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Research Article

Field tests reveal acoustic variation of call types in a subterranean rodent, the Northern Mole Vole *Ellobius talpinus*

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Abstract

This study investigates acoustic variation of human-audible sonic (below 20 kHz) and human-inaudible ultrasonic (above 20 kHz) calls in a wild subterranean rodent, the Northern Mole Vole (*Ellobius talpinus*), under 3 call-eliciting tests conducted during captures for 1 day. The Contact-in-Tunnel Test modeled contacts of 2 individuals during digging earth in a burrow tunnel. The Restraint Test modeled restraint of an animal by a surrogate predator (human hand). The Release-to-Burrow Test modeled acoustic communication of many family members returned to their home burrow after their isolation for about 8 h, from morning to evening. We described 8 call types: 3 sonic, 3 ultrasonic, and 2 expanding from sonic to ultrasonic range of frequencies; 6 call types were described for the first time for this species. No relationship was found between acoustic parameters and proxies of body size (body mass and the width of 2 upper incisors). No sex differences were found in body size or the acoustic parameters. Different call types prevailed in different tests: *wheeks* and *upsweeps* were made during peaceful interactions; *squeaks* and *squeals* were related to animal discomfort during the Restraint Test; *rasps* were only made in Release-to-Burrow Tests when animals were plugging the burrow entrance; and *variative* calls did not show any relationship with type of test. Based on presence or absence of certain call types in the tests, we evaluate their potential communicative role in comparison with published data on vocal repertoires of other subterranean rodents.

Key words: acoustic communication, Arvicolinae, audible and ultrasonic sounds, fossorial mammal, nonlinear phenomena, vocal repertoire**.**

All rodent species of the families Geomyidae, Spalacidae, Ctenomyidae, and Bathyergidae conduct their life underground (Nevo 1999; Lacey et al. 2000). Only some species of the Arvicolinae family are subterranean, e.g., the Mandarin Vole (*Lasiopodomys mandarinus*; Smorkatcheva 1999; Liu et al. 2010), the Long-clawed Vole (*Prometheomys schaposchnikowi*; Ognev 1926), and the Northern Mole Vole (*Ellobius talpinus*; Herbin et al. 1994; Volodin et al. 2022), providing opportunity for comparative studies of subterranean and surface-dwelling species to understand the effects of their lifestyle on communication.

Life in permanent darkness results in ocular reduction in many subterranean rodents (Němec et al. 2007) including the Arvicolinae species Long-clawed Vole (Ognev 1926; Kryštufek and Shenbrot 2022) and Northern Mole Vole (Herbin et al. 1994). The small eyes suggest impaired vision and enhanced role of acoustic communication, which is supported by modifications of ear morphology (e.g., Pleštilova et al. 2021) and shifts to low frequencies acoustic parameters of sonic (below 20 kHz) calls in some subterranean species

(Begall et al. 2007; Schleich and Francescoli 2018; Dymskaya et al. 2022).

A single comparative study of subterranean and surface-dwelling Arvicolinae species by Dymskaya et al. (2022) suggests that subterranean lifestyle solely affects the acoustic parameters of human-audible sonic calls (below 20 kHz), but not ultrasonic calls (above 20 kHz). In the previous study of vole vocalizations (Dymskaya et al. 2022), we hypothesized that similar values of acoustic parameters of ultrasonic calls between surface-dwelling and subterranean vole species may indicate that selection pressure for sound propagation was unimportant for ultrasonic calls used at close distance (Dymskaya et al. 2022), but this hypothesis has yet to be tested. In this study, we expected to find close-range ultrasonic calls in tests modeling contacts between subterranean northern mole voles in burrows.

So far, ultrasonic calls were only described for 2 subterranean species of rodents: 2 types for the Mandarin Vole (Dymskaya et al. 2022) and 2 types for the Northern Mole Vole (Volodin et al. 2022).

The 2 ultrasonic call types included calls with upward contour and a maximum fundamental frequency (f0max) of 35.32 kHz and calls with variable contour and f0max of 31.40 kHz; both call types were found in captivity and in the wild (Volodin et al. 2022). Compared to ultrasonic calls with variable contours, calls with upward contour were longer, more intense, more deeply modulated in frequency, and distinctive by being emitted in regular series (Volodin et al. 2022).

Acoustic parameters of sonic calls were previously described for a single subterranean Arvicolinae rodent, the Mandarin Vole (Rutovskaya 2011; Dymskaya et al. 2022). In other subterranean rodents, repertoires of sonic calls were described for the genera *Spalax*, *Heterocephalus*, *Fukomys*, *Ctenomys*, and *Spalacopus* (Pepper et al. 1991; Credner et al. 1997; Veitl et al. 2000; Bednářová et al. 2013; Dvořáková et al. 2016). Comparative studies revealed richer repertoires of sonic calls in social than in solitary subterranean rodent species (Schleich et al. 2007; Schleich and Francescoli 2018). In this study, we therefore hypothesized that the highly social northern mole voles, living in family groups of 2 to 19 (Evdokimov 2001) and up to 22 individuals (Novikov et al. 2007) may use for communication a variety of sonic call types.

A family group of northern mole voles commonly consists of 1 adult breeding female and 1 or several adult males and their offspring of several generations; each family lives in its own home burrow for several years (Evdokimov 2001). Animal age can be estimated by fur color (lighter-gray in adults and darker-gray in subadults) and by the width of 2 enlarged upper incisors used for earth-digging (Nikonova et al. 2024). Mole voles prepare their underground tunnels by scratching the soil with their incisors and pushing the loosened soil behind the body with their fore and hind limbs (Nikonova et al. 2024). The aim of this study was to investigate the acoustic structure of sonic and ultrasonic calls of wild-living northern mole voles tested under 3 conditions: (1) Contact-in-Tunnel Test, modeling a meeting of 2 diggers in a burrow tunnel; (2) Restraint Test, modeling a capture of the caller by a surrogate predator (human hand); and (3) Release-to-Burrow Test, modeling acoustic communication of many family members repairing the damaged tunnel of their home burrow.

Materials and methods.
Study area, animals, and dates.
Vocalizations of wild-living northern mole voles were recorded during field tests in the Saratov province, Russia, near Djakovka settlement (50.714215 N, 46.716292 E) in August to September 2021. The study area included 2 plots of steppe, about 40,350 m² and about 67,900 m² separated with a distance of about 1 km, both near the Eruslan River. Study plots had a variable grass cover (5 cm to 1 m) because of irregular haying and everyday grazing of a mixed sheep/cattle herd.

During the data collection period, each study plot counted at least 10 active burrows. In total, we captured 143 different individuals (89 males, 54 females). Individuals were recognized by microtransponders 1.25*7 mm (Star Security Technologies Co., Shanghai, China) implanted at the given or previous captures, made during a parallel study of population genetics.

All applicable international, national, and institutional guidelines for the care and use of animals were followed. During our work, we adhered to the "Guidelines for the treatment of animals in behavioral research and teaching" (Anim. Behav., 2020, 159, I-XI) and to the American Society of Mammalogists guidelines (Sikes et al. 2016). The Northern Mole Vole is not an endangered species in Russia. All tests were done in the shade, not one animal physically suffered due to experiments; many individuals that were tested were captured in the same area in the following years (2022 and 2023) in frames of the study of dental radiography (Nikonova et al. 2024). Data collection protocol #131-03-2(2021) was approved by the Ethical Committee in the Area of Animal Research of Saint-Petersburg State University.

Captures and daylong holding in the field.
Each day of data collection we tried to capture as many individuals as possible from up to 5 different burrows. Active parts of burrow systems were detected by presence of fresh soil mounds and by small ventilation holes of about 4 cm diameter appearing at 8:00 to 9:00 in the morning and sometimes later during the day. Animals were captured with metallic-spiral live traps (Golov 1954) placed in the burrow after slight excavating of the tunnel with a spade. The live traps were checked every 20 min. For each individual, we obtained GPS coordinates of the burrow entrance from which it was captured using the respective option on a smartphone.

After capture each animal was isolated in a 10-L bucket (bottom diameter 20 cm, height 28 cm) with a 5-cm layer of soil taken near the place of capture and pieces of cardboard and wood cork. The animals did not burrow down in this soil, but used the cardboard and cork as shelters. To avoid animal overheating, the buckets with animals were placed under shade trees and additionally on especially hot days in a depression in earth of about 0.5 m depth dug up under the trees. Food (oat and carrot as a source of water) was provided ad libitum to the animals immediately after capture; water was not provided because these animals do not drink in nature.

Call-eliciting tests.
Calls were recorded in 3 tests: (1) Contact-in-Tunnel Test (when 2 individuals came into contact during digging soil in a circular tunnel); (2) Restraint Test (measuring incisors of 1 handheld animal with calipers); and (3) Release-to-Burrow Test (release of all captured family members together to their home burrow tunnel at the end of the capture day). All test trials were conducted outdoor in the wild, at the distance of about 100 m from animal burrows, at a distance of 5 to 10 m from the buckets with other animals (to prevent recording calls of non-focal individuals), in daytime under the shade of trees, at an ambient temperature of 25 to 30 °C. Before the tests, the animals spent at least 1 h isolated in their individual buckets. During 1 experimental day, Restraint Tests were conducted first, Contact-in-Tunnel Tests were second, and Release-to-Burrow Tests were the last: in the evening all captured and tested animals were released to their home burrow tunnels.

