles and describe the phenomenon of joint startle calling of this species.

2. Methods

2.1. Study site, animals and dates

Alarm calls of Harting's voles *Microtus hartingi ankaraensis* (Golenishchev et al., 2022) were automatically recorded from 16 July to 3 September 2023 at the Joint Usage Center "Live collection of wild species of mammals" at A.N. Severtsov Institute of Ecology and Evolution (the biological station "Tchernogolovka"), Moscow Region, Russia, located 50 km NE from Moscow city. The laboratory population of Harting's voles initially started from 3 females and 4 males obtained in 2003 from surroundings of Ankara city: Kırşehir, Turkey (39°9′56.38″N, 34°6′6.99″E). The Harting's voles breed easily in captivity for many generations without appearing any signs of inbred depression or incest-tabu (Zorenko et al., 2016; Golenishchev et al., 2022; Zorenko, 2023).

In March 2023, we obtained from a captive population of Harting's voles of Zoological Institute of Russian Academy of Sciences (Saint Petersburg, Russia) 15 adult individuals aged 2 months or older (6 males, 9 females) and 10 (4 males, 6 females) offspring aged below 1 month. At the biological station 'Tchernogolovka', the animals were kept and bred under a natural light regime at room temperature (22–24°C) in the vivarium room 20 m^2, together with other vole species. The plastic home cage of each family group of $55 \times 35 \times 20$ cm contained the bedding of sawdust, various shelters and hay as enrichment. The voles received custom-made small rodent chow with mineral supplements, fruits, grass and vegetables. Water was available ad libitum.

By the time the study of alarm calls began in mid-July, we already had 15 family groups of Harting's voles. The groups consisted of a pair of adults (male-female, 10 groups) or one adult female with a removed male (5 groups) and their offspring from 1–3 subsequent litters (in total, over 100 offspring in 15 groups). Ten of 15 groups were used in experiments for eliciting the alarm calls, 6 contained both male and female parents and 4 contained only the female parent. In these 10 groups, the number of sexually mature animals (2 months of age and older) varied from 4 to 15 per group (10.5 ± 3.1 individuals on average). Three of the 10 groups additionally contained from 1–4 dependent pups below 10 days of age.

2.2. Attempts to elicit alarm calls indoor in cages

Preliminary observations showed that Harting's voles sometimes produced short series of high-frequency calls at sudden entrance of a human to the vivarium room. These calls were strongly reminiscent of the alarm call described for one wild-living individual Harting's vole (Pandourski, 2011). However, repeated attempts to elicit the alarm calls in the Harting's voles by sudden entrances of researchers to the vivarium room only enabled to record one series of 10 alarm calls from one cage. Attempts to elicit alarm calling from Harting's voles kept in the vivarium room by flapping over the cage with a baseball cap (following the procedure for eliciting alarm calls in live-trapped ground squirrels, Matrosova et al., 2009, 2010a) did not evoke the alarm calling, instead, the animals silently dived under the sawdust or escaped to shelters.

2.3. Eliciting alarm calls in outdoor enclosures

Successful eliciting the alarm calls from Harting's voles was achieved by placement the family groups of Harting's voles in outdoor enclosures (2 × 1 × 0.6 m), under natural temperature and light regime. Two outdoor enclosures were standing on the floor in a summer pavilion with wire-mesh walls and a roof, protecting from rain. Each enclosure had 40-cm bedding of sawdust and hay. Large size of the enclosures and thick sawdust layer enabled the voles to create the system of underground burrows, which imitated natural burrow systems of these voles (Çolak et al., 1998).

Two experimental groups of Harting's voles were released simultaneously to the two-neighbouring wire-mesh enclosures for recording the alarm calls and after 1–2 weeks replaced by next two groups and so on. The enclosures of Harting's voles were perfectly protected from predation, but potential predators could visit the pavilion, frighten the Harting's voles and provoke their alarm calling. The potential predators were feral cats, mustelids, different species of corvids, primarily *Pica pica*, and owls, primarily *Asio otis*. The alarm calls were produced by Harting's voles toward predators trying to catch them through the wire mesh of the outdoor enclosures. Close-vicinity calls of predators (cats, corvids, etc.) were sometimes present in the audio recordings along with alarm calls of Harting's voles. The voles also occasionally produced the alarm calls toward people visiting the enclosures once a day for animal feeding; otherwise, people rarely approached to the enclosures. Thus, release of family groups of Harting's voles in the large outdoor enclosures allowed them to create the system of subterranean runs and shelters, enhanced their vocal alertness and provoked the alarm calling toward potential danger.

2.4. *Audio recording*

For recording the alarm calls we used an automated recorder SongMeter SM2+ (Wildlife Acoustics, Maynard, MA, USA), established between the two enclosures. The device had two omnidirectional microphones at the angle of 180 degrees to each other. One microphone was directed to the first enclosure and the second to the second enclosure. The distance from microphone to voles ranged from 30 to 300 cm. The device recorded calls every day, in the mode 48 kHz, 16-bit, stereo. The recording schedule was set at 14-min and 1-min pause, 3 h around dusk and 3 h around down, 5 h 36 min in total per 24-h cycle.

From 4 of 10 experimental groups of Harting's voles we obtained recordings for the duration of 14 days (78.4 h of recordings per group). From other 4 groups, we obtained recordings for 7 days (39.2 h of recording per group). From remaining 2 groups, we obtained recordings only for 2 days (11.2 h of recording per group) because of refusals of the recording device. The total of 2112 14-min digital stereo audio files provided 492.8 h of recordings; each file contained recordings of two neighbouring groups. Based on ratios of amplitude of call recording on wave-forms of the left and right channels of the stereo audio file, we assigned each alarm call to one or another simultaneously recorded group.

2.5. *Verifying the automated recordings as belonging to Harting's voles*

For verifying the automated recordings as belonging to Harting's voles, were also received reference recordings of the alarm calls of Harting's voles toward researchers. For the six referential recording sessions, we used a solid-state recorder Marantz PMD-660 (D&M Professional, Kanagawa, Japan) with a hand-held AKG-C1000S (AKG-Acoustics, Vienna, Austria) cardioid electret condenser microphone, at sampling rate 48 kHz, 16-bit resolution. In addition, we used a hand-held Echo Meter Touch 2 PRO recorder (Wildlife Acoustics) attached to a compatible smartphone, at sampling rate 256 kHz, 16-bit resolution. The distance to alarm callers during the referential recordings was about 1–2 m for both recording devices. These recordings were not used in the acoustic and statistical analyses, but confirmed that the automatically recorded alarm calls belonged to the Harting's voles and that they are used in the alarm context.

2.6. Call samples and acoustic analysis

Visual inspection of call spectrograms was made using Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany). Preliminary visual inspection of the spectrograms showed that the recordings contained, aside the alarm calls of Harting's voles, also some number of squeaks of this species. The main difference of the squeaks from the alarm calls was a substantially lower fundamental frequency and the-rise-and-fall contour of the fundamental frequency (Rutovskaya, 2019a). For spectrographic analysis, we only selected the alarm calls, distinctive from the squeaks by a prominent rise of fundamental frequency without a subsequent fall to the lower frequencies (Pandourski, 2011).

From 2112 14-min stereo audio files 369 contained at least one alarm call. From 309 audio files containing alarm calls of good quality, we selected for analysis the alarm calls non-overlapped with noise and with a visible start of a call. In total, from the 10 groups of Harting's voles, we analysed spectrographically 1888 alarm calls, from 12 to 409 alarm calls per group (on average, 188.8 $\pm$ 129.5 calls). If the call belonged to a long series of similar calls, potentially emitted by the same individual, we only took 2–10 calls per series, to decrease potential pseudo-replication.

