

Acoustic communication in four species of subgenus *Alexandromys* (Rodentia, Cricetidae)

Marina V. Rutovskaya

ABSTRACT. The acoustic communication in four species of voles of the subgenus *Alexandromys* (*Microtus oeconomus*, *M. limnophilus*, *M. maximowiczii*, and *M. middendorffii*) includes two signals: squeaks in the context of discomfort, and singing during courtship for the female. Comparison of signal parameters shows a rather large similarity in the structure of sounds, especially between the lacustrine and Middendorf's voles, the squeaks of which have almost no differences in characteristics when using discriminant analysis. The most different in the squeak parameters is the root vole, which has recently been included in the subgenus *Alexandromys*. Singing is the most characteristic element of sexual behavior among species of the subgenus along with other behavioral characteristics of species and is used by animals more often than voles of subgenera *Microtus* and *Sumeriomys*.

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KEY WORDS: rodents, Arvicolinae, vocal repertoire, vocal behaviour, *Microtus*, subgenus *Alexandromys*.

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Акустическая коммуникация у четырех видов полевок подрода *Alexandromys* (Rodentia, Cricetidae)

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РЕЗЮМЕ. Звуковая сигнализация 4 видов полевок подрода *Alexandromys* (*Microtus oeconomus*, *M. limnophilus*, *M. maximowiczii* и *M. middendorffii*) включает два сигнала: писк в ситуации дискомфорта и пение при ухаживании за самкой. Сравнение параметров сигналов показывает довольно большое сходство строения звуков, особенно между приозерной полевкой и полевкой Миддендорфа, писк которых почти не различаются по характеристикам при использовании дискриминантного анализа. Наиболее отличающаяся по параметрам писк является полевка-экономка. Пение является наиболее характерным для видов подрода элементом полового поведения наряду с другими особенностями поведения видов подрода и используются зверьками чаще, чем полевками подродов *Microtus* и *Sumeriomys*.

КЛЮЧЕВЫЕ СЛОВА: грызуны, Arvicolinae, вокальный репертуар, акустическое поведение, *Microtus*, подрод *Alexandromys*.

Introduction

Communicative behavior is the basis for the formation and maintenance of social relationships among individuals (Nikol'skii, 1984; Bradbury & Vehrenkamp, 1998). Originally, mammals were nocturnal animals and their evolution was highly dependent on olfactory cues (Walker, 1998). Chemical communication has remained the leading sensory modality for obtaining information in most of the small mammal species (Doty, 2010; Wyatt, 2014; Kotenkova *et al.*, 2017). Comparatively vocalization is a more recent and advanced mode of communication (Brudzynski, 2010). Vocalization also has its own evolutionary history within the mammalian

taxa, from simple vocal displays, through complex vocal signaling to semiotically- and referentially-organized vocal communication (Brudzynski, 2010).

A vocal repertoire of a particular species may consist of a number of functional signals that are formed from non-specific sounds in the evolution process. The primary function of sound signals is the transmission of information about the state of the signal source such as emotional or motivational state (Nikol'skii, 1984). Kiley (1972) postulated that sound reactions mainly convey information not about the specific state of the animal, such as aggressive or sexual state, but rather about the level of interest of the animal in the stimulus. This is a reflection of the primary motivation level of animal's

arousal and represents typological continuums of sounds, in which the parameters of the extreme in a series of signals are related to each other by a complete series of intermediate values (Kiley, 1972). Non-specific, variable signals in the auditory range (distress signals) are typical of protective behavior during aggressive interactions in many animals, including Muroidea rodents.

Functional communicative signals can appear when the social structure of species became more complex to maintain this structure. Among these signals may be alarm signals that are widely developed for ground squirrels (Nikol'skii, 1984; Blumstein, 2007), or courtship sounds in sexual behavior that can be developed to stimulate reproductive behavior (Zorenko, 1990) or coordinate sexual behavior between the partners (Pomerantz *et al.*, 1983).

Despite the fact that the vocal repertoire of different species may include signals similar in function, it is species-specific. The differences lie both in the number of various acoustic signals of different species or lines (Yang *et al.*, 2013), and in the sound parameters (Nevo *et al.*, 1987; Dempster & Perrin, 1991, 1994; Miller & Engstrom, 2007; Kalcounis-Rueppell *et al.*, 2010; Rutovskaya, 2018 and others), as well as in various vocal reactions to similar situations (Hanson & Hurley, 2012; Brunelli, 2005; Yang *et al.*, 2013 and others). The parameters of the sound signals can diverge, owing to complete or partial geographic isolation (Nikol'skii, 1984; Campbell *et al.*, 2010; Merten *et al.*, 2014), acoustic properties of the habitat, or the ability of the signal recipient (Blumstein, 2007). The species-specificity of signal parameters may be associated with the morphology of the body and voice apparatus. In accordance with the source filter theory, the main frequency F_0 of mammalian sounds is generated by vibration of the vocal cords located in the larynx (source), but, passing through the vocal tract, sound frequencies are filtered out, revealing resonant frequencies — formants (Fitch & Reby, 2001; Taylor & Reby, 2010). According to the formula proposed by Fletcher (2010), the optimal frequency of the signal type, taking into account the size of the vocal cords and the distance between the ears, is proportional to the length of the body or its mass. Changes in the spectral characteristics, primarily the peak frequency, under the natural selection to optimize the signal passage through the environment can be directed both to lowering and increasing the frequency. For example, a number of tropical squirrels of the same size have alarm vocalizations that vary greatly in frequency. Thus, the peak frequency of the signal of *Aethosciurus poensis*, which lives in the most lightened forest area at an altitude of about 15 m, was 5.5 kHz, while the signal of the same in size *Funisciurus isabella*, which settles in a very dense undergrowth, was only about 1 kHz. Naturally, attenuation of high frequencies will be greater in dense undergrowth than in lightened crowns (Emmons, 1978). On the contrary, an increase in the peak frequency of alarm vocalization can be associated with an increase in the noise immunity, for example, the peak frequency of the Brandt's vole (*Lasiopodomys brandti* Radde, 1861)

alarm signal is about 10 kHz, which is higher than the frequency range occupied by bird singing (Rutovskaya, 2012). The variability of the sound signals may not be a result of directional selection also. Campbell (Campbell *et al.*, 2010) suggested that population differentiation in the advertisement song of neotropical singing mice (*Scotinomys teguina* and *S. xerampelinus*) is largely shaped by genetic drift. According to Somers (1973), sound signals are not subject to strong selection pressure and can be an “indicator of origin”. The phylogeny of species can play a significant role in the formation of the vocal repertoire. So to study the evolution of calling in 209 species of rodents phylogenetic analyses supported the hypothesis that calling was likely to evolve following the evolution of diurnality, but not following the evolution of sociality (Shelley & Blumstein, 2005). Wherein alarm call repertoire size in marmots was explained by social complexity (Blumstein, 2007).