During Restraint Test trials, calls were recorded on an individual basis from individually identified callers. During Contact-in-Tunnel Test trials, calls were recorded on a dyad basis, without identifying callers within dyads. During Release-to-Burrow Test trials, calls were recorded on a collective basis, without identifying callers from family members.

Contact-in-Tunnel Test.
The 5-min Contact-in-Tunnel Test trial included soil digging and contacts of 2 individuals in a test arena composed of a 10-L bucket (28 cm height, with 20-cm bottom diameter), in which a 3-L bucket (17 cm height, with 14-cm bottom diameter) was placed bottom up in the center. A 5-cm-deep soil-filled gap between the walls of the buckets imitated a burrow tunnel. Any 2 individuals placed in this setup started digging in a circle and soon met, commonly vocalizing during the first and sometimes also during following contacts. The test trial started when the second animal of the experimental dyad was placed into the test arena. After the end of a trial, each animal was returned to its bucket.

Before a new test trial, a fresh layer of soil was placed between the bucket walls, to prevent the effects of odor on the behavior of the next dyad of animal participants. The soil, as cool as possible to avoid overheating the animals, was taken from a neutral territory away from mole vole burrows under tree shade.

In total, we conducted 58 Contact-in-Tunnel Test trials—32 male–male trials, 17 female–female, and 9 male–female. In 40 of the trials, the dyads included animals from different burrow tunnels and in 18 of the trials the dyads included animals from the same burrow tunnel. During 1 experimental day, each animal participated in the Contact-in-Tunnel Test only once. A total of 84 animals (51 males, 33 females) participated in the Contact-in-Tunnel Tests. In total, 21 of 58 trials included repeatedly participating animals: 32 males and 25 females participated in this test once, 17 males and 6 females twice, 1 male and 2 females thrice, and 1 male 4 times. The interval between repeated trials with the same individuals was 3.2 ± 2.5 days (range: 1 to 10 days); the same dyads were not tested repeatedly.

Restraint Test.

For the 2- to 10-min (usually 4 to 5 min) Restraint Test trial, the animal was taken from its bucket, held by fingers under cheekbones head up, and the transverse width of both upper incisors was measured with electronic calipers (Kraftool, Germany) with 0.01 mm accuracy (Nikonova et al. 2024). Restraining by the experimenter's hands, and teeth touched with calipers were considered uncomfortable for the animals because the animals tried to escape or bite the experimenter's hand during this procedure and could produce the calls. After the trial, the animal was sexed by external sexual traits, weighted on the electronic scale G&G TS-100 (G&G GmbH, Neuss, Germany) with 0.01 g accuracy and then returned to its bucket. In total, we conducted 47 Restraint Test trials, 26 with males and 21 with females.

Release-to-Burrow Test.

A Release-to-Burrow Test trial (2 to 20 min depending on animal presence aboveground) included a simultaneous release of all family members captured during that day to their home burrow tunnel (slightly excavated by researchers, because normally the burrow has no open entrances) about 18:00, followed by recording their calls near-and-from the burrow entrance. As all released animals were isolated in individual buckets during the day, they started contacting each other and noncaptured family members, and could produce calls. In addition, 1 or 2 individuals started to bury an opened entrance to the burrow tunnel, sometimes with calls. Some released animals were agonistic toward researchers or just toward a handheld microphone and sometimes vocalized toward them. In total, we conducted 40 Release-to-Burrow Test trials, releasing 154 individuals, 1 to 10 individuals per trial (mean ± SD = 3.7 ± 2.0).

Call recording.

During each test trial, we continuously recorded the calls. For recording sonic calls, we used a recorder Zoom H1 (Zoom Corporation, Tokyo, Japan, sampling rate 48 kHz, 16 bit) with built-in microphone. For recording calls in both sonic and ultrasonic ranges of frequencies, we used the recorder Pettersson D1000X (Pettersson Electronik AB, Uppsala, Sweden, sampling rate 250 kHz, 16 bit) with built-in microphone and the recorder Echo Meter Touch 2 PRO (Wildlife Acoustics, Inc., Maynard, Massachusetts, sampling rate 256 kHz, 16 bit) attached to a smartphone enabling us also to inspect spectrograms in real-time mode on the smartphone display. Microphones were kept in a researcher's hand during the recording at a distance of 20 to 30 cm over the animals, providing a high signal-to-noise

ratio during recording. Two audio tracks per test trial were stored as wav-files, 1 for each recording system.

Call samples.

From 2 audio files for each trial, we analyzed up to 10 calls of each of the 8 call types (see description of call types in the Results). For analysis, we took calls of good quality, with high signal-to-noise ratio, not broken with wind nor superimposed with alien noises and calls of other individuals. As call type *rasp* occurred rarely in Release-to-Burrow Test trials (*n* = 17) we analyzed from 4 to 46 *rasps* per trial.

In total, from 145 test trials, we included in the analysis 2,370 calls with 1,113 being from files in the sonic range and 1,257 from files in the ultrasonic range. From 58 Contact-in-Tunnel Test trials, we analyzed 1,065 calls; from 47 Restraint Test trials, we analyzed 596 calls; and from 40 Release-to-Burrow Test trials we analyzed 709 calls.

Call measurements.

Acoustic parameters were measured using Avisoft SasLab Pro (Avisoft Bioacoustics, Berlin, Germany). Before the start of measurements, we filtered out the low frequencies in all wav-files for removal of low-frequency noise, at 0.2 kHz in files for the sonic range and at 10 kHz in files for the ultrasonic range (except the USV files with *rasps*, which were filtered out at 1 kHz). For creating spectrograms, we used the following settings: Hamming window; Fast Fourier Transform 1,024; frame 50%; sampling rate of 48 kHz for files in the sonic range and 250 to 256 kHz for files in the ultrasonic range; overlap 96.87% for the sonic and 93.75% for the ultrasonic range. For sonic calls, these settings provided 43 Hz frequency resolution and 0.73 ms time resolution; for ultrasonic calls, these settings provided 250 Hz frequency resolution and 0.25 ms time resolution. All measurements were exported automatically to Microsoft Excel (Microsoft Corp., Redmond, Washington). The *twits* and *rasps* were calls of low intensity hardly separable from background noise, so for their analyses we used recordings made in the ultrasonic range of frequencies, because twits and rasps spanned both the sonic and ultrasonic frequencies.

For each call, we measured in the spectrogram window of Avisoft the duration with the standard marker cursor (Fig. 1A and B). In the power spectrum window of Avisoft, we measured the peak frequency (fpeak) and 3 power quartiles: the lower, medium, and upper (q25, q50, q75), covering, respectively, 25%, 50%, and 75% of call energy. In addition, for each call except for *rasps*, we measured the maximum fundamental frequency (f0max), the minimum fundamental frequency (f0min), the fundamental frequency at the beginning of a call (f0beg), and the fundamental frequency at the end of a call (f0end) with the reticule cursor (Fig. 1A and B). Because *rasps* could be produced singly or in bouts of 2 to 3 calls, for those produced in bouts we measured acoustic parameters in the last *rasps* of the bouts. If the *rasp* contained a whistle component in the form of a narrow frequency band (Fig. 1C), we additionally measured f0max and f0min of this component.

In addition, the frequencies of formants (acoustic resonances of vocal tract) in *rasps* were tracked using the PRAAT DSP package (Boersma and Weenink 2013). To establish the settings of Linear Predictive Coding (LPC) for measuring formants using PRAAT, we estimated the oral vocal tract length (oral vtl) of the Northern Mole Vole based on skull length of this species (Sineva and Evdokimov 2007) as about 30 mm, because in rodents the larynx position is immediately behind the skull at the level of first to second neck vertebras (Fitch 2000; Pasch et al. 2017; Riede et al. 2017).
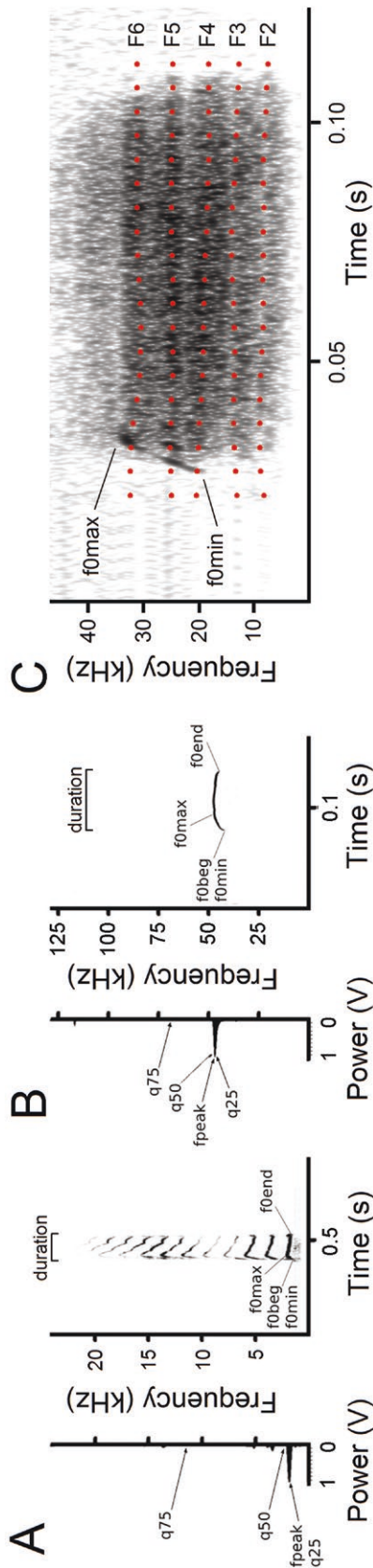
Fig. 1. Spectrograms and power spectra illustrating the measured acoustic parameters for (A) sonic (below 20 kHz) and (B) ultrasonic (above 20 kHz) call types; (C) dots indicate tracks of the first 5 formants (F2 to F6) of rasp with PRAAT (the F1 formant track expected at 3 to 4 kHz is missing, probably because of the weaker sensitivity of the Pettersson D1000X recorder at frequencies below 10 kHz). Designations: duration—call duration; f0beg—the fundamental frequency at the beginning of the call; f0end—the fundamental frequency at the end of the call; f0max—the maximum fundamental frequency; f0min—the minimum fundamental frequency; fpeak—the peak frequency; q25, q50, q75—the lower, medium, and upper quartiles of the power spectrum.