Acoustic parameters of alarm calls were measured manually with Avisoft and automatically exported to Microsoft Excel (Microsoft, Redmond, WA, USA). For measuring, we used the following settings: sampling frequency 48 kHz, Hamming window, FFT (Fast Fourier Transform) length 1024 points, frame 50%, and overlap 93.75%, providing 47 Hz frequency resolution and 1.33 ms time resolution. As visual inspection of spectrograms showed that the minimum f0 of the calls always exceeded 2 kHz, we applied Gauss high-pass filtering at 2 kHz to remove low-frequency noise.

For each alarm call, we measured, in the spectrogram window of Avisoft, the duration with the standard marker cursor (Figure 1). We measured, with the reticule cursor, the fundamental frequency (f0) parameters: the f0 at the onset of a call (f0beg), which was always equal to the minimum f0 of a call, the maximum f0 (f0max), the f0 at the end of a call (f0end), and the local minimum f0 between f0max and f0end (f0minlocal), if its value was lower than f0end (Figure 1). The rise of fundamental frequency from call

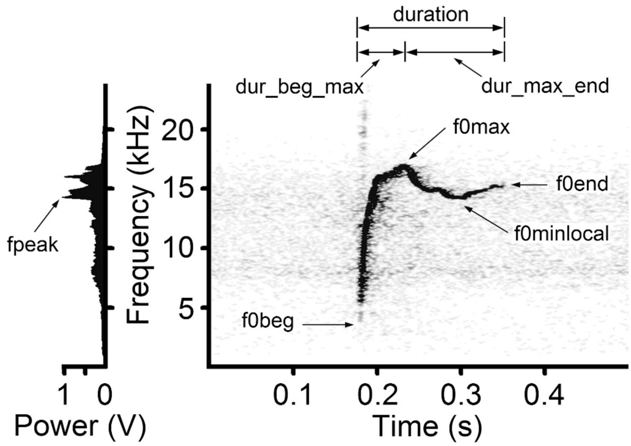

Figure 1. Measured acoustic parameters of alarm calls of Harting's voles. Spectrogram (right) and mean power spectrum of call (left). Designations: duration, call duration; dur_beg_max, duration from the beginning of a call to the point of maximum fundamental frequency; dur_max_end, duration from the point of maximum fundamental frequency to the end of a call; f0beg, fundamental frequency at the onset of a call; f0max, maximum fundamental frequency; f0end, fundamental frequency at the end of a call; f0minlocal, local minimum fundamental frequency between f0max and f0end; fpeak, peak frequency. The spectrogram was created using a sampling frequency of 48 kHz, Hamming window, FFT 1024 points, frame 50% and overlap 96.87%.

beginning to call maximum (df0_max_beg) was calculated as the difference between f0max and f0beg, and the fall of fundamental frequency from maximum to minimum (df0_max_min) was calculated as the difference between f0max and f0minlocal (or f0end, if f0end=f0minlocal). We calculated call duration from the beginning of a call the point of the maximum fundamental frequency (dur_beg_max) and duration from the point of maximum fundamental frequency to the end of a call (dur_max_end) (Figure 1). In addition, we measured, in the power spectrum of Avisoft, the frequency of maximum amplitude (fpeak) from the call mean power spectrum (Figure 1). For alarm calls produced in series, we measured the inter-call interval from the end of a preceding call to the start of the next call.

Based on visual inspection of audio recordings in the spectrogram window of Avisoft, one researcher (IAV) classified the alarm calls to one of four contours (Figure 2): flat, chevron, upward and complex (partially following Dymskaya et al., 2022). The upward contour was noted if the f0max was equal to f0end. The flat contour was noted if the difference between f0max

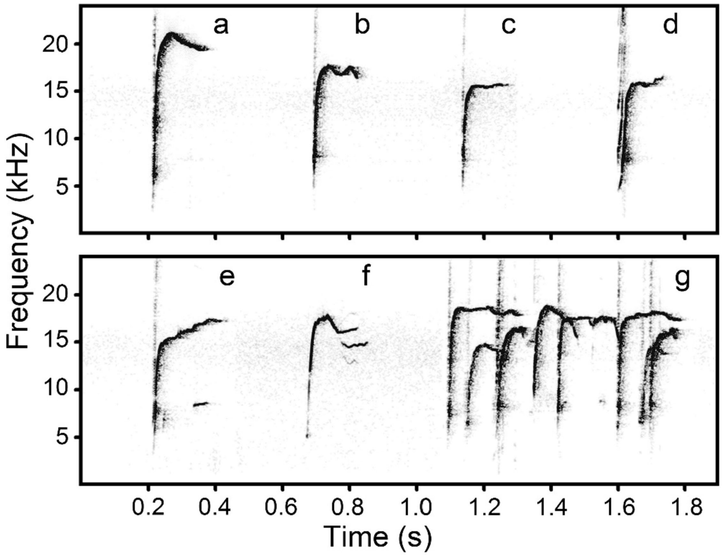

Figure 2. Spectrogram illustrating the Harting's vole alarm call (a–c) four contours of fundamental frequency, (e-f) nonlinear phenomena and (g) the burst of superimposing spectrograms of alarm calls pointing to the phenomenon of collective shouting. Designations: a, call with chevron contour; b, call with complex contour; c, call with flat contour; d, call with upward contour; e, call with subharmonics; f, call with biphonation; g, collective shouting of alarm calls by 8 individual voles (family group B2, the group contains in total 9 individuals, the alarms of different individuals superimpose each other). The spectrogram was created using a sampling frequency of 48 kHz, Hamming window, FFT 1024 points, frame 50% and overlap 93.75%. The audio file is available as Audio 1 at https://stream.cadmore.media/player/289bbe79-4622-4948-9ba3-d50c826ccbf0.

and f0end or f0minlocal was less than 0.6 kHz. If the difference between f0max and f0end or f0minlocal was equal or larger than 0.6 kHz, call contour could be classified as chevron (up-and-down) or complex (up-and-down a few times) (Figure 2).

We also noted in the alarms the occurrence of nonlinear vocal phenomena: subharmonics or biphonations (Wilden et al., 1998; Yurlova et al., 2020; Dymskaya et al., 2022; Rutovskaya et al., 2024). Subharmonics were noted if intermediate frequency band of 1/2 of f0 was present. Biphonation was noted when two independent fundamental frequencies and their combinatory frequency bands were present in call spectrum (Figure 2).