The subfamily Arvicolinae Gray, 1821, a large group of vole species with different degrees of kinship and acoustic system development, is suitable for the study of communicative system evolution. The distress signals (squeaks) during aggressive interactions have been described for several species of voles (genera *Microtus* Schrank, 1798, *Lasiopodomys* Lataste, 1887, *Lagurus* Gloger, 1841, and *Myodes* Pallas, 1811 (Giannoni *et al.*, 1997; Rutovskaya & Kovalskaya, 1999; Kapusta *et al.*, 1999, 2007; Rutovskaya, 2007, 2011, 2012, 2017; Kapusta & Sales, 2009; Rutovskaya & Nikol'skii, 2014). Males of the genera *Microtus*, and *Lasiopodomys* also sing during courtship of females. Singing constitutes a signal with relatively low amplitude (Zorenko & Rutovskaya, 2006). Voles from different subgenera have differential propensities to emit songs: voles from the “arvalis” group and social voles sing rarely, whereas voles from the subgenus *Alexandromys* Ognev, 1914 sing more often which may play a significant role in their social life, for example in pairing and synchronizing sexual behavior (Zorenko, 1990). The singing vole (*Microtus miurus* Osgood, 1901) emits songs that may serve as a territorial signal (Cole & Wilson, 2010). Several species of the subfamily Arvicolinae are known to emit alarm signals, including Brandt's vole (Nikol'skii, 1979; Rutovskaya, 2012) and narrow-skulled vole (*Microtus gregalis* Pallas, 1779) (Rutovskaya & Nikol'skii, 2014).

The voles of subgenus *Alexandromys* noted to have a number of behavioral peculiarities, compared with other species of subfamily Arvicolinae (Zorenko, 1990). They mark their territories with femoral and anal gland secretions by specific actions, and dance in conflicts. Males waltz, emit sexual singing, and bite females, stimulating them to copulate (Zorenko, 1990; Zorenko & Atanasov, 2018). Zorenko (1990) identified two main trends of sexual behavior with different degrees of genital stimulation: many intromissions and few thrusts during mountings of the males, which is typical for the genus *Microtus* (subgenera *Sumeriomys*, *Terricola*, and “arvalis” group). In the first case, singing is rare and only 30% of the males sing. The second trend includes few intromissions and many thrusts during

mountings of the males, which is typical of the genera *Alexandromys*, *Blanfordimys*, and *Lasiopodomys*. In this case, 70–90% of the males sing in genera *Alexandromys* and *Lasiopodomys*. Whereas singing is completely absent in genera *Blanfordimys* and *Neodon* (Zorenko, 1990), possibly because these taxonomic groups are not as primitive as previously thought and had a parallel evolution with other genera of gray voles (Bannikova *et al.*, 2009). Zorenko (1990) postulated that the evolution of sexual behavior is related to the emergence and development of singing in genus *Alexandromys*. Singing allows an individual to evaluate a possible partner at a distance, and therefore close contacts between unfamiliar individuals in this genus, such as sniffing and grooming, are less recorded than that in the genus *Microtus* (Zorenko, 1990). All species of subgenus *Alexandromys* exhibit a high aggressiveness and low tolerance (Zorenko, 1990). But the vocal behavior of this species has been studied only minimally.

The purpose of this study was to describe the acoustic communication of adult voles in four species of the subgenus *Alexandromys*: the root vole *M. oeconomus*, the lacustrine vole *M. limnophilus*, the Maximowicz's vole *M. maximowiczii*, and the Middendorf's vole *M. middendorffii*, to compare and to identify the species-specific parameters of sounds and to discuss the possible value of singing in this subgenus.

Methods

Some characteristics of the studied species

Subgenus *Alexandromys* (subfamily Arvicolinae, Rodentia) includes a group of large hydrophilic voles, found predominantly in the Far East: Zabaykalsky Krai, Amur Oblast, the north of Siberia, Mongolia, Northeastern China, and Korea, while only the root vole is spread over the tundra and taiga zones all over Eurasia and Alaska. The taxonomy of voles is still controversial. Pavlinov (2006) distinguished the subgenera *Alexandromys* and *Pallasiinus* Kretzoi, 1964, within the genus *Microtus*, whereas Musser & Carleton (2005) combined them together into one subgenus *Alexandromys*. Similarly, the lacustrine vole (*M. limnophilus* Büchner, 1889) was considered as a close relative of the root vole (*M. oeconomus* Pallas, 1776) in the subgenus *Pallasiinus* (Malygin *et al.*, 1990; Pavlinov, 2006). The latest molecular studies, however, suggest that the lacustrine voles are more likely to be related to the reed vole (*Microtus fortis* Büchner, 1889) (Bannikova *et al.*, 2010; Lissovsky *et al.*, 2018). Based on craniometric data, the lacustrine vole from Mongolia has been combined with the Evoron vole (*Microtus evoronensis* Kovalskaya et Sokolov, 1980), Muya vole (*Microtus mujanensis* Orlov et Kovalskaya, 1978) and Maximowicz's vole (*M. maximowiczii* Schrenk, 1859) (Lissovsky & Obolenskaya, 2011) in a single clade. These species differ in details of the karyotype structure and are all reproductively isolated from each another. Hybrids of the Evoron voles with Maximowicz's voles in different combinations are either sterile or have

meiotic disturbances (Meyer *et al.*, 1996). Middendorf's voles (*M. middendorffii* Poljakov, 1881), together with the North Siberian vole (*M. hyperboreus* Vinogradov, 1933) are identified as a separate group "middendorffii" (Ellerman, 1941). Following modern splitting tendency, the taxonomic status of *Alexandromys* was elevated from subgeneric within the genus of *Microtus* Schrank, 1798 to full generic rank (Abramson & Lissovsky, 2012), confirmed by analysis of various fragments of nuclear and mtDNA (Conroy & Cook, 2000; Jaarola *et al.*, 2004; Galewsky *et al.*, 2006; Bannikova *et al.*, 2010).