The first 6 formants (F1 to F6) of *rasps* were tracked over the entire duration of a call (following Lapshina et al. 2012; Volodin et al. 2014; Fig. 1C). Point values of formant tracks were extracted, exported to Excel and the values of each formant for a given *rasp* were calculated as the average values from the point values. The LPC settings were: Burg analysis; window length 0.04 s; time step 0.01 s; maximum number of formants 5 to 6; and the upper limits of the frequency range of 34 to 37 kHz. While formants F2 to F6 were tracked in most *rasps*, the F1 could only be tracked in 3 *rasps*, probably because of weaker sensitivity of the Pettersson D1000X recorder at frequencies below 10 kHz.

We calculated formant dispersion (dF) from average values of the 6 formant frequencies of all *rasps* using the linear regression method (Reby and McComb 2003). Then, the vocal tract length (vtl) was calculated as vtl = C/2 * dF, where C is the sound speed in air, 350 m/s (Reby and McComb 2003).

Call contours.

By visual inspection of call spectrograms in the spectrogram window of Avisoft, we classified calls to 1 of 5 contours (Fig. 2; Supplementary Data SD1): flat, chevron, upward, downward, and complex (Yurlova et al. 2020; Kozhevnikova et al. 2021; Dymskaya et al. 2022). Flat contour was determined if the difference between f0min and f0max was less than 0.6 kHz (for files in the sonic range) or less than 6 kHz (for files in the ultrasonic range). In cases where the difference between f0min and f0max was equal or larger than 0.6 kHz or 6 kHz, respectively, a call contour could be classified as chevron (up and down), upward (ascending from start to end), downward (descending from start to end), or complex (up and down a few times or U-shaped; Fig. 2).

Nonlinear phenomena.

For each call, we also noted a presence/absence of 4 kinds of nonlinear phenomena (Fig. 3; Supplementary Data SD1): sidebands, deterministic chaos, subharmonics, and frequency jumps (Wilden et al. 1998; Yurlova et al. 2020; Kozhevnikova et al. 2021; Dymskaya et al. 2022; Piastolov et al. 2023; Rutovskaya et al. 2023). Sidebands were identified in a call when we observed additional frequency bands above and below the fundamental frequency band. Deterministic chaos was identified when a call had a chaotic segment, sometimes containing residual tonal elements. Subharmonics were identified by presence of frequency bands of 1/2 or 1/3 of f0 (Fig. 3). Deterministic chaos and subharmonics were only registered if total duration of fragments with these nonlinear phenomena was at least 10% of the entire call duration (following Yurlova et al. 2020; Kozhevnikova et al. 2021). Frequency jump was only identified when it was 1 kHz or more in files recorded in the sonic range or 10 kHz or more in files recorded in the ultrasonic range (Fig. 3). For understanding the contour shape in calls broken with frequency jumps, we virtually smoothed the broken line of call contour (following Yurlova et al. 2020; Kozhevnikova et al. 2021).

Statistical analyses.

Statistical analyses were carried out with STATISTICA, v. 8.0 (StatSoft, Tulsa, Oklahoma) and R 4.3.1 (R Development Core Team 2023). Means are given as mean ± SD, all tests were 2-tailed, and differences were considered significant whenever $P < 0.05$.

We used GLMM for comparison of acoustic parameters among 3 fully sonic and among 3 fully ultrasonic call types and for estimating the effect of call-eliciting test on the acoustic parameters. Call type, call-eliciting test, and interaction between these factors were introduced in the analyses as fixed factors, while trial ID (nested in call-eliciting test) was introduced as a random factor.

For estimating the effect of sex on animal body mass and the width of incisors, we used a 1-way ANOVA. For estimating the effects of sex on the acoustic parameters, we used a nested design of 2-way ANOVA, with animal sex introduced as a fixed factor and test trial ID (nested in sex) as a random factor. For estimating the relationship between the 2 body size proxies (body mass and the width of incisors) and the acoustic parameters, we used Pearson correlation with Bonferroni correction.

We used the standard procedure of discriminant function analysis (DFA) for calculating the probability of correct assignment of calls to type, 1 DFA for 3 fully sonic call types and another DFA for 3 fully ultrasonic call types. We included in DFAs all 9 measured acoustic parameters: duration, f0max, f0min, f0beg, f0end, fpeak, q25, q50, and q75. Parameters mostly introducing in discrimination were determined by Wilks' lambda. We did not include in DFAs 2 sonic-to-ultrasonic call types, because 1 of them (*twit*) was too rare to be included in the analysis and the second (*rasp*) had a fully different set of measured acoustic parameters.

To validate our DFA results, we calculated the chance of values being correctly assigned to call type by applying a randomization test for misclassification probability in discriminant analysis (Solow 1990) with macros, created in R. The values by chance were calculated from DFAs performed on 1,000 randomized permutations on the actual data sets (Solow 1990; Mundry and Sommer 2007). If the observed value exceeded 95%, 99%, or 99.9% of values within the distribution of 1,000 chance values, we established that the observed value did differ significantly from the chance value with a probability $P < 0.05$, $P < 0.01$, or $P < 0.001$, respectively (Solow 1990; Briefer et al. 2010; Chelysheva et al. 2023).
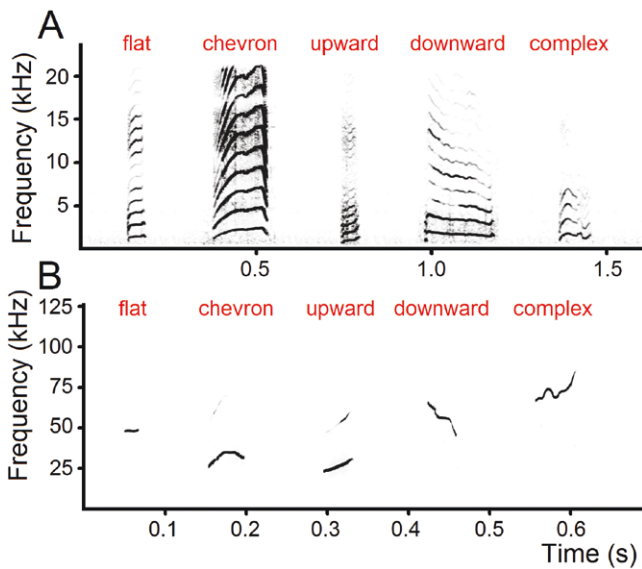
Results

Based on values of the acoustic parameters and on contour shapes, we classified calls into 8 call types (Fig. 4; Supplementary Data SD1). Three call types (*wheek*, *squeak*, and *squeal*) were fully sonic (below 20 kHz). Three call types (*upsweep*, *variative*, and *squeeze*) were fully ultrasonic (above 20 kHz). Two call types (*twit* and *rasp*) spanned across both sonic and ultrasonic ranges (Fig. 4).

Sonic call types.

The 3 sonic call types differed by duration, f0max, and fpeak (Table 1). Values of all acoustic parameters were the highest in *squeals*, lowest in *wheeks*, and intermediate in *squeaks* (Table 1). The *wheeks* were faint short tonal calls with low f0, commonly produced in long series (Fig. 4A). The *squeaks* were tonal calls with intermediate values of duration and f0 values close to those of *wheeks* and *squeals*. The *squeals* were tonal calls of higher-intensity, longer in duration, higher in f0 and with call energy shifted toward higher frequencies compared to *wheeks* or *squeaks* (Fig. 4A). In *wheeks*, fpeak coincided with f0 band; in *squeaks*, fpeak either coincided with f0 band or coincided with its first harmonic; in *squeals*, fpeak did not

Fig. 2. Spectrogram illustrating 5 contour shapes for (A) sonic calls (below 20 kHz) and (B) ultrasonic calls (above 20 kHz).