We noted whether the alarm call was urgent alarm based on characteristic attending noises (e.g., cat meows, strikes, human voices and rustle noise evoked by animal fleeing to burrow). We noted whether the caller was only

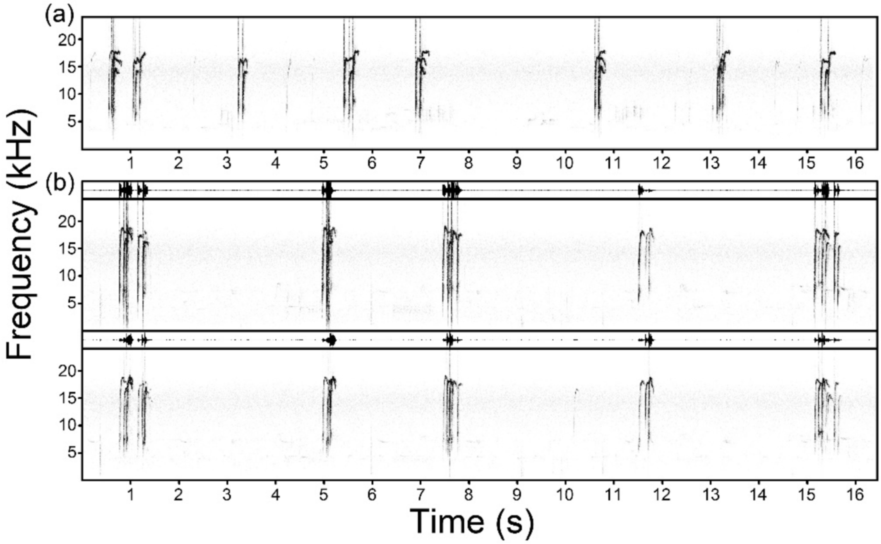

Figure 3. Spectrograms illustrating natural series of collective bursts of alarm calls (alarm bursts) produced by Harting's voles. Simultaneous calling is evident from superimposed spectrograms of alarm calls produced nearly synchronously by different individuals. A, mono-mode spectrogram, illustrating overlapping alarm calls of Harting's voles within one family group (group B2, containing 9 individuals); b, stereo-mode spectrograms and wave-forms, illustrating overlapping alarm calls of Harting's voles within and between two neighboring family groups (above group B8, containing 12 individuals, below group B10, containing 10 individuals). Wave-forms enable to establish the belonginess of alarm calls to this or those group. For example, at 11.6 s, the first call outcomes from group B8 and the second and third calls outcome from group B10. The spectrograms were created using a sampling frequency of 48 kHz, Hamming window, FFT 1024 points, frame 50% and overlap 75%. The audio files are available as Audio 2 (https://stream.cadmore.media/player/891adf87-09df-46d6-a349-fdb68b064a2d) and Audio 3 (https://stream.cadmore.media/player/2adf1a14-78da-434c-ba30-8cdce12762cb).

one or more, based on presence of alarms of other callers within 5 s. We also noted the phenomenon of collective shouting if the call spectrogram was superimposed by alarm calls of other individuals (Figure 3).

2.7. Statistical analyses

Statistical analyses were carried out with STATISTICA, v.8.0 (StatSoft, Tulsa, OK, USA). Means are given as mean ± SD, all tests were two-tailed, and differences were considered significant whenever $p < 0.05$.

We used two-way ANOVA with Unequal N HSD post-hoc test for unequal samples to compare variability of acoustic parameters between the alarms with different contours of fundamental frequency and also to compare the acoustic parameters of urgent alarms and superimposed alarms with a total sample of alarms, with inclusion in analysis the identity of the experimental group as fixed factor. We used Fisher's exact test to compare percentages.

2.8. *Ethical note*

The authors adhered to the "Guidelines for the treatment of animals in behavioural research and teaching" (Anim. Behav. 2020, 159, I-XI) and the legal requirements of Russia pertaining to the protection of animal welfare. Management of animals and experimental procedures for this study were approved by the Regulatory Commission of Experimental Research (Bioethics Commission) of A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences (permission no. 38 of 27.07.2020).

3. Results

Alarm calls of Harting's voles displayed a rapid increase of f0 from on average 3.98 kHz (ranging from 2.01 to 7.40 kHz at call beginning) to on average 17.35 kHz (ranging from 12.42 to 22.12 kHz at the point of the maximum of fundamental frequency, followed by a slight decrease of fundamental frequency to 15.92 kHz to the end of a call (ranging from 10.64 to 21.04 kHz) (Table 1). The entire call duration was, on average, 126 ms (ranging from 32 to 410 ms), in particular, the duration from the beginning of a call to the point of the maximum fundamental frequency comprised 65 ms (ranging from 14 to 305 ms) and the duration from the point of the maximum fundamental frequency to the end of a call comprised 57 ms (ranging from 0 to 224 ms) (Table 1). The peak frequency of the alarm calls was, on average, 16.67 kHz (ranging from 5.25 to 21.28 kHz) and in 1739 (92.1%) alarm calls the values of the peak frequency was located in the high-frequency range between f0max and f0minlocal.

Nonlinear phenomena in the alarm calls occurred rarely: subharmonics were only noted in 44 alarm calls (2.3%) and biphonations were only noted in 22 alarm calls (1.2%) (Figure 2). The alarm calls could either be produced in series of similar calls (398 calls in 120 series, 21.1%) or singly (1490 calls, 78.9%). The series were revealed by uniformity of the acoustic structure of the calls, which repeated with quasi-regular intervals suggesting the belonging of these calls to the same individual. The inter-call interval between the

Table 1.
Values (mean ± SD) of the acoustic variables of alarm calls of Harting's voles and two-way ANOVA results for comparisons between calls with different contours of fundamental frequency with inclusion in analysis the identity of the experimental group as fixed factor.

Acoustic parameter	All calls ($N = 1888$)	Chevron ($N = 1390$)	Complex ($N = 155$)	Flat ($N = 257$)	Upward ($N = 86$)	ANOVA results) ($F_{3,1875}$)
Duration (ms)	126 ± 49	120 ± 42^{a}	175 ± 66^{b}	130 ± 53^{a}	130 ± 39^{a}	69.90; $p < 0.001$
dur_beg_max (ms)	65 ± 32	58 ± 22^{a}	86 ± 52^{b}	69 ± 37^{c}	117 ± 40^{d}	128.30; $p < 0.001$
dur_max_end (ms)	57 ± 39	57 ± 35^{a}	85 ± 50^{b}	57 ± 39^{a}	8 ± 14^{c}	97.81; $p < 0.001$
f0beg (kHz)	3.98 ± 1.11	4.02 ± 1.12^{a}	3.66 ± 1.07^{b}	3.99 ± 1.04^{a}	$3.85 \pm 1.11^{a,b}$	5.08; $p = 0.002$
f0max (kHz)	17.35 ± 1.65	17.51 ± 1.65^{a}	17.49 ± 1.46^{a}	16.66 ± 1.67^{b}	16.62 ± 1.14^{b}	22.42; $p < 0.001$
f0end (kHz)	15.92 ± 1.70	15.80 ± 1.72^{a}	$15.94 \pm 1.61^{a,b}$	16.34 ± 1.69^{b}	16.52 ± 1.17^{b}	18.33; $p < 0.001$
fpeak (kHz)	16.67 ± 2.14	16.85 ± 2.15^{a}	$16.72 \pm 1.71^{a,b}$	16.16 ± 2.07^{b}	15.30 ± 2.22^{c}	13.61; $p < 0.001$
df0_max_beg (kHz)	13.37 ± 1.85	13.49 ± 1.86^{a}	13.82 ± 1.64^{a}	12.66 ± 1.74^{b}	12.77 ± 1.62^{b}	21.64; $p < 0.001$
df0_max_min (kHz)	1.50 ± 0.94	1.75 ± 0.81^{a}	1.90 ± 0.95^{a}	0.38 ± 0.20^{b}	0.11 ± 0.19^{b}	329.90; $p < 0.001$

Duration, call duration; dur_beg_max, duration from the beginning of a call to the point of the maximum fundamental frequency; dur_max_end, duration from the point of the maximum fundamental frequency to the end of a call; f0beg, the fundamental frequency at the onset of a call; f0max, the maximum fundamental frequency; f0end, the fundamental frequency at the end of a call; fpeak, the frequency of maximum amplitude; df0_max_beg, the rise of fundamental frequency from the beginning of a call to the point of maximum; df0_max_min, the fall of fundamental frequency from maximum to minimum; *n*, number of calls. Different superscripts (^{a}, ^{b}, ^{c}, ^{d}) indicate statistically different values (Unequal N HSD, $p < 0.05$).

alarm calls of the series was, on average, 1.97 ± 1.46 s and ranged from 0.40 to 8.89 s.