All voles of the subgenus *Alexandromys* are large in size. Maximowicz's vole has body length up to 152 mm. Middendorf's vole is smaller; the body length is up to 143 mm (Gromov & Erbaeva, 1995). The root vole has a wide distribution and its body length varies greatly (105–150 mm) depending on geographical location. The subspecies with which I worked (*M. oeconomus hohlovi* Skalon, 1935) are large voles, with a body length of 120–155 mm. The lacustrine vole is the smallest among the studied species, with a body length of 109–118 mm (Ognev, 1950).

Study site and housing

The study was carried out at the A.N. Severtsov Institute of Ecology and Evolution, Chernogolovka Biological Station, using a collection of animal sounds (1983–1999) and equipment from the Joint Usage Center's «Collection of live mammals». Collections included recording of vole's vocalizations from four species of subgenus *Alexandromys* (Table 1). Animals were kept in family groups in 44 × 56 cm plastic cages under natural light. Sawdust was used as bedding and hay was used as the nesting material. Water, grain, and vegetables were available ad libitum. Specimens included animals caught in nature and voles with 1–2 generations of captive breeding.

Acoustic recordings

The animal sounds were recorded during interactions of same- and different-sex pairs in the laboratory during 1983–1999. I used Sony TC75, Sony Walkman, Jupiter-203, and Rostov-102 tape recorders, and microphones MKE-5, MKE-9, and MD-80 (Oktava, USSR) with a frequency response of 50 Hz–15 kHz. Each individual participated in two experiments, once in a same-sex pair and once in a different-sex pair. Before the experiment, the animals were kept alone. Exceptions were animals that were represented by only one formed pair: Middendorf's vole and root vole from Yamal. The microphone was located 50 cm above the boxes in a special room without reverberation, maintained at 18–20°C, 20% humidity, and low light. The experiment lasted for 15 minutes in the evening (20:00–22:00) when the voles show most activity. The recording procedure was standardized. Encounters between unfamiliar voles of the same sex were conducted in boxes (44 × 28 cm) on sawdust with a neutral odor. Unfamiliar male and female interacted within the female's territory. The recordings of the singing from mated pairs were made at

Table 1. Species, location of collection of live subject's ancestors and number of recordings obtained of each type.

Species	The location of the forefathers of the vivarium population	Origin of animals	Tape recorder/microphone, year	Number of males		Number of females
				squeaks	singing	squeaks
<i>M. middendorffii</i>	Taimyr, Khatanga Area, Kotui River	from nature	Sony TC 765/MKE-9, 1992	2	1	3
<i>M. maximowiczii</i>	Amur Region, Zeysky Nature Reserve	1–2 generation	Jupiter-203 / MD-80, 1988	4	6	4
<i>M. oeconomus oeconomus</i>	Yamalo-Nenets Autonomous District, Noyabrsk	1 generation	Walkman Sony WM-701, 1999	4		4
<i>M. oeconomus tschuktschorum</i>	Chukotka	from nature	Jupiter-203 / MD-80, 1987		1	
<i>M. limnophilus</i>	Mongolia, Tsap Khan	1–2 generation	Jupiter-203 / MD-80, 1987	8	9	7

the living cage. The observer was in the same room and commented on the behavior accompanying the recordings. The animals vocalized with an opened mouth, so the vocalizations were easily identified. The typology of interactions was based on Johst's (Johst, 1967) description of the behavior of Gapper's red-backed vole (*Myodes gapperi* Vigors, 1830). The author identified the following types of interactions between voles: aggressive (persecution, attacks, bites and boxing), identification (nasal, naso-anal sniffing and sniffing of other parts of the body), amicable (sitting side-by-side and grooming), and sexual (following, mounting, and copulation).

Call analysis

Magnetic tapes were digitized in a Pentium IV PC using a DMX 6 Fire professional sound card, at a recording rate of 16 bits and 48 kHz. Sound analysis program Avisoft SASLab Pro ver. 4.2 was used to analyze the sounds. I measured the call duration onscreen using the standard marker cursor in the spectrogram window (Hamming window, FFT 512 points, frame 100%, and overlap 87.5%). For each vocalization, I measured the following parameters in automatic mode: maximum amplitude frequency (peak frequency), medium quartile, and entropy. The maximum value of the fundamental frequency (hereafter, fundamental frequency — the lowest frequency of a harmonic signal produced by the vocal cord oscillation) was measured, using the harmonic cursor from the harmonic power spectrum (logarithmic) at the maximum value of the modulated signal. All measured signals were divided by structure into harmonic, noise and mixed. If it was impossible to distinguish the signal harmonics at the window "harmonic power spectrum", the signal was classified as noise. The fundamental frequency of the noise sounds was not measured. The mixed signals included the fundamental frequency and broadband noise.

The three quartiles of the spectrum (lower, medium, and upper) represent the frequencies that are lower than 25%, 50%, and 75% of the energy spectrum, respectively. The entropy parameter, calculated as the ratio of the

geometric mean to the arithmetic mean of the spectrum, reflects the ratio of noise and harmonic energy in the energy spectrum. The frequency modulation range was calculated as the difference between the maximum and minimum values of the fundamental frequency.

Statistics

The results were processed using the Statistica Ultimate Academic 13 program for Windows En (StatSoft, Russia). A statistical sample comprised, selected 18–25 sounds of each type (squeaks and singing) for each individual of different species. Values are provided as mean \pm standard deviation. The measured parameters of sounds for each animal were tested for compliance with a normal distribution by Kolmogorov-Smirnov test. I compared the squeak parameters of different species using nested-design ANOVA with Tukey post-hoc tests (the sex factor was embedded into the species factor). To take into account the individual differences, I conducted an additional analysis using nested-design ANOVA, where the factor of individuality was embedded in the species factor. I used one-way ANOVA to compare the parameters of male singing by species. The parameters with non-normal distributions (e.g., peak frequency), were compared using the nonparametric Kruskal-Wallis ANOVA median test. All statistical tests were two-tailed and differences were considered significant for $p < 0.05$.