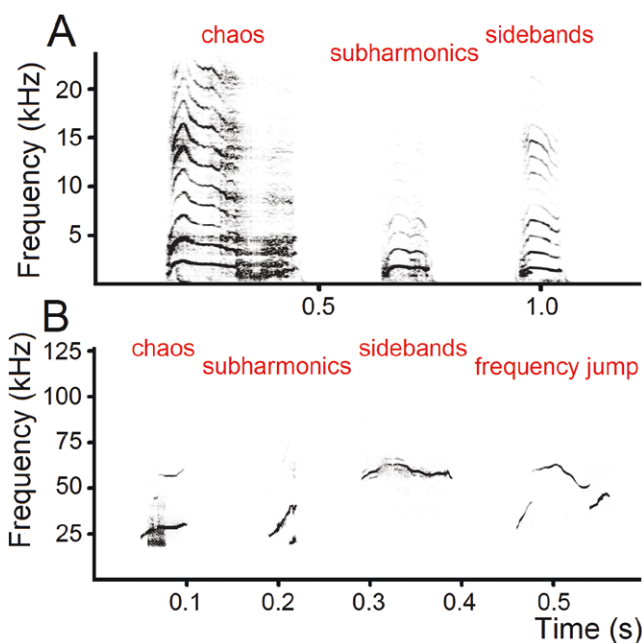**Fig. 3.** Spectrogram illustrating nonlinear phenomena in (A) sonic calls (below 20 kHz) and (B) ultrasonic calls (above 20 kHz).
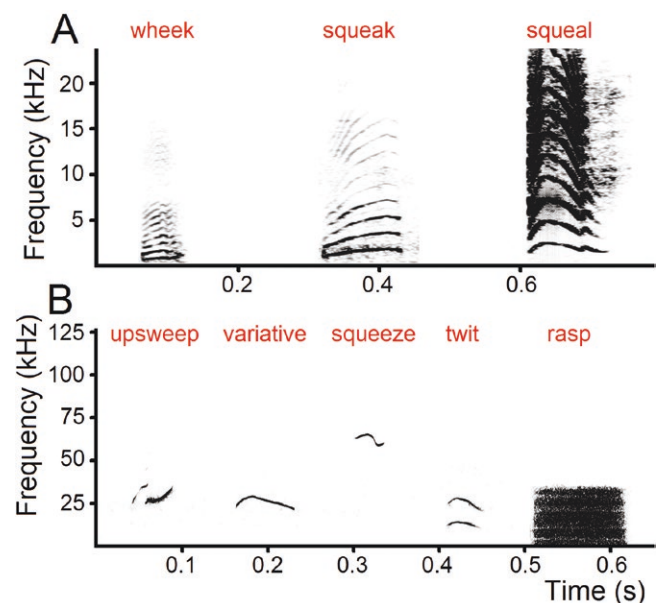

Fig. 4. Spectrogram illustrating 8 call types of wild-living northern mole voles. (A) 3 sonic call types (*wheek, squeak, squeal*); (B) 3 ultrasonic call types (*upsweep, variative, squeeze*); and 2 sonic-to-ultrasonic call types (*twit, rasp*).

Table 1. Values (means ±SD, min–max) of acoustic parameters and GLMM results for comparison for sonic and ultrasonic call types. Test trial ID was introduced as a random factor. Different superscripts indicate statistically different values (Tukey post hoc, $P < 0.05$), n—number of calls.

Acoustic parameter	Sonic call types				Ultrasonic call types			
	wheek (n = 398)	squeak (n = 408)	squeal (n = 307)	GLMM	upsweep (n = 292)	variative (n = 325)	squeeze (n = 261)	GLMM
duration (ms)	48 ± 13[a] (25 to 140)	115 ± 45[b] (47 to 340)	135 ± 49[c] (47 to 320)	$F_{2,1006} = 151.77; P < 0.001$	33 ± 12[a] (7 to 80)	25 ± 23[b] (6 to 160)	30 ± 28[a] (5 to 176)	$F_{2,781} = 8.13; P < 0.001$
f0max (kHz)	1.31 ± 0.20[a] (0.75 to 1.96)	2.03 ± 0.33[b] (1.16 to 3.14)	2.41 ± 0.37[c] (1.37 to 3.70)	$F_{2,1006} = 356.75; P < 0.001$	36.8 ± 6.9[a] (22.5 to 71.0)	36.9 ± 8.5[a] (19.0 to 57.5)	66.5 ± 10.6[b] (46.5 to 98.5)	$F_{2,781} = 265.33; P < 0.001$
f0min (kHz)	0.57 ± 0.16[a] (0.20 to 1.17)	1.04 ± 0.31[b] (0.28 to 1.78)	1.19 ± 0.28[c] (0.55 to 1.87)	$F_{2,1006} = 127.48; P < 0.001$	23.5 ± 4.1[a] (15.5 to 35.0)	29.4 ± 8.5[b] (13.0 to 47.7)	49.2 ± 11.5[c] (25.6 to 92.7)	$F_{2,781} = 144.41; P < 0.001$
f0beg (kHz)	0.60 ± 0.18[a] (0.20 to 1.29)	1.10 ± 0.36[b] (0.32 to 2.39)	1.27 ± 0.32[c] (0.60 to 2.20)	$F_{2,1006} = 99.29; P < 0.001$	24.8 ± 5.2[a] (15.5 to 43.0)	32.3 ± 8.9[b] (15.0 to 57.5)	54.1 ± 11.9[c] (27.5 to 98.5)	$F_{2,781} = 165.13; P < 0.001$
f0end (kHz)	1.20 ± 0.26[a] (0.23 to 1.96)	1.40 ± 0.24[b] (0.42 to 2.15)	1.38 ± 0.22[b] (0.55 to 2.02)	$F_{2,1006} = 8.71; P < 0.001$	33.2 ± 5.7[a] (17.5 to 63.5)	32.7 ± 9.2[a] (13.0 to 52.5)	58.5 ± 13.1[b] (26.2 to 97.2)	$F_{2,781} = 144.11; P < 0.001$
fpeak (kHz)	0.98 ± 0.21[a] (0.51 to 1.73)	1.94 ± 0.71[b] (0.93 to 5.43)	9.48 ± 3.77[c] (4.04 to 18.04)	$F_{2,1006} = 736.91; P < 0.001$	29.1 ± 4.6[a] (19.5 to 44.2)	33.2 ± 8.6[b] (17.7 to 50.5)	57.5 ± 12.8[c] (28.2 to 124.2)	$F_{2,781} = 145.36; P < 0.001$
q25 (kHz)	0.10 ± 0.23[a] (0.55 to 2.28)	2.27 ± 1.02[b] (0.98 to 6.45)	7.21 ± 1.39[c] (2.67 to 12.18)	$F_{2,1006} = 1,685.69; P < 0.001$	25.7 ± 3.9[a] (17.2 to 36.6)	27.2 ± 8.3[a] (11.0 to 49.0)	45.0 ± 13.4[b] (16.5 to 81.7)	$F_{2,781} = 108.43; P < 0.001$
q50 (kHz)	0.15 ± 0.62[a] (0.70 to 4.59)	4.17 ± 2.42[b] (1.12 to 12.98)	11.66 ± 1.78[c] (5.34 to 14.71)	$F_{2,1006} = 1,228.20; P < 0.001$	29.6 ± 5.2[a] (20.7 to 64.9)	33.4 ± 9.3[b] (20.2 to 70.2)	56.2 ± 11.7[c] (25.5 to 94.5)	$F_{2,781} = 159.36; P < 0.001$
q75 (kHz)	3.17 ± 1.83[a] (0.84 to 12.18)	8.25 ± 3.9[b] (1.45 to 17.39)	15.28 ± 1.47[c] (9.56 to 18.42)	$F_{2,1006} = 629.36; P < 0.001$	34.4 ± 9.0[a] (24.0 to 83.0)	44.5 ± 17.5[b] (21.5 to 106.5)	71.4 ± 14.9[c] (34.5 to 110.7)	$F_{2,781} = 106.01; P < 0.001$

coincide with f0 band or its first harmonic but was located at frequencies above 4 kHz (Table 1).

The 3 sonic call types differed by prevalent contour shapes (Fig. 5A): upward in *wheeks* (73.4% of calls), chevron or upward in *squeaks* (47.8% and 36.0% calls), and chevron in *squeals* (90.2% calls). Nonlinear phenomena were only detected in 11.3% *wheeks*, 11.3% *squeaks*, and 7.5% *squeals* (Fig. 5B). The most widespread nonlinear phenomenon was chaos, detected in 9.3% *wheeks*, 8.1% *squeaks*, and 5.2% *squeals*; subharmonics or sidebands were rare (Fig. 5B).

We conducted a DFA for correct classification of 1,113 sonic calls to 3 call types based on 9 measured acoustic parameters: duration, f0max, f0min, f0beg, f0end, fpeak, q25, q50, and q75. The average value of call correct assignment to type was 94.2%, which was significantly higher than the level expected by chance of 36.8 ± 1.1%, min = 33.2%, max = 40.3% (permutation test, 1,000 permutations, $P < 0.001$). DFA correctly assigned to type 98.5% *wheeks*, 88.0% *squeaks*, and 96.7% *squeals* (Fig. 6A). Parameters mostly introducing in discrimination, in order of decreasing importance, were q25, duration, and f0max.

Ultrasonic call types.

The *squeeze* was distinctive from other ultrasonic call types (Fig. 4B) with a very high f0 (f0max exceeding 47 kHz; Table 1). The *upsweep* and *variative* call types had close values of f0 parameters although f0min, f0beg, and fpeak were higher in *variative* calls (Table 1). The duration was the shortest in *variative* calls and did not differ between *upsweep* calls and *squeezes* (Table 1).