In the total sample of 1888 alarm calls, the most abundant contour was chevron (1390 calls, 73.6%), followed by flat (257 calls, 13.6%), complex (155 calls, 8.2%) and upward contours (86 calls, 4.6%) (Table 1, Figure 2). The duration and the dur_max_end were the longest in calls with complex contour, dur_beg_max was the longest in calls with upward contour and the shortest in calls with chevron contour (Table 1). The peak frequency was the highest in the alarms with the contour chevron and the lowest in the alarms with upward contour. The f0beg was higher in calls with contours chevron and flat, f0max was higher in calls with contours chevron and complex, and f0end was higher in calls with contours flat and upward. Thus, the rise of fundamental frequency from call beginning to call maximum and then the fall of fundamental frequency from maximum to minimum were substantially more prominent in the alarms with contours chevron and complex compared to the alarms with contours flat and upward (Table 1).

There were 201 urgent alarms (10.6% of calls), which, compared with other alarm calls, had a shorter duration (108 ± 46 ms, $F_{1,1877} = 31.43$; $p < 0.001$), shorter dur_max_end (37 ± 30 ms, $F_{1,1877} = 55.01$; $p < 0.001$), lower f0beg (3.84 ± 1.09 kHz, $F_{1,1877} = 7.79$; $p = 0.005$), higher f0max (17.59 ± 1.45 kHz, $F_{1,1877} = 5.94$; $p = 0.02$), higher f0end (16.16 ± 1.54 kHz, $F_{1,1877} = 6.58$; $p = 0.01$) and longer df0_max_beg (13.75 ± 1.66 kHz, $F_{1,1877} = 15.04$; $p < 0.001$). However, the urgent alarms did not differ from other alarms by the percentage of calls with different contours (chevron: 70.6%, flat 13.9%, complex: 10.0%, upward: 5.5%; Fisher's exact test, $p > 0.05$ for all comparisons). Thus, more threatening situation during production of urgent alarms resulted in changes of their time and frequency characteristics.

The Harting's voles often produced their alarm calls collectively. Alarm calls were concentrated only in 369 from 2112 (17.5%) audio files. Most alarm calls, 1426 from 1888 (75.5%), were emitted when there were two or more callers, and only 462 (24.5%) alarm calls were produced when the caller was only one. We also found that Harting's voles display the phenomenon of collective shouting, evident from superimposing the alarm call spectrograms from two or more individuals (from 2 to 10, 4.4 ± 1.9 calls on average) (Figure 3).

Superimposing alarm calls (330 of 1888 alarm calls, 17.5%) did not differ from the total sample of alarm calls by the occurrence of alarm calls with different contours (chevron: 73.6%, flat 15.8%, complex: 7.6%, upward: 3.0%; Fisher's exact test, $p > 0.05$ for all comparisons). Compared with other alarm calls, the superimposing alarm calls had a longer duration (135 ± 49 ms, $F_{1,1877} = 16.38$; $p < 0.001$), longer dur_max_end (65 ± 35 ms, $F_{1,1877} = 8.71$; $p = 0.003$), lower f0beg (3.62 ± 1.05 kHz, $F_{1,1877} = 17.07$; $p < 0.001$), higher f0max (17.61 ± 1.78 kHz, $F_{1,1877} = 7.41$; $p = 0.007$), higher f0end (16.16 ± 1.79 kHz, $F_{1,1877} = 7.49$; $p = 0.007$), larger df0_max_beg (13.99 ± 1.91 kHz, $F_{1,1877} = 24.49$; $p < 0.001$) and higher fpeak (16.97 ± 2.21 kHz, $F_{1,1877} = 5.04$; $p = 0.03$).

4. Discussion

This study confirmed the presence of alarm calls in Harting's voles. Previously, the alarm calls of Harting's voles were only known from spectrographic description of one single alarm call recorded in the wild (Pandourski, 2011). We found, in the Harting's vole, a previously unknown phenomenon of collective bursts of alarm calls, at which a few individuals synchronize the rhythm of their alarm calls, resulting in a series of collective bursts of alarm calls (Figure 3). To our knowledge, such phenomenon was not previously known for mammals, but it may be also potentially present in related species of voles.

Different shapes of spectrograms and superimposed (overlapping) spectrograms of alarm calls in the bursts clearly indicated that the bursts include the calls of many different individuals vocalizing simultaneously (Figure 3). Adaptive significance of such synchronization of alarm calling in Harting's vole now remains unclear. In order to understand the reasons and to reveal situation attending with collective emission of alarm calls in Harting's voles, observations of vocal vigilance of this species in natural environment are necessary.

In Harting's voles, series of collective bursts of alarm calls of many individuals were noted both within family groups and also occasionally between two family groups, sitting in the two neighbouring enclosures. The observed mobbing behaviour was partly reminiscent of the collective mobbing predators reported for passerine birds (Curio, 1978; Lima, 1993). Alarm calling by multiple individuals toward a human was also noted in Brandt's voles

(Rutovskaya, 2012), however, neither Brandt's voles nor passerine birds do synchronize their alarm calls and each individual vocalizes independently of the others.

We also showed that, in Harting's voles, urgent alarm calls followed with fleeing to burrow differed from remaining sample of alarm calls by shorter duration, lower f0beg and higher f0max. Commonly, increase of f0 is characteristic for mammalian calls produced in situation of higher arousal (Briefer, 2012). In particular, for rodents, the Brandt's vole and great gerbil *Rhombomys opimus*, increase the maximum and end fundamental frequencies of there calls at urgent danger (Nikolskii & Sukhanova, 1992).

The alarm calls of Harting's voles are the highest-frequency among alarm calls of other vole species (on average 17.35 kHz and up to 22.12 kHz, Table 1). The alarm calls of all other studied vole species are also high-frequency, with f0max of 8.9–10.4 kHz on the Brandt's vole (Nikolskii & Sukhanova, 1992) and f0max of 7.5–8.2 kHz in the narrow-headed and Raddey's voles (Rutovskaya & Nikolskii, 2014).

Consistently to the wide ranges of f0 in vole alarms, of 7–22 kHz (Pandourski, 2011; Rutovskaya, 2012; Rutovskaya & Nikolskii, 2014; this study), the discomfort calls of these species are also high-frequency, with f0 ranging from 10.2–17.6 kHz in the Harting's vole (Rutovskaya, 2019a), from 3.6–5.6 kHz in the narrow-headed and Raddey's voles (Rutovskaya & Nikolskii, 2014), and from 4.4–6.5 kHz in the Brandt's vole (Rutovskaya, 2012; Dymskaya et al., 2022). In other studied vole species, the f0max of discomfort calls does not exceed 3 kHz (Rutovskaya, 2018, 2019a–c; Yurlova et al., 2020; Dymskaya et al., 2022).