I used the Discriminant Function Analysis (DFA) standard procedure to calculate the probability of the assignment of calls to the correct species. I included three measured call variables (duration, medium quartile, and entropy) in all DFAs. I used Wilks' lambda values to estimate how strongly the acoustic variables of the calls contributed to the discrimination among species or sex. Using a 2×2 Yates' chi-square test, I compared the percentages of correct assignments of calls. To validate the DFA results, I calculated the random values of correct assignment of calls by species or sex by applying a randomization procedure. The random values were averaged from DFAs performed on 100 randomized permutations of the data sets, as described by Solow (1990). I noted

whether the observed value exceeded 95% of the values within the distribution obtained by the permutations. If the observed value exceeded 95% of the values within this distribution, I concluded that the observed value differed significantly from random with a probability $p < 0.05$ (Solow, 1990).

As the recording of singing in three species was available only for one male, it was deemed inappropriate to compare species by discriminant analysis, because the differences may have been induced by the individual characteristics.

Ethics

During this study, I adhered to the 'Guidelines for the treatment of animals in behavioral research and teaching', published by the Animal Behavior Society (Guidelines for the Use of Animals, 2012) and to the laws on animal welfare for scientific research of the Russian Federation, where the study was conducted. A.N. Severtsov Institute of Ecology and Evolution provided full approval for this purely observational research.

Results

The vocal repertoire in the audible range of the voles from subgenus *Alexandromys* includes two main signals in captivity: squeaks by both sexes and singing by males. Squeaks constitute a widely variable signal depending on varying degrees of animal discomfort. As the males and females were seated, the contacts were of an amicable or aggressive character. In the first case, in which I observed courtship, females produced low-intensity squeaks and males sang. In the second case, the animals produced the same high intensity squeaks as ones emitted during the same-sex encounters.

The duration of squeaks varied from 0.3 s to 0.7 s in different species (Table 2). The root voles emitted the longest squeaks and the lacustrine voles emitted the shortest squeaks. Despite the wide variability of sound parameters within each sample, the squeak duration was significantly different among species except between Middendorf's and Maximowicz's voles. The squeak duration of females was significantly longer than that of males only in the Middendorf's voles. The duration differences across species remained significant if I compared the samples for each individual using nested-design ANOVA, where the factor of individuality was embedded in the factor of species ($F_{(3,35)} = 58.96, p < 0.001$).

The fundamental frequencies of squeaks varied from 1 to 3.5 kHz. The minimum fundamental frequency of squeaks was observed in the root and Maximowicz's voles as 1.3–1.5 kHz, which differed significantly from the fundamental frequencies of squeaks in lacustrine and Middendorf's voles (2.9–3.5 kHz) (Table 3). Male squeaks had significantly higher fundamental frequency than female squeaks in lacustrine and root voles. The differences in fundamental frequencies across species remained significant if I compared the samples for each

individual using a nested-design ANOVA, where the factor of individuality was embedded in the factor of species ($F_{(3,35)} = 596.2, p < 0.001$).

The peak frequencies of squeaks varied across species from 1 to 10 kHz. The root vole's squeaks had the highest peak frequency (median 4.5 kHz), whereas the Maximowicz's voles emitted squeaks with the lowest peak frequency (1.5 kHz). The peak frequencies of the lacustrine and the Middendorf's vole squeaks lay in the range of 3 to 4 kHz and did not differ significantly between species ($p = 0.106$). The peak frequencies of squeaks in males were usually higher compared with females in all species, except in the root voles where the opposite trend was apparent (Table 4).

The entropy index reflected the structure of squeaks (harmonic, mixed or noise). The maximum entropy index ($0.642 \pm 0.051, n = 162$) was detected in the root vole (Table 5). Only 7% of the signals of the root vole had harmonic structure, the rest were approximately equally mixed, or noise. The Middendorf's vole squeaks had the lowest value of entropy ($0.481 \pm 0.087, n = 119$), but mixed signals (49%) and noise signals (35%) predominated. Squeak entropy in the lacustrine voles was 0.421 ± 0.058 ($n = 375$), and mixed signals (62%) were more prevalent than noise (21%). The lowest entropy was observed in Maximowicz's vole squeaks ($0.369 \pm 0.079, n = 172$), although mixed (56%) and noise (34%) signals remained predominant. The squeak entropy differed significantly among species ($F_{(3,820)} = 571.24, p = 0.001$) and between sexes in all the species ($F_{(3,820)}$) (Table 5). In all species the squeak entropy of females was lower than that of males, except among root voles, where the female squeak entropy was higher than that in males. The entropy differences between species remained significant if I compared the samples for each individual using a nested-design ANOVA, where the factor of individuality was embedded in the factor of species ($F_{(3,35)} = 696.5, p < 0.001$).

The modulation range of the fundamental frequency of squeaks in all species was noted. The fundamental frequency increased, then symmetrically decreased over the duration of the squeak, though sometimes the frequency only raised or decreased over the course of the signal's emission (Figs 1, 2). The modulation ranges of fundamental frequency of squeaks were between 0.4 to 1.5 kHz (Table 6). They were low (0.4–0.9 kHz) and similar for the lacustrine, and root voles ($p = 0.065$), but differed from the greater frequency modulation range (1.0 to 1.5 kHz) of Middendorf's, and Maximowicz's vole squeaks ($p = 0.001$). In the lacustrine voles, the modulation range of the fundamental frequency of male squeaks was much higher compared with females (Table 6). The modulation range of the fundamental frequency differences among species remained significant if I compared the samples for each individual using a nested-design ANOVA, where the factor of individuality was embedded in the factor of species ($F_{(3,35)} = 20.76, p < 0.001$).

Discriminant analysis revealed significant species differences among squeaks in the four species, based on three parameters: duration, medium quartile and

Table 2. Comparison of the squeak duration of different sexes voles from the subgenus *Alexandromys*.