The *upsweep* calls were distinctive from other ultrasonic call types by the upward contour (91.4% calls; Fig. 4B) and were commonly produced in short series. The *variative* calls commonly had a flat contour (50.5% calls; Fig. 5A) and were emitted as single calls, not in series. In *squeezes*, the most widespread contour was upward (44.4% calls), and the remaining 4 contours occurred at approximately equal percentages (Fig. 5A). Nonlinear phenomena were found in 37.7% of *upsweep* calls, in 14.2% of *variative* calls, and in 41.38% of *squeezes* (Fig. 5B). The most common nonlinear phenomenon was frequency jump, detected in 35.6% *upsweep* calls, 11.1% *variative* calls, and 32.2% *squeezes*. Sidebands were found in 1.7% *upsweep* calls, 2.8% *variative*, and 6.5% *squeezes*; subharmonics and chaos were rare (Fig. 5B).

We conducted DFA for correct assignment of all 878 measured ultrasonic calls to 3 call types based on 9 measured acoustic parameters: duration, f0max, f0min, f0beg, f0end, fpeak, q25, q50, and q75. The average value of call correct assignment to type was 83.8%, which was significantly higher than the level expected by chance of 37.2 ± 1.3%, min = 33.2%, max = 41.6% (permutation test, 1,000 permutations, $P < 0.001$). DFA correctly assigned to type 85.3% *upsweeps*, 76.6% *variative* calls, and 91.2% *squeezes* (Fig. 6B). Parameters mostly introducing in discrimination, in order of decreasing importance, were f0max, q75, and f0beg.

Sonic-to-ultrasonic call types.

The tonal *twits* (n = 39) had f0 values marginal between sonic and ultrasonic ranges of frequencies (Fig. 4B). The *twits* were faint and short, produced singly, not in series. The *twits* had the shortest duration (19 ± 12 ms, ranging from 8 to 77 ms) among the 8 call types and had values of f0 parameters and of fpeak intermediate between the sonic and ultrasonic call types. The f0max of *twits* was 17.1 ± 3.4 kHz and ranged from 11.7 to 26.5 kHz in sonic-to-ultrasonic range of frequencies, the mean f0min was 12.3 ± 2.7 kHz, mean f0beg was 13.9 ± 3.7 kHz, and mean f0end was 13.9 ± 3.3 kHz. The fpeak of *twits* was 15.9 ± 4.1 kHz and ranged from 9.7 to 26.5 kHz; the mean values of power quartiles were 15.3 ± 2.3 kHz for q25, 21.5 ± 4.1 kHz
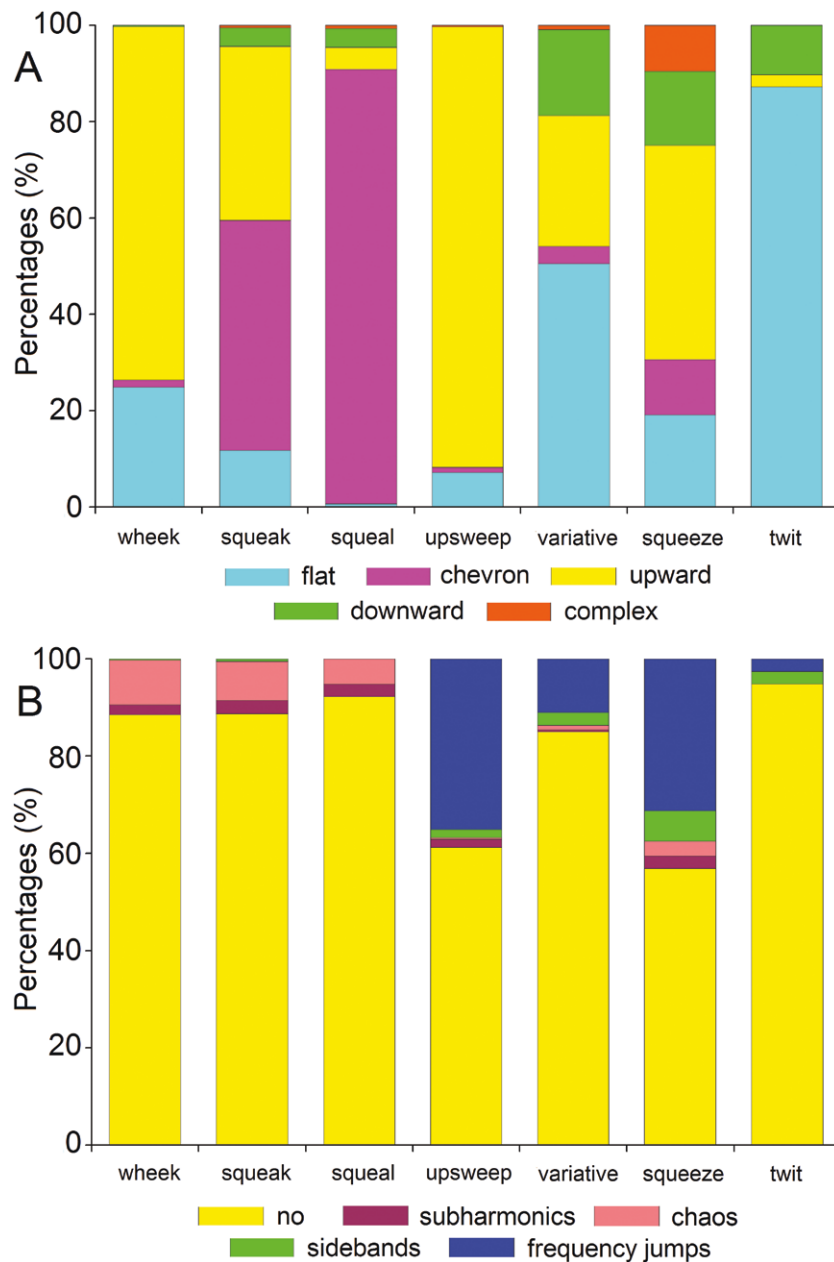
Fig. 5. Percentages of (A) 5 different contour shapes and (B) 4 kinds of nonlinear phenomena in 7 call types.

for q50 and 38.9 ± 11.8 kHz for q75. Most *twits* (87.2%) had flat contours, but some *twits* had downward or upward contours (Fig. 5A). Nonlinear phenomena were only present in 2 (5.1%) *twits*: 1 *twit* contained frequency jump and 1 *twit* contained sidebands (Fig. 5B).

The *rasp* (*n* = 340) was the broadband noisy call type expanding from sonic-to-ultrasonic range of frequencies (Figs. 1C and 4B). The *rasps* were single calls (62.4%) or bouts of 2 (32.1%) or 3 (5.6%) *rasps* with very short intervals between calls. The *rasps* were produced in long series with irregular intervals between them. About half of *rasps* (156 *rasps*, 45.9%) contained a tonal component with f0max 21.18 ± 9.09 kHz and f0min 13.10 ± 5.69 kHz. Duration of *rasps* was 105 ± 32 ms ranging from 34 to 213 ms, the fpeak was 17.8 ± 7.2 kHz ranging from 1.2 to 34.1 kHz. Frequencies of power quartiles were 13.2 ± 2.8 kHz for q25, 20.7 ± 3.8 kHz for q50, and 28.9 ± 2.9 kHz for q75. Frequencies of the first 6 formants were 2.6 ± 0.3 kHz (F1, *n* = 3), 8.0 ± 0.7 kHz (F2, *n* = 314), 13.9 ± 0.9 kHz (F3, *n* = 314), 19.4 ± 1.2 kHz (F4, *n* = 314), 25.7 ± 1.1 kHz (F5, *n* = 314), and 31.3 ± 1.2 kHz (F6,

n = 314). Formant dispersion of *rasps*, calculated by the method of linear regression (Reby and McComb 2003), comprised 5.652 kHz (Fig. 7). This formant dispersion indicates the oral vocal tract length of 30.96 mm, which is very close to the value of the basal skull length in the Northern Mole Vole (29.0 to 30.3 mm; Sineva and Evdokimov 2007).

Call type and context.