Among other rodent taxa, very high-frequency alarm calls were also reported for whistling rats from the genus *Parotomys*, ranging in f0max from 10–13 kHz (le Roux et al., 2002), for Townsend chipmunks from the genus *Eutamias*, ranging in f0max from 11.1–14.5 kHz (Gannon & Lawlor, 1989), and for Siberian chipmunks *Tamias sibiricus*, with f0max of 11.8 kHz (Lissovsky et al., 2006). Some rodents even have ultrasonic alarm calls, e.g., rats (Litvin et al., 2007; Chen et al., 2023), Mongolian gerbils *Meriones unguiculatus* (Ter-Mikaelian et al., 2012; Volodin et al., 2024) and Richardson's ground squirrels *Urocitellus richardsonii* (Wilson & Hare, 2004).

We can propose that high-frequency alarm calls in the surface-dwelling Harting's voles could evolve for better propagation in the open landscapes. The voles produce their alarm calls very close to ground level. As the result, these calls are strongly affected by sound shadow zones created by temperature and/or wind gradients and by the effect of ground attenuation (Wiley & Richards, 1978). The strong effect of ground attenuation was reported for transmission of sounds below 2 kHz at the ground level in the open environments (Marten & Marler, 1977). At the same time, the least ground attenuation in the open environments for sounds produced at ground level was reported for frequencies over 6 kHz (Marten & Marler, 1977); that is, just for the range of frequencies of alarm calls of the three studied vole species (Pandourski, 2011; Rutovskaya, 2012; Rutovskaya & Nikolskii, 2014; this study).

Furthermore, in primates and in rodents, the low-frequency and low-intense call starts and ends degrade with distance much stronger than frequencies around call f0max (Matrosova et al., 2010b; Maciej et al., 2011). Also, a study of perceptibility of orangutan *Pongo pygmaeus* high-frequency calls (with f0max of 4 kHz) and low-frequency calls (with f0max of 0.3 kHz) across increasing savannah distances up to 400 m showed that overall detection of the low-frequency calls was significantly compromised compared with high-frequency calls from 100 m onwards (Gannon et al., 2023).

The role of sound production mechanism is also relevant for emission of the high-frequency audible alarms of Harting's voles. The alarm calls of Harting's voles have a very high f0max (on average 17.35 kHz and up to 22.12 kHz, Table 1). For rodents, two call-producing mechanisms were reported, the voice-based mechanism and the whistle-based mechanism (Fernández-Vargas et al., 2022; Riede et al., 2022, 2024). While 'voice-based' calls are produced with vibration of the vocal folds (Riede et al., 2011), the 'whistle-based' calls are produced by an aerodynamic whistle mechanism based on airflow vorticities in the vocal tract (Mahrt et al., 2016; Riede et al., 2017, 2022; Håkansson et al., 2022). Both voice and whistle-based calls can be sonic (below 20 kHz) or ultrasonic (above 20 kHz) (Fernández-Vargas et al., 2022; Riede et al., 2022).

For rodent calls at the range of frequencies about 20 kHz, experiments in heliox are necessary to confirm the mode of sound production, because both whistle- and voice-based mechanisms are possible. In the Norway rat *Rattus norvegicus*, the alarm calls at 22 kHz are whistle-based (Riede, 2011, 2013). At the same time, in California deer mice *Peromyscus californicus*, both sustainable calls of adults (with f0 of 12–19 kHz) and pup isolation calls (with f0 of 18–22 kHz) were voice-based calls (Riede et al., 2022). In the harvest mouse *Reithrodontomys megalotis*, the long-distance calls of about 10 kHz were voice-based, whereas high-frequency calls used in close-distant social interactions (about 80 kHz) were generated by a whistle mechanism (Riede et al., 2024).

Further research is necessary to evaluate the effects of caller's individuality, sex and age on the acoustic structure of alarm calls in the Harting's vole. The individualistic traits are found in the alarm calls of many rodents, including the Brandt's vole (Rutovskaya, 2012), marmots (McCowan & Hooper, 2002; Blumstein & Munos, 2005), ground squirrels (Matrosova et al., 2009, 2010a, 2011; Schneiderová et al., 2017) and Gunnison's prairie dogs, *Cynomys gunnisoni* (Loughry et al., 2019). Among the non-rodent colonial surface-dwelling species, the individualistic traits are well-expressed in the alarm calls of meercats *Suricata suricatta*, although the conspecific listener does not discriminate between the alarm calls of different individuals (Schibler & Manser, 2007). At the same time, sex and age effects on the acoustics of alarm calls were small or lacking for ground squirrels (Matrosova et al., 2007; Swan & Hare, 2008; Volodina et al., 2010).

This study opens an interesting perspective of searching the alarm calls in other species and subspecies of social voles of the taxonomic "guentheri" group (Kryštufek et al., 2012; Abramson et al., 2021; Kryštufek & Shenbrot, 2022). As the alarm calls of Harting's voles are very high-frequency and expand beyond the well-audible for humans range of frequencies, people may do not pay attention to these calls in the wild, because they only hear the short initial part of a call at raising of fundamental frequency and do not hear the high-frequency high-amplitude part of the alarm call. Moreover, on human ear, the alarm calls of Harting's voles are dissimilar with vole calls and are more similar to bird chirps. It would be very interesting to reveal the potential geographical variation of the acoustic structure of alarm calls, related to both phylogeography of social voles of the 'guentheri' group (Kryštufek et al., 2012; Yiğit et al., 2017; Thanou et al., 2020; Golenishchev et al., 2022), and probable effects of habitat structure (Campbell et al., 2010; Matrosova et al., 2016; Schneiderová et al., 2020).

Another potential branch of research is studying geographical variation of alarm calls in cryptic species, the narrow-headed and Raddey's voles, which have a very large distribution areas, including both tundra regions and steppes from Northern Eurasia to Northern China and have a few well-separated genetic lineages (Petrova et al., 2021, 2022, 2023). In addition, for the singing vole (*Mynomes miurus*) and taiga vole (*Mynomes xanthognathus*), there are published verbal descriptions of calls in human-audible range of frequencies emitted in the wild toward people, but without presenting spectrograms (Wolff & Lidicker, 1980; Cole & Wilson, 2010). These two vole species may also potentially have alarm calls.

Acknowledgements

We thank Andrey Popov, Margarita Dymskaya and Svetlana Sablina for help and support. This study was not supported by any foundation.

References

Abramson, N.I., Bodrov, S.Y., Bondareva, O.V., Genelt-Yanovskiy, E.A. & Petrova, T.V. (2021). A mitochondrial genome phylogeny of voles and lemmings (Rodentia: Arvicolinae): Evolutionary and taxonomic implications. — PLoS ONE 16: e0248198. DOI:10.1371/journal.pone.0248198.

Blumstein, D.T. (2007a). The evolution, function, and meaning of marmot alarm communication. — Adv. Stud. Behav. 37: 371-401. DOI:10.1016/S0065-3454(07)37008-3.

Blumstein, D.T. (2007b). The evolution of alarm communication in rodents: structure, function, and the puzzle of apparently altruistic calling. — In: Rodent societies: An ecological and evolutionary perspective (Wolff, J.O. & Sherman, P.W., eds). University of Chicago Press, Chicago, IL, p. 317-327. DOI:10.7208/9780226905389-029.

Blumstein, D.T. & Munos, O. (2005). Individual, age and sex-specific information is contained in yellow-bellied marmot alarm calls. — Anim. Behav. 69: 353-361. DOI:10.1016/j.anbehav.2004.10.001.

Briefer, E.F. (2012). Vocal expression of emotions in mammals: mechanisms of production and evidence. — J. Zool. 288: 1-20. DOI:10.1111/j.1469-7998.2012.00920.x.

Brudzynski, S.M. & Holland, G. (2005). Acoustic characteristics of air puff-induced 22-kHz alarm calls in direct recordings. — Neurosci. Biobehav. Rev. 29: 1169-1180. DOI:10.1016/j.neubiorev.2005.04.007.