Species*	Sex	X ± SD, s	Confidence limits (± 95%), s	Number of sounds	Sex comparing, nested design ANOVA, $F_{(3, 820)} = 5.08$ Tukey HSD test**
<i>M. oeconomus</i>	female	0.066 ± 0.029	0.060–0.073	73	$p = 0.987$
	male	0.064 ± 0.027	0.058–0.069	89	
<i>M. limnophilus</i>	female	0.034 ± 0.019	0.031–0.037	197	$p = 0.244$
	male	0.039 ± 0.017	0.036–0.042	178	
<i>M. middendorffii</i>	female	0.056 ± 0.025	0.051–0.062	84	$p = 0.005$
	male	0.041 ± 0.006	0.038–0.043	35	
<i>M. maximowiczii</i>	female	0.023 ± 0.013	0.020–0.026	60	$p = 1.000$
	male	0.023 ± 0.014	0.020–0.025	112	

* Average squeak duration of all the species differed significantly $F_{(3, 820)} = 58.45, p = 0.001$.

** The bold type indicates significant differences.

Table 3. Comparison of the squeak fundamental frequencies of different sexes of voles from the subgenus *Alexandromys*.

Species*	Sex	X ± SD, kHz	Confidence limits (±95%), kHz	Number of sounds	Sex comparing, nested design ANOVA, $F_{(3, 549)} = 6.55$ Tukey HSD test**
<i>M. oeconomus</i> ^a	female	1.19 ± 0.50	1.00–1.37	31	$p = 0.002$
	male	1.46 ± 0.41	1.33–1.60	47	
<i>M. limnophilus</i> ^b	female	3.16 ± 0.40	3.10–3.23	160	$p = 0.001$
	male	3.49 ± 0.47	3.41–3.57	136	
<i>M. middendorffii</i> ^b	female	3.46 ± 0.79	3.10–3.23	62	$p = 0.810$
	male	3.57 ± 0.47	3.29–3.85	13	
<i>M. maximowiczii</i> ^c	female	2.73 ± 0.72	2.52–2.96	43	$p = 0.063$
	male	3.03 ± 1.29	2.71–3.36	65	

* Average squeak fundamental frequencies of the species differed significantly $F_{(3, 561)} = 592.8, p = 0.001$, different indices denote significantly different values between species with $p < 0.001$.

** The bold type indicates significant differences.

Table 4. Comparison of medians of the squeak peak frequencies of different sexes of voles from the subgenus *Alexandromys*.

Species*	Sex	Median, kHz	Min-max, kHz	Number of sounds	Sex comparing, Kruskal-Wallis ANOVA, Median Test
<i>M. oeconomus</i> ^a	female	4.56	2.75–8.93	73	$\chi^2 = 0.07$ $p = 0.788$
	male	4.37	1.62–7.93	89	
<i>M. limnophilus</i> ^b	female	3.18	2.15–7.40	197	$\chi^2 = 46.53$ $p = 0.001$
	male	3.61	1.11–8.87	178	
<i>M. middendorffii</i> ^b	female	3.35	1.70–10.24	84	$\chi^2 = 5.16$ $p = 0.023$
	male	3.87	0.94–9.99	35	
<i>M. maximowiczii</i> ^c	female	1.10	0.65–3.35	60	$\chi^2 = 12.98$ $p = 0.001$
	male	1.40	0.65–5.60	112	

* different indices denote significantly different values with $p < 0.001$ by Kruskal-Wallis ANOVA, Median Test: $\chi^2 = 290.30, p = 0.001$.

** The bold type indicates significant differences.

Table 5. Comparison of the squeak entropy of different sexes of voles from the subgenus *Alexandromys*.

Species*	Sex	X ± SD	Confidence limits (±95%)	Number of sounds	Sex comparing, nested design ANOVA, $F_{(3, 820)} = 31.78$ Tukey HSD test**
<i>M. oeconomus</i>	female	0.660 ± 0.043	0.649–0.671	73	$p = 0.006$
	male	0.627 ± 0.066	0.613–0.641	89	
<i>M. limnophilus</i>	female	0.410 ± 0.070	0.400–0.419	197	$p = 0.039$
	male	0.434 ± 0.067	0.425–0.445	178	
<i>M. middendorffii</i>	female	0.445 ± 0.064	0.430–0.459	84	$p = 0.001$
	male	0.568 ± 0.041	0.554–0.583	35	
<i>M. maximowiczii</i>	female	0.339 ± 0.039	0.329–0.350	60	$p = 0.001$
	male	0.386 ± 0.074	0.370–0.401	112	

*Average squeak entropy of the all species differed significantly $F_{(3, 820)} = 571.24, p = 0.001$.

** The bold type indicates significant differences.

Table 6. Comparison of the squeak modulation range of the fundamental frequencies of different sexes of voles from the subgenus *Alexandromys*.

Species*	Sex	X ± SD, kHz	Confidence limits (±95%), kHz	Number of sounds	Sex comparing, nested design ANOVA, $F_{(3, 549)} = 16.07$ Tukey HSD test**
<i>M. oeconomus</i> ^a	female	0.4 ± 0.6	0.4–0.5	31	$p = 1.000$
	male	0.5 ± 0.7	0.3–0.6	47	
<i>M. limnophilus</i> ^a	female	0.4 ± 1.3	0.3–0.5	160	$p = 0.001$
	male	0.9 ± 1.1	0.8–1.0	136	
<i>M. middendorffii</i> ^b	female	1.1 ± 0.8	0.9–1.3	62	$p = 0.556$
	male	1.4 ± 0.7	1.0–1.9	13	
<i>M. maximowiczii</i> ^b	female	1.2 ± 0.7	1.0–1.3	43	$p = 0.684$
	male	1.4 ± 0.8	1.2–1.6	65	

* Different indices denote significantly different values with $p < 0.001$ by post-hoc Tukey HSD test, $F_{(4, 560)} = 23.9, p = 0.001$.

** The bold type indicates significant differences.

Table 7. Assignment of vole's calls to a predicted species, based on discriminant analysis of the squeak.

Species	Predicted group membership				Total	Correctly classified (%)
	<i>M. oeconomus</i>	<i>M. limnophilus</i>	<i>M. middendorffii</i>	<i>M. maximowiczii</i>		
<i>M. oeconomus</i>	147	12	3	0	162	90.7
<i>M. limnophilus</i>	3	342	12	18	375	91.2
<i>M. middendorffii</i>	15	70	16	18	119	13.4
<i>M. maximowiczii</i>	3	65	5	99	172	57.6
Total	163	459	42	164	828	72.3

entropy. The average percentage of correct assignments was 72.3%. All three parameters contribute to the differences between the species. The percentage of correct assignments did not differ from each other using the chi-square test while determining the keys for discrimination and validating these keys ($\chi^2 = 0.102, p = 0.750$). The percentage of correct assignments with randomization was $46.9 \pm 9.6\%$ ($n = 100$), which differed significantly

from the average percentage of correct assignments using chi-square test ($\chi^2 = 27.14, p = 0.001$). However, the squeaks of the Middendorf's and the lacustrine voles have similar parameters and were clustered together as one group (Table 7).