The *wheek* was the most common call type attending all peaceful contacts. Judging by some superimposed calls on spectrograms, 2 or more animals could produce their *wheeks* simultaneously. As a rule, northern mole voles produced the *wheeks* in long series with irregular intervals. The *wheeks* were often produced in Contact-in-Tunnel Tests during digging or during tactile interactions, when 2 animals met in tunnel and interfered with each other's digging (Table 2). The *wheeks* were also frequently produced in Release-to-Burrow Tests and probably attended the meetings of animals in a burrow. The
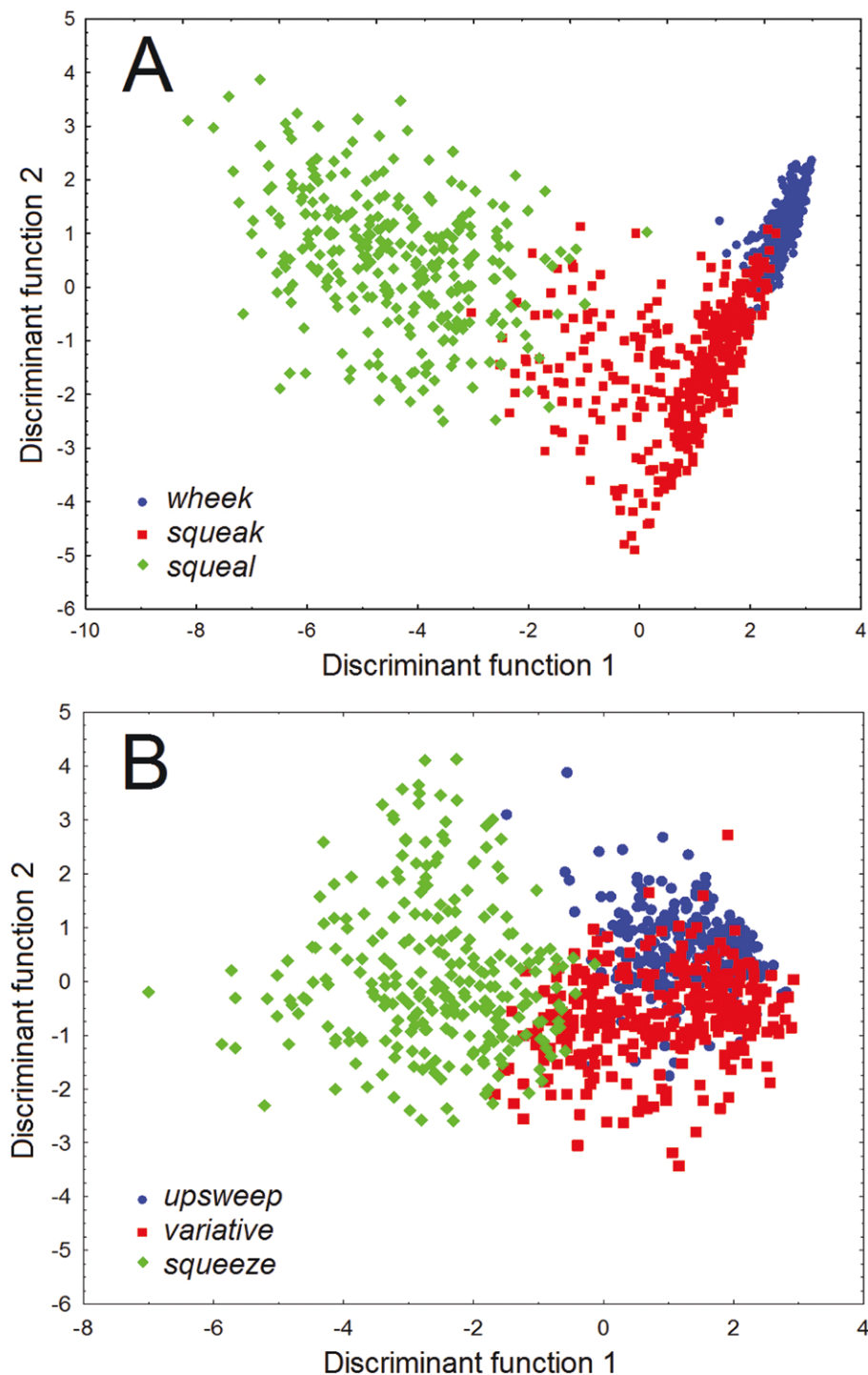
Fig. 6. Scatterplots illustrating DFA results for classifying calls to correct call type. (A) Sonic calls to 3 call types: *wheek*, *squeak*, and *squeal*. (B) Ultrasonic calls to 3 call types: *upsweep*, *variative*, and *squeeze*. Average percent of correct assignment to call type was 94.2% for sonic and 83.8% for ultrasonic calls.

wheeks were very rare during the Restraint Tests (were only recorded in a few trials; Table 2). We have never heard or recorded the *wheeks* from animals isolated in their individual buckets.

The *squeaks* occurred in all the 3 call-eliciting tests and were related to moderate arousal of animals (Table 2). The *squeaks* could be produced singly or in short series. The *squeaks* were common in Contact-in-Tunnel Tests during tactile contacts of 2 animals trying to dig in the same place simultaneously or climbing over one another. The *squeaks* were also common in the Restraint Tests and in the Release-to-Burrow Tests, in which they were probably produced during animal encounters in a burrow or when climbing over one another.

The *squeals* attended situations of high arousal, primarily during Restraint Tests (Table 2). The *squeals* were commonly produced in series for the entire duration of unpleasant handling. The animals also produced the *squeals* during Contact-in-Tunnel Tests immediately after releasing to the experimental setup or at high arousal during jumps to the walls in attempts to escape from the experimental setup. During the Release-to-Burrow Tests, *squeals* were rare.

The *upsweeps* were most often emitted during the Contact-in-Tunnel Tests when both animals were in a calm state. The *upsweeps* attended peaceful contacts and sometimes movements of noncontacting animals (Table 2). The *upsweeps* were commonly produced
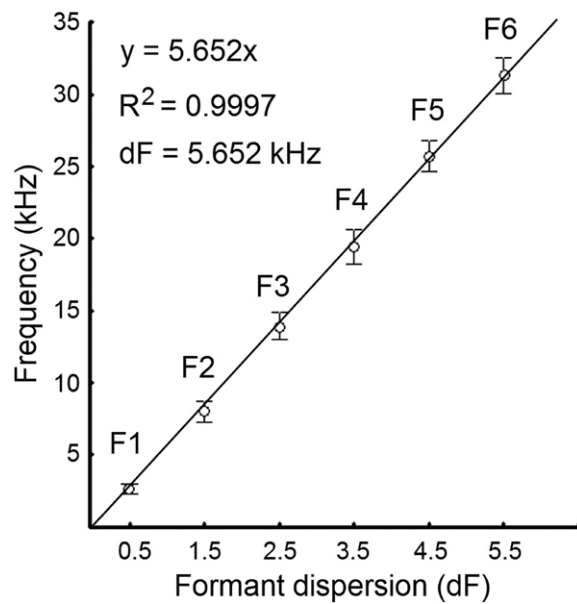
Fig. 7. Estimation of formant dispersion (dF) by average values of formant frequencies of *rasps* by the method of linear regression following Reby and McComb (2003). Central points show the average frequencies of the first 6 formants (F1 to F6), whiskers show SD.

in series of 3 to 8 (sometimes up to 30) calls, primarily during naso-nasal contacts. Both animals could vocalize simultaneously, which was visible from superimposed calls on the spectrogram. If animals from different burrows (even adult males) emitted *upsweeps* during their first contact in the Contact-in-Tunnel Test, all subsequent interactions between them were peaceful. The *upsweeps* also often occurred in the Release-to-Burrow Tests, probably during contacts between family members (Table 2). The *upsweeps* were never registered during the Restraint Tests.

The *variative* calls were found in all 3 call-eliciting tests (Table 2). It seems that this call type was not related to a particular situation or certain level of arousal.

The *squeezes* were most often produced during the Restraint Tests (Table 2). Rarely, *squeezes* were also produced during Release-to-Burrow Tests, probably during situations of high arousal.

The *twits* were most often made during the Release-to-Burrow Tests and rare during the Contact-in-Tunnel Tests or during Restraint Tests (Table 2). They were either produced singly or among series of *rasps*.

The *rasps* occurred exclusively in Release-to-Burrow Test trials. These calls were produced from the tunnel hole or in those moments when caller(s) were plugging the opened entrance to a damaged tunnel and shortly showed the fore part of its body in the hole (Table 2). It appeared that the animal *rasps* produced from the hole were directed toward a microphone, handheld by a researcher in about 10 cm near the hole.

Acoustic parameters of sonic call types could differ in different call-eliciting tests (Table 2). Test type affected the values of f0max ($F_{4,1006} = 8.12$, $P < 0.001$) and fpeak ($F_{4,1006} = 9.99$, $P < 0.001$), but did not affect call duration ($F_{4,1006} = 1.67$, $P = 0.155$). The *wheeks* had a lower f0max during the Release-to-Burrow Tests than during the Contact-in-Tunnel Tests (Table 2). The f0max of *squeaks* was highest during Restraint Tests, intermediate during Contact-in-Tunnel Tests, and the lowest during Release-to-Burrow Tests (Table 2). The f0max of *squeals* was higher during the Contact-in-Tunnel Tests or Restraint Tests than during Release-to-Burrow Tests. The fpeak of *squeals* was the highest during the Contact-in-Tunnel Tests, intermediate during the

Restraint Tests, and the lowest during the Release-to-Burrow Tests (Table 2).

For ultrasonic call types, Test type also affected the values of f0max ($F_{3,781} = 3.88$, $P = 0.009$) and fpeak ($F_{3,781} = 4.11$, $P = 0.007$), but did not affect call duration ($F_{3,781} = 0.18$, $P = 0.909$). The duration, f0max, and f0peak of *upsweeps* did not differ between Contact-in-Tunnel and Release-to-Burrow Tests (Table 2). The f0max of *variative* calls was lower during Release-to-Burrow Tests, but fpeak was higher during Restraint Tests compared to other tests (Table 2). The f0max of *squeezes* was the lowest in the Contact-in-Tunnel Test, and fpeak was the highest during the Restraint Tests compared to other tests (Table 2).

Sex and acoustic parameters.

One-way ANOVA did not reveal significant differences between males (*n* = 24) and females (*n* = 22) in body mass (males 42.6 ± 5.4 g, females 42.9 ± 6.7 g; $F_{1,45} = 0.02$, $P = 0.90$) or in the width of the 2 upper incisors (males 3.26 ± 0.24 mm, females 3.23 ± 0.28 mm; $F_{1,45} = 0.13$, $P = 0.73$). We also did not find differences in duration, f0max, and fpeak between male and female calls in any call type, sonic or ultrasonic (Supplementary Data SD2).