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. DOI:10.1111/j.1558-5646.2010.00962.x.

Chen, Y., Xiang, Z., Su, Q., Qin, J. & Liu, Q. (2023). Vocal signals with different social or non-social contexts in two wild rodent species (*Mus caroli* and *Rattus losea*). — Anim. Cogn. 26: 963-972. DOI:10.1007/s10071-023-01745-6.

Çolak, E., Sözen, M., Yiğit, N. & Özkurt, S. (1998). A study on ecology and biology of *Microtus guentheri* Danford & Alston, 1880 (Mammalia: Rodentia) in Turkey. — Tr. J. Zool. 22: 289-295.

Cole, F.R. & Wilson, D.E. (2010). *Microtus miurus* (Rodentia: Cricetidae). — Mamm. Spec. 42: 75-89. DOI:10.1644/855.1.

Curio, E. (1978). The adaptive significance of avian mobbing. I. Teleonomic hypotheses and predictions. — Z. Tierpsychol. 48: 175-183. DOI:10.1111/j.1439-0310.1978.tb00254.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. DOI:10.1007/s00265-022-03213-6.

Fernández-Vargas, M., Riede, T. & Pasch, B. (2022). Mechanisms and constraints underlying acoustic variation in rodents. — Anim. Behav. 184: 135-147. DOI:10.1016/j.anbehav.2021.07.011.

Fichtel, C. & Kappeler, P.M. (2002). Anti-predator behavior of group-living Malagasy primates: mixed evidence for a referential alarm call system. — Behav. Ecol. Sociobiol. 51: 262-275. DOI:10.1007/s00265-001-0436-0.

Gannon, C., Hill, RA. & Lameira, A.R. (2023). Open plains are not a level playing field for hominid consonant-like versus vowel-like calls. — Sci. Rep. 13: 21138. DOI:10.1038/s41598-023-48165-7.

Gannon, W.L. & Lawlor, T.E. (1989). Variation of the chip vocalizations of three species of the Townsend chipmunks (Genus *Eutamias*). — J. Mammal. 70: 740-753. DOI:10.2307/1381708.

García-Navas, V. & Blumstein, D.T. (2016). The effect of body size and habitat on the evolution of alarm vocalizations in rodents. — Biol. J. Linn. Soc. 118: 745-751. DOI:10.1111/bij.12789.

Golenishchev, F.N. & Malikov, V.G. (2011). The systematics and distribution of the grey voles of the tribe *Microtini* (Rodentia, Arvicolinae) in the Caucasus and Asia Minor. — In: Proc. Internat. Conf. "Biological diversity and conservation problems of the fauna of the Caucasus". LLC Spika, Yerevan, p. 101-105 (in Russian).

Golenishchev, F.N., Malikov, V.G., Nazari, F., Vaziri, A.S., Sablina, O.V. & Polyakov, A.V. (2003). New species of vole of "*guentheri*" group (Rodentia, Arvicolinae, *Microtus*) from Iran. — Russ. J. Theriol. 1: 117-123. DOI:10.15298/rusjtheriol.1.2.05.

Golenishchev, F.N., Sablina, O.V., Borodin, P.M. & Gerasimov, S. (2002). Taxonomy of voles of the subgenus *Sumeriomys* Argyropulo, 1933 (Rodentia, Arvicolinae, *Microtus*). — Russ. J. Theriol 1: 43-55. DOI:10.15298/rusjtheriol.1.1.03.

Golenishchev, F.N., Zorenko, T.A., Petrova, T.V., Voyta, L.L., Kryuchkova, L.Y. & Atanasov, N. (2022). Evaluation of the "bottleneck" effect in an isolated population of *Microtus hartingi* (Rodentia, Arvicolinae) from the Eastern Rhodopes (Bulgaria) by methods of integrative analysis. — Diversity 14: 709. DOI:10.3390/d14090709.

Gromov, V.S. (2023). Ecology and social behavior of the Brandt's vole: A generalized review. — J. Arid Environ. 214: 104994. DOI:10.1016/j.jaridenv.2023.104994.

Håkansson, J., Jiang, W., Xue, Q., Zheng, X., Ding, M., Agarwal, A.A. & Elemans, C.P.H. (2022). Aerodynamics and motor control of ultrasonic vocalizations for social communication in mice and rats. — BMC Biol. 20: 3. DOI:10.1186/s12915-021-01185-z.

Kislyi, A.A., Ravkin, Y.S., Bogomolova, I.N., Tsybulin, S.M. & Starikov, V.P. (2021). Number and distribution of the narrow-headed vole *Lasiopodomys gregalis* (Pallas, 1779) (Cricetidae, Rodentia) in Western Siberia. — Biol. Bull. Russ. Acad. Sci. 48: 1822-1831. DOI:10.1134/S1062359021100162.

Kryštufek, B. & Shenbrot, G.I. (2022). Voles and lemmings (Arvicolinae) of the Palaearctic region. — University of Maribor Press, Maribor. DOI:10.18690/um.fnm.2.2022.

Kryštufek, B., Zorenko, T. & Buzan, E. (2012). New insights into taxonomy and phylogeny of social voles inferred from mitochondrial cytochrome *b* sequences. — Mammal. Biol. 77: 178-182. DOI:10.1016/j.mambio.2011.11.007.

le Roux, A., Jackson, T.P. & Cherry, M.I. (2002). Differences in alarm vocalizations of sympatric populations of the whistling rats, *Parotomys brantsii* and *P. littledalei* (Rodentia: Muridae). — J. Zool. 257: 189-194. DOI:10.1017/S0952836902000791.

Lima, S.L. (1993). Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. — Wilson Bull. 105: 1-47.

Lissovsky, A.A., Obolenskaya, E.V. & Emelyanova, L.G. (2006). The structure of voice signals of Siberian chipmunk (*Tamias sibiricus* Laxmann, 1769; Rodentia: Sciuridae). — Russ. J. Theriol. 5: 93-98. DOI:10.15298/rusjtheriol.5.2.07.

Litvin, Y., Blanchard, D.C. & Blanchard, R.J. (2007). Rat 22 kHz ultrasonic vocalizations as alarm cries. — Behav. Brain. Res. 182: 166-172. DOI:10.1016/j.bbr.2006.11.038.

Loughry, W.J., Oeser, M., Anderson, C.D. & Hoogland, J.L. (2019). The importance of individual variation in the alarm calls of Gunnison's prairie dogs. — Anim. Behav. 150: 59-68. DOI:10.1016/j.anbehav.2019.01.019.

Maciej, P., Fischer, J. & Hammerschmidt, K. (2011). Transmission characteristics of primate vocalizations: implications for acoustic analyses. — PLoS ONE 6: e23015. DOI:10.1371/journal.pone.0023015.

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: R865-R881. DOI:10.1016/j.cub.2016.08.032.

Manser, M.B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. — Proc. Roy. Soc. Lond. B: Biol. Sci. 268: 2315-2324. DOI:10.1098/rspb.2001.1773.

Markov, G., Yiğit, N., Çolak, E., Kocheva, M. & Gospodinova, M. (2014). Epigenetic diversity and similarity of the voles of "*guentheri*" group (Mammalia: Rodentia) in Anatolian Peninsula and southeastern part of the Balkan Peninsula. — Acta Zool. Bulg. 66: 159-164.