Males actively sing during encounters with females. The lacustrine and Maximowicz's voles demonstrate singing activity: all the males sang during encounters

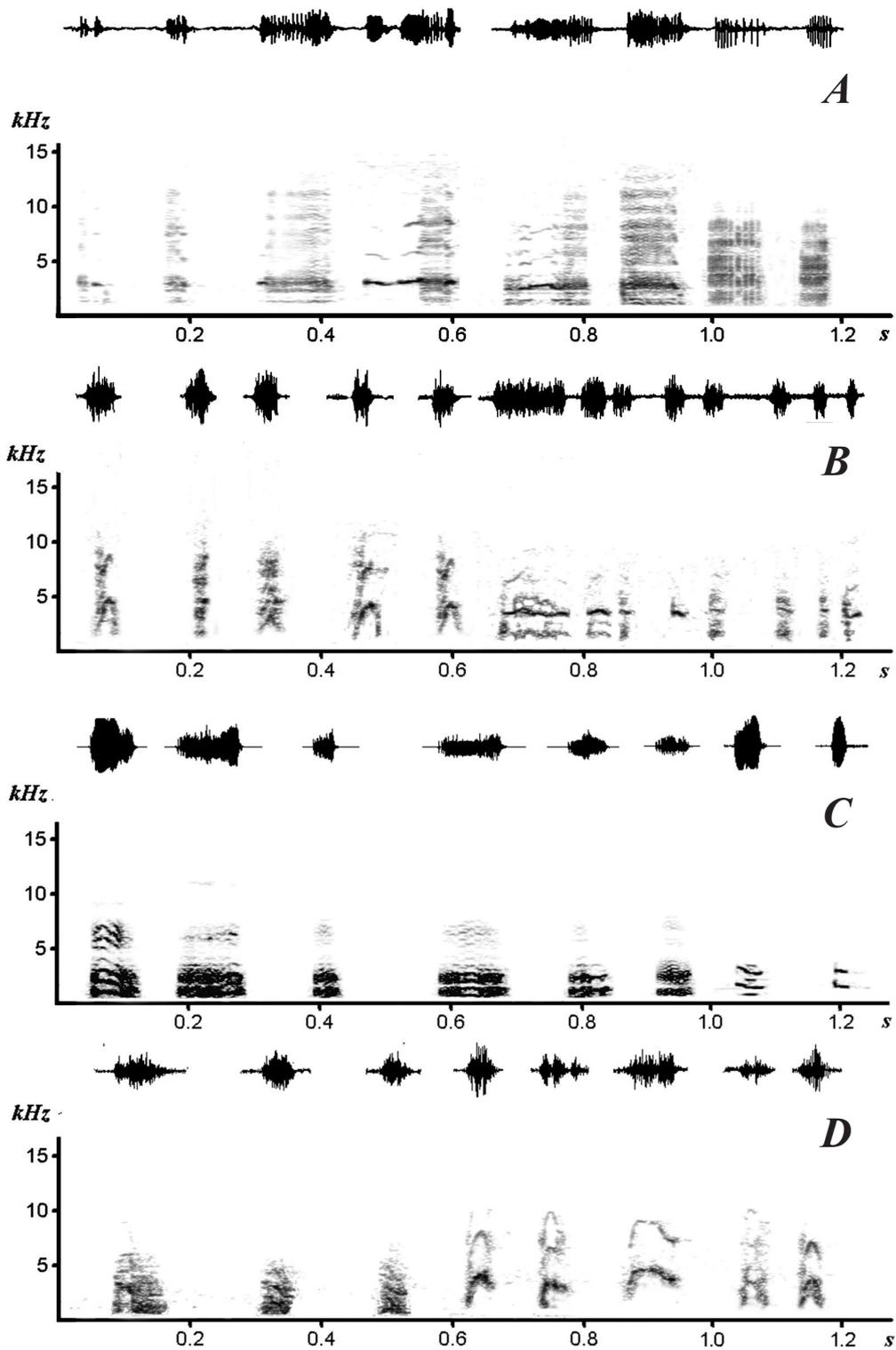


Fig. 1. Sonograms and oscillograms of female squeaks, made by voles of subgenus *Alexandromys*: A — the root voles *M. oeconomus*; B — the lacustrine voles *M. limnophilus*; C — the Maximowicz's voles *M. maximowiczii*; D — the Middendorf's vole *M. middendorffii*.