Body size and acoustic parameters.

We did not find correlations between proxies of animal body size (body mass or the width of 2 upper incisors) and the acoustic parameters of sonic and ultrasonic calls (Supplementary Data SD3). Only duration and fpeak of *squeals* showed marginally significant positive correlations with parameters related to body size (Supplementary Data SD3).

Discussion
Call-eliciting tests.

This study investigated call types in a subterranean rodent, northern mole voles, produced in the field under 3 experimental conditions: Contact-in-Tunnel Test, Restraint Test, and Release-to-Burrow Test. Two of the 3 tests were specially developed for this study and were never used previously; the third test (Restraint Test) was previously used in different modifications in studies of calls of different species of rodents (e.g., Volodin et al. 2018; Klenova et al. 2021). The novelty of this study was also the analysis of both ultrasonic and sonic calls, which have never been applied previously for any species of subterranean rodents. The experimental design of the Contact-in-Tunnel Test was well-applicable for provoking acoustic contacts of 2 animals because the digging for northern mole voles in burrow tunnels entirely fitted to the situations regularly occurring in the wild. Our previous attempts to provoke the acoustic contacts of 2 wild animals through the gap in a wall of 2-chamber cage were unsuccessful because the animals were either motivated to escape from the experimental setup or to hide (personal observations by the authors).

Call types.

We found that northern mole voles use for communication a variety of call types: 3 fully sonic (*wheek*, *squeak*, and *squeal*), 3 fully ultrasonic (*upsweep, variative,* and *squeeze*), 1 marginally sonic-to-ultrasonic narrowband *twit*, and the broadband noisy *rasp*, expanding from sonic to ultrasonic frequency range. Previously for northern mole voles we described 2 ultrasonic call types (*upsweep* and *variative*; Volodin et al. 2022). The correctness of classifying the calls to types based on visual inspection of spectrograms was confirmed by the results of ANOVA and DFA (Table 1; Fig. 6).

Table 2. Values (mean ± SD) of acoustic parameters of sonic and ultrasonic call types and the occurrence of different call types in 3 call-eliciting tests. GLMM results for the effects of test type on the acoustic parameters are given in the text. Different superscripts indicate statistically different values (Tukey post hoc, $P < 0.05$), n—number of calls. Relative occurrence designations are: – not present or present very rarely; + present; +++ present very often.

Call type	Acoustic parameter	Contact-in-Tunnel Test	Restraint Test	Release-to-Burrow Test
Sonic call types		(n = 629)	(n = 243)	(n = 241)
wheek (n = 398)	duration (ms)	49 ± 14	48 ± 14	44 ± 10
	f0max (kHz)	1.35 ± 0.20[a]	1.42 ± 0.17[a,b]	1.23 ± 0.18[b]
	fpeak (kHz)	1.03 ± 0.21	1.11 ± 0.23	0.89 ± 0.18
	occurrence	+++	–	+
squeak (n = 408)	duration (ms)	119 ± 45	112 ± 36	107 ± 54
	f0max (kHz)	2.02 ± 0.30[a]	2.20 ± 0.35[b]	1.84 ± 0.28[c]
	fpeak (kHz)	1.92 ± 0.67	2.23 ± 0.84	1.65 ± 0.51
	occurrence	+	+++	+++
squeal (n = 307)	duration (ms)	129 ± 48	142 ± 48	131 ± 55
	f0max (kHz)	2.49 ± 0.35[a]	2.42 ± 0.35[a]	2.14 ± 0.38[b]
	fpeak (kHz)	10.26 ± 3.90[a]	9.23 ± 3.58[b]	7.64 ± 3.19[c]
	occurrence	+	+++	–
Ultrasonic call types		(n = 433)	(n = 342)	(n = 103)
upsweep (n = 292)	duration (ms)	34 ± 12		30 ± 13
	f0max (kHz)	36.7 ± 7.0		37.0 ± 6.5
	fpeak (kHz)	28.9 ± 4.7		30.5 ± 3.8
	occurrence	+++	–	+
variative (n = 325)	duration (ms)	24 ± 13	28 ± 26	19 ± 9
	f0max (kHz)	36.7 ± 7.5[a]	38.4 ± 9.0[a]	31.7 ± 8.1[b]
	fpeak (kHz)	32.6 ± 6.9[a,b]	34.8 ± 9.5[a]	29.0 ± 8.4[b]
	occurrence	+	+	+
squeeze (n = 261)	duration (ms)	25 ± 27	33 ± 30	23 ± 13
	f0max (kHz)	61.1 ± 8.2[a]	68.1 ± 10.8[b]	65.3 ± 10.3[a,b]
	fpeak (kHz)	51.8 ± 10.7[a]	59.6 ± 12.7[b]	52.8 ± 14.7[a]
	occurrence	+	+++	+
Sonic-to-ultrasonic calls		(n = 3)	(n = 11)	(n = 365)
twit (n = 39)	occurrence	+	–	+++
rasp (n = 340)	occurrence	–	–	+++

In this study, we classified calls to types on the basis of their acoustic structure, following previous studies describing vocal repertoire of subterranean rodents (Pepper et al. 1991; Francescoli 1999; Devries and Sikes 2008; Bednářová et al. 2013). At the same time, many previous studies of vocal communication in subterranean rodents classified the calls by contexts of their emission (Credner et al. 1997; Veitl et al. 2000; Knotková et al. 2009; Vanden Hole et al. 2014; Dvořáková et al. 2016). This approach to classification is questionable, because calls of the same acoustic structure may occur in different situations (e.g., Credner et al. 1997; Salmi et al. 2013; Smirnova et al. 2016; Romani et al. 2022), so vocal repertoires of different subterranean rodents are not immediately comparable. Therefore, call classification by acoustic structure was considered less subjective.

We showed for the first time for a rodent species that spectral peaks of *rasps* in northern mole voles represent formants of the vocal tract (Fig. 7). In rodents, the vocal tract is very short, so the formants

are widely spaced (Fitch and Hauser 2003) and can therefore be exclusively measured in calls in which energy is present in a broad band of frequencies, from hundreds of Hertz to dozens of kiloHertz. *Rasps* of northern mole voles have just this kind of acoustic structure. Our finding indirectly suggests that well-expressed spectral peaks in rasps of *Neotoma* cricetids (Soltis et al. 2012; Kobrina et al. 2023) also represent formants. Comparison of skull length in the Northern Mole Vole and the length of the vocal tract calculated on the basis of formant dispersion of *rasps* (Reby and McComb 2003) showed that the sound source for producing this call type is located in the larynx or in its vicinity. It is known that low-frequency sonic calls of rodents are produced with vocal folds in the larynx (Pasch et al. 2017; Fernández-Vargas et al. 2022), whereas the ultrasonic calls of rodents are produced in the vocal tract (Pasch et al. 2017; Riede et al. 2017; Fernández-Vargas et al. 2022). Our finding for the first time provides arguments in use that the broadband sonic-to-ultrasonic noisy rasp-like calls of rodents are also produced in the vicinity of the larynx.

Call contexts.

This study showed that at the discomfort level of the Restraint Test, northern mole voles produced both sonic calls (primarily *squeals*) and ultrasonic calls (primarily *squeezes*). This is consistent with previous data on other Arvicolinae vole species, e.g., yellow steppe lemmings and the mandarin and Brands's voles, which use both sonic and ultrasonic calls in the Restraint Test (Klenova et al. 2021; Volodin et al. 2021; Dymskaya et al. 2022).

So far, contexts of ultrasonic vocalizations investigated in Arvicolinae and other rodents did not include vocalizations during peaceful interactions of animals, aside from the previous pilot study of northern mole voles (Volodin et al. 2022) and experiments with sibling prairie voles (*Microtus ochrogaster*; Ma et al. 2014). This study is filling this gap of research by modeling peaceful contacts in animal dyads (in Contact-in-Tunnel Tests) or groups (in Release-to-Burrow Tests). This study confirmed previous preliminary data that *upsweeps* function as friendly contact calls at dyad interactions between northern mole voles on neutral territory, with olfactory and tactile contacts (Volodin et al. 2022). Our results therefore provide partial support of a hypothesis that *upsweeps*, used by northern mole voles as close-contact peaceful signals, might not be under selection pressure for long-distant propagation in burrows.

We found that the *variative* ultrasonic calls did not show a relationship with a certain situation, possibly representing the baseline default-state ultrasonic calls providing a reservoir for natural selection for developing context-specific call types. In the previous study, the *variative* ultrasonic calls were the only call type produced by wild northern mole voles when a caller moved to the damaged place of the underground burrow tunnel to plug it with soil (Volodin et al. 2022).

We found that very faint sonic call type *wheek* also attended the peaceful contacts of animals. In northern mole voles, the *wheeks* were permanently heard during movements with digging and at peaceful contacts during the Contact-in-Tunnel and Release-to-Burrow Tests. In this respect, the *wheeks* were reminiscent of soft chirps of naked mole-rats (*Heterocephalus glaber*), using these calls very often in captive colonies (Pepper et al. 1991; Barker et al. 2021a, 2021b) to vocally interact with each other (Yosida et al. 2007). Other subterranean rodents also have low-frequency contact calls. For example, coruros (*Spalacopus cyanus*) produce cooing, whenever they come into contact after brief separation (Veitl et al. 2000). The Mashona mole-rats (*Fukomys darlingi*) use the low-frequency twitters as contact calls when passing each other in tunnels (Dvořáková et al. 2016).