Marten, K. & Marler, P. (1977). Sound transmission and its significance for animal vocalization. I. Temperate habitats. — Behav. Ecol. Sociobiol. 2: 271-290. DOI:10.1007/BF00299740.

Matrosova, V.A., Volodin, I.A., Volodina, E.V. & Babitsky, A.F. (2007). Pups crying bass: Vocal adaptation for avoidance of age-dependent predation risk in ground squirrels? — Behav. Ecol. Sociobiol. 62: 181-191. DOI:10.1007/s00265-007-0452-9.

Matrosova, V.A., Volodin, I.A. & Volodina, E.V. (2009). The short-term and long-term individuality in speckled ground squirrel alarm calls. — J. Mammal. 90: 158-166. DOI:10.1644/08-MAMM-A-032.1.

Matrosova, V.A., Volodin, I.A., Volodina, E.V., Vasilieva, N.A. & Kochetkova, A.A. (2010a). Between-year stability of individual alarm calls in the yellow ground squirrel *Spermophilus fulvus*. — J. Mammal. 91: 620-627. DOI:10.1644/09-MAMM-A-143.1.

Matrosova, V.A., Volodin, I.A., Volodina, E.V. & Vasilieva, N.A. (2010b). Stability of acoustic individuality in the alarm calls of wild yellow ground squirrels *Spermophilus fulvus* and contrasting calls from trapped and free-ranging callers. — Naturwissenschaften 97: 707-715. DOI:10.1007/s00114-010-0686-7.

Matrosova, V.A., Blumstein, D.T., Volodin, I.A. & Volodina, E.V. (2011). The potential to encode sex, age, and individual identity in the alarm calls of three species of Marmotinae. — Naturwissenschaften 98: 181-192. DOI:10.1007/s00114-010-0757-9.

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

Matrosova, V.A., Rusin, M.Y., Volodina, E.V., Proyavka, S.V., Savinetskaya, L.E., Shekarova, O.N., Rashevska, 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. DOI:10.1016/j.mambio.2016.01.001.

McCowan, B. & Hooper, S.L. (2002). Individual acoustic variation in Belding's ground squirrel alarm chirps in the High Sierra Nevada. — J. Acoust. Soc. Am. 111: 1157-1160. DOI:10.1121/1.1446048.

McRae, T.R. (2020). A review of squirrel alarm-calling behavior: what we know and what we do not know about how predator attributes affect alarm calls. — Anim. Behav. Cognit. 7: 168-191. DOI:10.26451/abc.07.02.11.2020.

McRae, T.R. & Green, S.M. (2017). Gray squirrel alarm call composition differs in response to simulated aerial versus terrestrial predator attacks. — Ethol. Ecol. Evol. 29: 54-63. DOI:10.1080/03949370.2015.1087433.

Nikolskii, A.A. (1979). Species specificity of alarm call in ground squirells (*Citellus*, Sciuridae) of Eurasia. — Zool. Zh. 58: 1183-1194. (in Russian).

Nikolskii, A.A. & Sukhanova, M.V. (1992). Situation dependent variations of a call emitted by great gerbil, *Rhombomys opimus* and by Brandt's vole, *Microtus brandtii*, retreating to burrows. — Zool. Zh. 71: 125-132. (in Russian).

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

Petrova, T.V., Genelt-Yanovskiy, E.A., Lissovsky, A.A., Chash, U.-M.G., Masharsky, A.E. & Abramson, N.I. (2021). Signatures of genetic isolation of the three lineages of the narrow-headed vole *Lasiopodomys gregalis* (Cricetidae, Rodentia) in a mosaic steppe landscape of South Siberia. — Mammal. Biol. 101: 275-285. DOI:10.1007/s42991-020-00099-7.

Petrova, T., Skazina, M., Kuksin, A., Bondareva, O. & Abramson, N. (2022). Narrow-headed voles species complex (Cricetidae, Rodentia): Evidence for species differentiation inferred from transcriptome data. — Diversity 14: 512. DOI:10.3390/d14070512.

Petrova, T.V., Dvoyashov, I.A., Bazhenov, Y.A., Obolenskaya, E.V. & Lissovsky, A.A. (2023). An invisible boundary between geographic ranges of cryptic species of narrow-headed voles (*Stenocranius*, *Lasiopodomys*, Cricetidae) in Transbaikalia. — Diversity 15: 439. DOI:10.3390/d15030439.

Randall, J.A. & Rogovin, K.A. (2002). Variation in and meaning of alarm calls in a social desert rodent *Rhombomys opimus*. — Ethology 108: 513-527. DOI:10.1046/j.1439-0310.2002.00797.x.

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

Riede, T. (2013). Stereotypic laryngeal and respiratory motor patterns generate different call types in rat ultrasound vocalization. — J. Exp. Zool. A 319: 213-224. DOI:10.1002/jez.1785.

Riede, T., York, A., Furst, S., Müller, R. & Seelecke, S. (2011). Elasticity and stress relaxation of a very small vocal fold. — J. Biomech. 44: 1936-1940. DOI:10.1016/j.jbiomech.2011.04.024.

Riede, T., Borgard, H.L. & Pasch, B. (2017). Laryngeal airway reconstruction indicates that rodent ultrasonic vocalizations are produced by an edge-tone mechanism. — Roy. Soc Open Sci 4: 170976. DOI:10.1098/rsos.170976.

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. DOI:10.1242/jeb.243695.

Riede, T., Kobrina, A. & Pasch, B. (2024). Anatomy and mechanisms of vocal production in harvest mice. — J. Exp. Biol. 227: jeb246553. DOI:10.1242/jeb.246553.

Rutovskaya, M.V. (2012). The sound signals of Brandt's vole (*Lasiopodomys brandti*). — Sens. Systems 26: 31-38. (in Russian).

Rutovskaya, M.V. (2018). Audible acoustic communication in voles of Arvicolinae subfamily. — KMK Press, Moscow. (in Russian).

Rutovskaya, M.V. (2019a). Sound communication in social voles (subgenus *Sumeriomys*). — Bioacoustics 28: 503-521. DOI:10.1080/09524622.2018.1482787.

Rutovskaya, M.V. (2019b). Vocal communication in *Microtus* (*Terricola*) *schelkovnikovi* and *M.* (*T.*) *daghestanicus* in the audible range of frequencies. — J. Ethol. 37: 187-195. DOI:10.1007/s10164-019-00587-5.

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

Rutovskaya, M.V. & Nikolskii, A.A. (2014). The sound signals of the narrow-skulled vole (*Microtus gregalis* Pall.). — Sens. Systems 28: 76-83 (in Russian).

Rutovskaya, M.V., Volodin, I.A., Feoktistova, N.Y., Surov, A.V., Gureeva, A.V. & Volodina, E.V. (2024). Acoustic complexity of pup isolation calls in Mongolian hamsters: 3-frequency phenomena and chaos. — Curr. Zool. 70: zoad036. DOI:10.1093/cz/zoad036.

Schibler, F. & Manser, M.B. (2007). The irrelevance of individual discrimination in meerkat alarm calls. — Anim. Behav. 74: 1259-1268. DOI:10.1016/j.anbehav.2007.02.026.

Schneiderová, I., Volodina, E.V., Matrosova, V.A. & Volodin, I.A. (2017). One plus one: Binary alarm calls retain individual signature for longer periods than single-note alarms in the European ground squirrel (*Spermophilus citellus*). — Behav. Process. 138: 73-81. DOI:10.1016/j.beproc.2017.02.014.