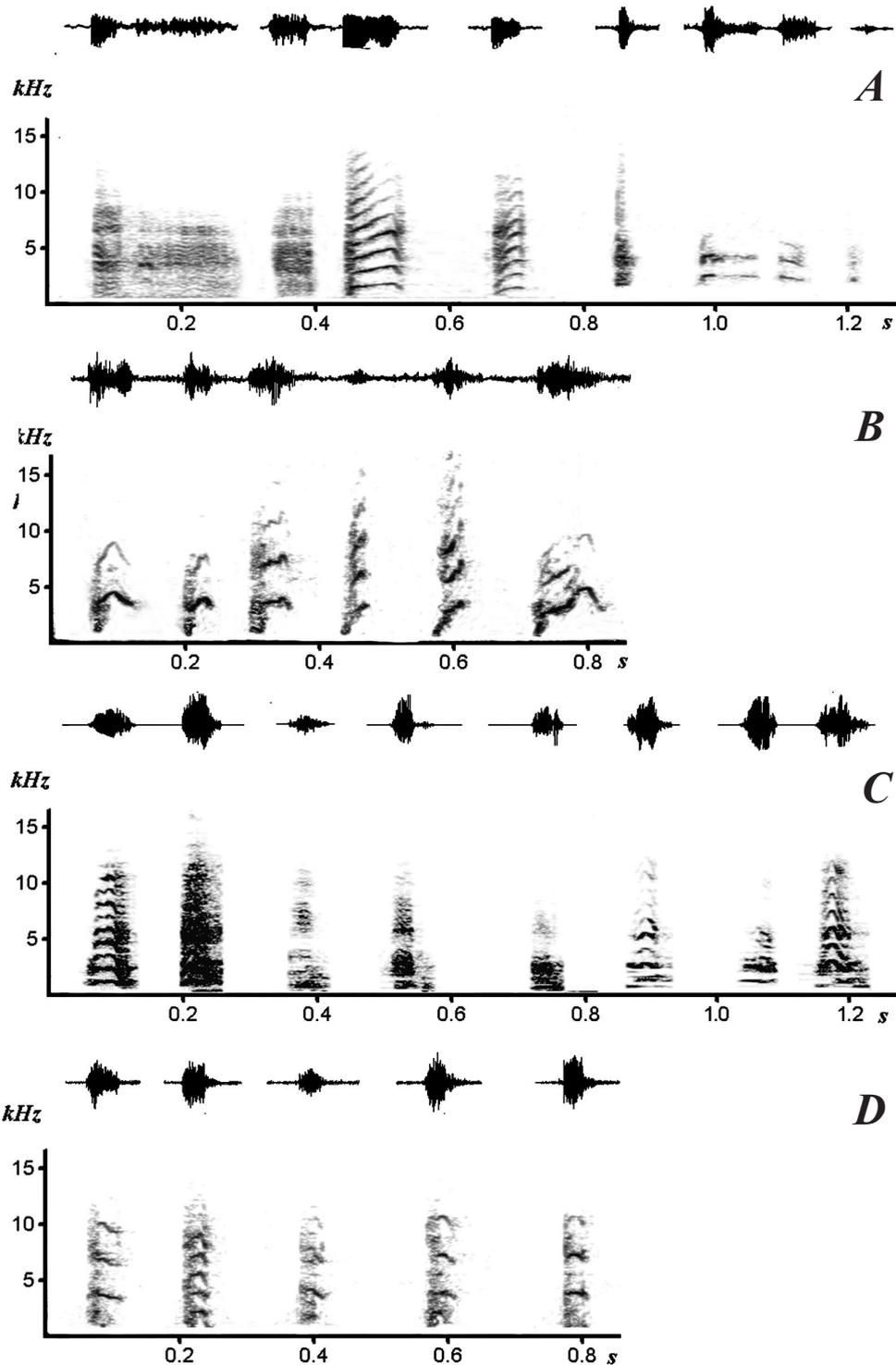


Fig. 2. Sonograms and oscillograms of male squeaks, made by voles of subgenus *Alexandromys*: A — the root voles *M. oeconomus*; B — the lacustrine voles *M. limnophilus*; C — the Maximowicz's voles *M. maximowiczii*; D — the Middendorf's vole *M. middendorffii*.

with females. The Middendorff's vole males sang only with their current female partner. During encounters of unfamiliar females with males, I observed fights, in which both animals emitted squeaks. The root voles also showed only aggressive interactions with squeaks, when unfamiliar individuals interacted. The single record of singing in the root vole was observed only for one pair of voles, referred to another subspecies *M. (A.) oeconomus tschuktschorum* Miller, 1899, caught in Chukotka. Singing is a low-intensity short sound (20–60 ms), often emitted in a series (Table 8). The fundamental frequency ranged from about 1.5–3 kHz. Male singing of the root, lacustrine, and Middendorff's voles had a slight modulation of the fundamental frequency (modulation range 0.3 kHz). The fundamental frequency of the male singing of the Maximowicz's voles has deep modulation range (0.4–0.7 kHz) (Table 8, Fig. 3). The peak frequencies of the singing varied across species.

Discussion

Voies emitted squeaks during both amicable and aggressive types of interactions. The patterns of regularities underlying the formation of vocal reactions in mammals allowed Morton (1977) to formulate “motivational and structural rules” in the behavioral spectrum. Morton emphasized the “end points”, — “antagonism and amicability”. While the former is characterized by high amplitude broadband sounds, the second is characterized by harmonic sounds with relatively higher frequency. However, the squeaks, for example, those of bank

voies (*Myodes glareolus* Schreber, 1780), represent one continuum of sounds produced in different situations. The attacked animal squeaks in aggressive interactions, and this signal has a high-amplitude. During amicable interactions, the animal squeaks when disturbed, or to avoid the contact. Low-intensity sounds accompany, as a rule, repulsion and boxing. Often, the latter situation is encountered during between-sex interactions, when the male tries to court, and the female is not yet receptive, so she demonstrates a soft aggression (Rutovskaya, 1998).

The continuum of these sound signals corresponds to the one described by Kiley (1972), i.e., a typological continuum reflecting the excitation of the animal. Earlier I had found that different intensity of sounds can lead to a change in some signal characteristics: high-intensity squeaks of steppe lemming (*Lagurus lagurus* Pallas, 1773) differ from low-intensity squeaks, in terms of longer duration, peak and fundamental frequencies and the modulation range of the fundamental frequency (Rutovskaya, 2017). This variability of the squeak parameters corresponded to the typical vocal expression of emotions in mammals, namely, with an increase in excitation, there was an increase in the vocal activity, fundamental and peak frequencies, range of frequency modulation, and the values of energy quartiles. This is a universal feature. The duration as well as the structure of the sound signal varies with the increase in emotional arousal in different ways, depending on the species (Volodin *et al.*, 2009; Briefer, 2012). That is, the intensive squeaks, with higher values of the parameters, seem to reflect higher level of emotional expression in animals. This is consistent with my data: higher average values of

Table 8. Parameters of male singing in voles of the subgenus *Alexandromys*.

	<i>M. oeconomus</i>	<i>M. limnophilus</i>	<i>M. middendorffii</i>	<i>M. maximowiczii</i>	ANOVA*
Number of males	1	9	1	6	
Number of sounds	21	195	20	100	
	Mean ± SD				
Duration, s	0.044 ± 0.032	0.037 ± 0.014 ^a	0.059 ± 0.018	0.066 ± 0.040 ^b	F_(1, 293) = 72.2, p = 0.001
Fundamental frequency, kHz	2.80 ± 0.14	2.88 ± 0.02 ^a	2.47 ± 0.13	1.48 ± 0.30 ^b	F_(1, 293) = 1391.8, p = 0.001
Entropy	0.511 ± 0.096	0.334 ± 0.098 ^a	0.040 ± 0.076	0.285 ± 0.80 ^b	F_(1, 293) = 18.6, p = 0.001
Number of harmonics	1.5 ± 0.5	1.4 ± 1.4 ^a	1.7 ± 0.4	1.8 ± 1.0 ^b	F_(1, 293) = 18.8, p = 0.001
Modulation range, kHz	0.3 ± 0.5	0.3 ± 1.4 ^a	0.3 ± 0.4	0.4 ± 1.0 ^b	F_(1, 293) = 5.9, p = 0.016
	Median				Kruskal-Wallis ANOVA, Median Test
Peak frequency, kHz	2.87	2.92 ^a	2.49	1.40 ^b	χ² = 119.1, p = 0.001

* Comparison of the characteristics of different species singing was carried out only between *M. limnophilus* and *M. maximowiczii*, since for other species singing was presented only for one male. Different indices denote significantly different values.