Short low-frequency *wheeks*, produced in series and supporting permanent spatial cohesion between groupmates, are characteristic of many social mammals, e.g., Guinea pigs (*Cavia porcellus*; Verzola-Olivio and Monticelli 2017; Verzola-Olivio et al. 2021), meerkats (*Suricata suricatta*; Rauber et al. 2020), and dwarf mongooses (*Helogale parvula*; Rubow et al. 2018). For the Guinea Pig, it was shown that their short rhythmic *wheeks* are resistant to accumulation of echo at propagation through the environment, thus being well-recognizable by the animals (Parida et al. 2023). For subterranean rodents, the propagation abilities of the *wheek*-like calls have yet to be investigated.

Calls, reminiscent of Northern Mole Vole *wheeks* in acoustic structure and contextual use, were found in all studied social subterranean rodents (Pepper et al. 1991; Credner et al. 1997; Veitl et al. 2000; Knotková et al. 2009; Bednářová et al. 2013; Dvořáková et al. 2016; Barker et al. 2021a). Such calls were not found in solitary subterranean rodents (Francescoli 1999; Schleich and Busch 2002; Devries and Sikes 2008), except for silvery mole-rats (*Heliophobius argenteocinereus*), producing low-frequency (0.81 to 2.5 kHz) and short (about 60 ms) high clucks at courting (Knotková et al. 2009).

The intense sonic calls *squeaks* and *squeals* were related to discomfort in the Restraint Test and did not occur during peaceful contacts between animals. Potentially, these calls might serve to distract the predator and force it to release its prey (Perrone 1980).

The sonic-to-ultrasonic *rasps* of northern mole voles were aggressive calls. Probably, the *rasp* may function as some kind of close-distant alarm call or as a threatening call toward a nondangerous object located in an immediate vicinity of the entrance to the burrow tunnel. The acoustic structure of *rasp* spectrum during spectrographic analysis is reminiscent of the acoustic structure of alarm hisses in some ruminants (Volodina et al. 2018). At the same time, in Key Largo woodrats (*Neotoma floridana smalli*) and white-throated woodrats (*Neotoma albigula*), the raspy vocalizations were associated with courtship behavior and copulations (Soltis et al. 2012; Kobrina et al. 2023).

Acoustic parameters of sonic calls in Arvicolinae rodents.

Our data only partly support a hypothesis of lower-frequency sonic calls in subterranean than in surface-dwelling rodents (Begall et al. 2007; Schleich and Francescoli 2018). To date, there are no comparative data on ultrasonic contact calls for other Arvicolinae species; however, such data are available for sonic calls related to discomfort. These comparative data only partially support the hypothesis, because only in some non-subterranean vole species tested in different variants of the Restraint Test, sonic "sharp squeaks" are indeed higher-frequency than in subterranean vole species. In the subterranean northern mole voles, the average f0max of discomfort-related sonic calls was 2.39 to 2.43 kHz (Supplementary Data SD2) and in the subterranean mandarin voles, the average f0max was 1.49 to 1.81 kHz (Rutovskaya 2011; Dymskaya et al. 2022).

In agreement with this hypothesis (Begall et al. 2007; Schleich and Francescoli 2018), some non-subterranean vole species produce relatively high-frequency discomfort calls: with f0max of 2.4 to 3.5 kHz in Daghestan pine voles (*M. daghestanicus*; Rutovskaya 2019a), 2.7 to 3.0 kHz in Maximowicz's voles (*M. maximowiczii*; Rutovskaya 2020), 3.3 to 4.1 kHz in steppe lemmings (*Lagurus lagurus*; Rutovskaya 2019b), 3.16 to 3.49 kHz in lacustrine voles (*M. limnophilus*; Rutovskaya 2020), 3.46 to 3.57 kHz in Middendorff's voles (*M. middendorffii*; Rutovskaya 2020), and 3.8 kHz in Tien Shan red-backed voles (*Myodes centralis*; Rutovskaya 2019c). Furthermore, some non-subterranean voles produce very high-frequency sonic discomfort calls, with average f0max of 6.49 kHz in Brandt's voles (Rutovskaya 2012; Dymskaya et al. 2022) and of 10.2 to 17.6 kHz in Harting's voles (*M. hartingi*; Rutovskaya 2019d).

In contradiction with this hypothesis (Begall et al. 2007; Schleich and Francescoli 2018), some non-subterranean Arvicolinae species produced even lower-frequency discomfort sonic calls than those found in the subterranean mole vole. For example, in non-subterranean vole species, the average f0max of discomfort calls could be relatively low: about 1.5 kHz in yellow steppe lemmings (Rutovskaya 2019b; Volodin et al. 2021), 1.0 to 1.1 kHz in short-tailed field voles (*M. agrestis*; Rutovskaya and Osipova 2018), 1.2 kHz in Schelkovnikov's pine voles (*M. schelkovnikovi*; Rutovskaya 2019a), 1.5 kHz in bank voles (*Myodes glareolus*; Rutovskaya 2019c), 1.19 to 1.46 kHz in root voles (*M. oeconomus*; Rutovskaya 2020), 1.6 to 2.2 kHz in social voles (*M. socialis*; Rutovskaya 2019d), and 1.9 to 2.0 kHz in paradox voles (*M. paradoxus*; Rutovskaya 2019d).

Acoustic parameters of ultrasonic calls in Arvicolinae rodents.

As was hypothesized, values of acoustic parameters of ultrasonic calls of northern mole voles (Table 1) were in the same range of frequencies as in non-subterranean Arvicolinae species. While comparative data for the acoustics of ultrasonic calls at friendly interactions in voles are unavailable, such comparative data are available in the aggressive and mating contexts for many vole species.

For example, during aggressive interactions, bank voles produce ultrasonic calls of 61 to 71 ms in duration and f0 of 25 to 33 kHz (Kapusta et al. 2007; Kapusta and Sales 2009; Kapusta and Pochroń 2011; Kapusta 2012), root voles produce ultrasonic calls of 15 to 20 ms in duration and f0 of 31 to 35 kHz (Kapusta et al. 1999), common voles (*M. arvalis*) produce ultrasonic calls of 66 to 68 ms in duration and f0 of 28 to 35 kHz (Kapusta et al. 2007; Kapusta and Sales 2009), and short-tailed field voles produce ultrasonic calls of 63 to 68 ms in duration and f0 of 42 to 45 kHz (Kapusta et al. 2007; Kapusta and Sales 2009).

During mating behavior, bank voles produce ultrasonic calls of 61 to 70 ms in duration and f0 of 22 to 37 kHz (Kapusta and Kruczek 2016), prairie voles produce ultrasonic calls of 30 to 150 ms in duration and f0 of 30 to 45 kHz (Mandelli and Sales 1997; Ma et al. 2014), steppe lemmings produce ultrasonic calls of 60 ms and f0 of 50 to 75 kHz (Sales 1972), pine voles (*M. pinetorum*) produce ultrasonic calls of 25 to 50 kHz (Geyer 1979), montane voles (*M. montanus*) produce ultrasonic calls of 31 kHz (Pierce et al. 1989), collared lemmings (*Dicrostonyx torquatus*) produced calls with f0 of 15 to 35 kHz (Brooks and Banks 1973).

At discomfort of the Restraint Test, in northern mole voles the ultrasonic calls were primarily *squeezes* with f0 of 49 to 66 kHz, well comparable with f0 values of ultrasonic calls (65 to 80 kHz) in both subterranean mandarin and non-subterranean Brandt's vole species produced in the situation of discomfort related to restraint in human hand (Dymskaya et al. 2022). In the same situation, yellow steppe lemmings produced calls about 30 ms in duration, with f0 of 25 to 39 kHz (Yurlova et al. 2020; Klenova et al. 2021).

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1. Calls used for creating spectrograms for Figs. 2–4. Wave-file provides the calls in order of their appearances on the figures.

Supplementary Data SD2. Values (mean ± SD) of acoustic parameters for sonic and ultrasonic call types in males and females in 2 call-eliciting tests and 2-way ANOVA results on the effects of sex on the acoustic parameters. Test trial ID was introduced as a random factor. *N*—number of test trials; *n*—number of calls, males/females.

Supplementary Data SD3. Coefficients of Pearson's correlation between acoustic parameters of call types in the Restraint Test with body mass and width of both upper incisors. Values of correlation marginally significant after Bonferroni correction ($P = 0.05/3 = 0.017$) are labeled in bold, *N*—number of individuals.

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Author contributions

Conceptualization: IAV, AVS, and EVV. Methodology: IAV, AVS, and EVV. Software: MMD and IAV. Validation: IAV. Formal analysis: MMD and IAV. Investigation: MMD, IAV, AVS, AR, and EVV. Resources: IAV and AVS. Data curation: MMD, IAV, AVS, AR, and EVV. Writing—original draft: MMD, IAV, AVS, AR, and EVV. Writing—review & editing: MMD, IAV, AVS, AR, and EVV. Visualization: MMD and IAV. Supervision: IAV, AVS, and EVV. Project administration: IAV and AVS.

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Conflict of interest

None declared.

Data availability

All relevant data can be found within the article and its Supplementary Information.

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