Schneiderová, I., Štefanská, L. & Kratochvíl, L. (2020). Geographic variability in the alarm calls of the European ground squirrel. — Curr. Zool. 66: 407-415. DOI:10.1093/cz/zoz055.

Seyfarth, R.M., Cheney, D.L. & Marler, P. (1980). Vervet monkey alarm calls: semantic communication in a free-ranging primate. — Anim. Behav. 28: 1070-1094. DOI:10.1016/S0003-3472(80)80097-2.

Shelley, E.L. & Blumstein, D.T. (2005). The evolution of vocal alarm communication in rodents. — Behav. Ecol. 16: 169-177. DOI:10.1093/beheco/arh148.

Sloan, J.L. & Hare, J.F. (2008). The more the scarier: adult Richardson's ground squirrels (*Spermophilus richardsonii*) assess response urgency via the number of alarm signalers. — Ethology 114: 436-443. DOI:10.1111/j.1439-0310.2008.01479.x.

Swan, D.C. & Hare, J.F. (2008). Signaler and receiver ages do not affect responses to Richardson's ground squirrel alarm calls. — J. Mammal. 89: 889-894. DOI:10.1644/07-MAMM-A-228.1.

Ter-Mikaelian, M., Yapa, W.P. & Rübsamen, R. (2012). Vocal behavior of the Mongolian gerbil in a seminatural enclosure. — Behaviour 149: 461-492. DOI:10.1163/156853912X639778.

Thanou, E., Paragamian, K. & Lymberakis, P. (2020). Social but lonely: Species delimitation of social voles and the evolutionary history of the only *Microtus* species living in Africa. — J. Zool. Syst. Evol. Res. 58: 475-498. DOI:10.1111/jzs.12325.

Volodin, I.A., Volodina, E.V., Frey, R., Karaseva, K.D. & Kirilyuk, V.E. (2021). Daurian pika (*Ochotona dauurica*) alarm calls: individual acoustic variation in a lagomorph with audible through ultrasonic vocalizations. — J. Mammal. 102: 947-959. DOI:10.1093/jmammal/gyab048.

Volodin, I.A., Klenova, A.V., Kirilyuk, V.E., Ilchenko, O.G. & Volodina, E.V. (2024). Ultrasonic alarm call of Mongolian gerbils (*Meriones ungiuculatus*) in the wild and in captivity: a potential tool for detecting inhabited colonies during population depression. — Mammal. Biol. 104. DOI:10.1007/s42991-024-00416-4.

Volodina, E.V., Matrosova, V.A. & Volodin, I.A. (2010). An unusual effect of maturation on the alarm call fundamental frequency in two species of ground squirrels. — Bioacoustics 20: 87-98. DOI:10.1080/09524622.2011.9753634.

Volodina, E.V., Volodin, I.A., Chelysheva, E.V. & Frey, R. (2018). Hiss and snort call types of wild-living giraffes *Giraffa camelopardalis*: acoustic structure and context. — BMC Res. Notes 11: 12. DOI:10.1186/s13104-017-3103-x.

Wilden, I., Tembrock, G., Herzel, H. & Peters, G. (1998). Subharmonics, biphonation, and deterministic chaos in mammal vocalization. — Bioacoustics 9: 171-196. DOI:10.1080/09524622.1998.9753394.

Wiley, R.H. & Richards, D.G. (1978). Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. — Behav. Ecol. Sociobiol. 3: 69-94. DOI:10.1007/BF00300047.

Wilson, D.R. & Hare, J.F. (2004). Ground squirrel uses ultrasonic alarms. — Nature 430: 523. DOI:10.1038/430523a.

Wolff, J.O. & Lidicker, W.Z. (1980). Population ecology of the taiga vole, *Microtus xanthognathus*, in interior Alaska. — Can. J. Zool. 58: 1800-1812. DOI:10.1139/z80-247.

Yiğit, N., Markov, G., Çolak, E., Kocheva, M., Saygılı, F., Yüce, D. & Çam, P. (2012). Phenotypic features of the '*guentheri'* group vole (Mammalia: Rodentia) in Turkey and southeast Bulgaria: Evidence for its taxonomic detachment. — Acta Zool. Bulg. 64: 23-32.

Yiğit, N., Çetintürk, D. & Çolak, E. (2017). Phylogenetic assessment of voles of the Guentheri Group (Mammalia: *Microtus*) in Turkish Thrace and Western Anatolia. — Eur. Zool. J. 84: 252-260. DOI:10.1080/24750263.2017.1317041.

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. DOI:10.1371/journal.pone.0228892.

Zorenko, T.A. (2023). Communal reproduction of females of two subspecies of Harting's vole *Microtus* (*Sumeriomys*) *hartingi* (Rodentia, Arvicolinae) under experimental conditions. — Biol. Bull. Russ. Acad. Sci. 50: 1603-1614. DOI:10.1134/S1062359023070336.

Zorenko, T.A. & Golenishchev, F.N. (2015). The spermatozoa structure peculiarities of the subgenus *Sumeriomys* (Rodentia, Arvicolinae, Microtus). — Russ. J. Theriol. 14: 105-111. DOI:10.15298/rusjtheriol.14.1.05.

Zorenko, T.A. & Kagainis, U. (2021). Discrimination of the two subspecies of *Microtus hartingi* (Rodentia: Arvicolinae) by shape and linear features of the spermatozoon. — Russ. J. Theriol. 21: 143-157. DOI:10.15298/rusjtheriol.20.2.04.

Zorenko, T.A., Atanasov, N. & Golenishchev, F.N. (2016). Behavioral differentiation and hybridization of the European and Asian forms of Harting' vole *Microtus hartingi* (Rodentia, Arvicolinae). — Russ. J. Theriol. 15: 133-150. DOI:10.15298/rusjtheriol.15.2.06.

Zorenko, T.A., Kagainis, U. & Baraškova, L. (2020). Does the geometric and linear morphometry of the brain reflect the divergence in the "*guentheri*" group (Arvicolinae; *Sumeriomys*)? — Russ. J. Theriol. 19: 45-57. DOI:10.15298/rusjtheriol.19.1.04.

Zorenko, T.A., Kagainis, U., Golenishchev, F.N. & Barashkova, L. (2023). Geometric morphometrics of the cranium and mandible in social voles of the "*guentheri*" group (Arvicolinae: *Sumeriomys*). — Diversity 15: 83. DOI:10.3390/d15010083.

Zuberbühler, K. (2009). Survivor signals: the biology and psychology of animal alarm calling. — Adv. Stud. Behav. 40: 277-322. DOI:10.1016/S0065-3454(09)40008-1.

Supplementary Material

Audio 1. The Harting's vole alarm calls with chevron contour, with complex contour, with flat contour, with upward contour, with subharmonics, with biphonation and collective shouting of alarm calls by 8 individual voles with the alarms of different individuals superimposing each other (WAV, mono).

This file can be accessed at https://stream.cadmore.media/player/289bbe79-4622-4948-9ba3-d50c826ccbf0.

Audio 2. A natural series of collective bursts of alarm calls (alarm bursts) produced by Harting's voles with overlapping alarm calls within one family group, containing 9 individuals (WAV, mono). This file can be accessed at https://stream.cadmore.media/player/891adf87-09df-46d6-a349-fdb68b064a2d.

Audio 3. A natural series of collective bursts of alarm calls (alarm bursts) produced by Harting's voles with overlapping alarm calls within and between two neighbouring family groups, containing 12 and 10 individuals, respectively (WAV, stereo). This file can be accessed at https://stream.cadmore.media/player/2adf1a14-78da-434c-ba30-8cdce12762cb.