** The bold type indicates significant differences.

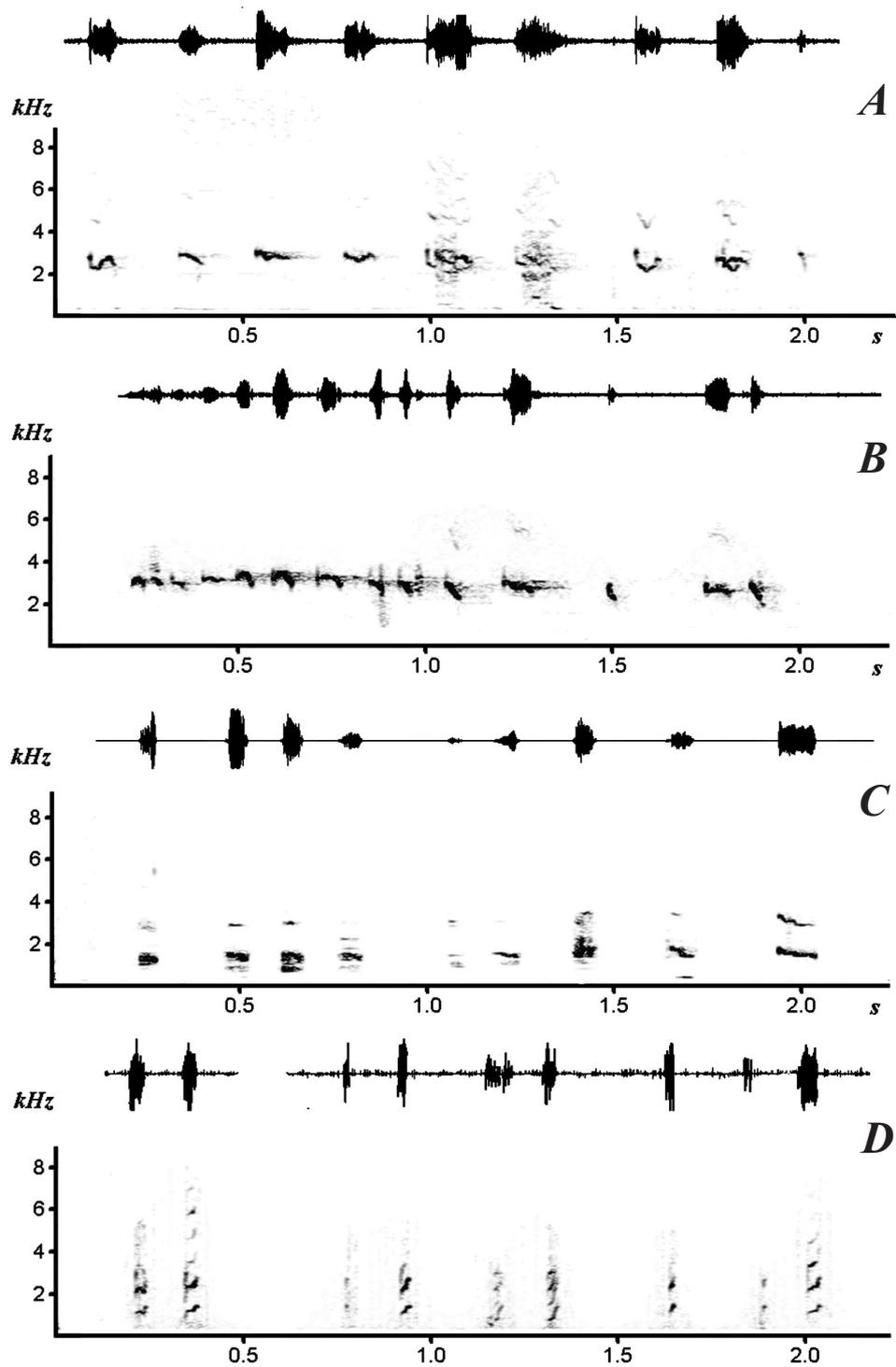


Fig. 3. Sonograms and oscillograms of male singing, made by voles of subgenus *Alexandromys*: A — the root voles *M. oeconomicus*; B — the lacustrine voles *M. limnophilus*; C — the Maximowicz's voles *M. maximowiczii*; D — the Middendorff's vole *M. middendorffii*.

the parameters of male squeaks reflect a more frequent use of high-intensity signals, in comparison with females. Sexual variability of the emitted squeaks in the studied species was apparent in the peak frequency (except for the root vole) and the sound entropy may reflect this sexual variability of squeaks.

Acoustic signals of the voles from the subgenus *Alexandromys* are very similar. Because these species are large voles, the fundamental and peak frequencies of their squeaks are low compared to the frequencies of smaller species of voles such as bank and common voles, whose squeak peak frequencies are between 5–8 kHz (Rutovskaya & Kovalskaya, 1999; Rutovskaya, 2007; Rutovskaya *et al.*, 2017). This corresponds to the concept that the primary-optimal frequency of animal sound signals is inversely proportional to the linear body dimensions (Nikol'skii, 1984). The “primary-optimal” frequency is determined by the resonance frequency of the vocal tract, the length of which is determined by the body size. This resonance frequency leads to the amplification of some frequencies and suppression of others (Fitch & Hauser, 1995). Later, Bradbury & Vehrenkamp (1998) reiterated the same principle, stating that the optimal frequency value is inversely proportional to the body length or proportional to the body mass to a power of $-1/3$. Moreover, the fundamental frequency of the signal is proportional to the body mass in relation to $M^{-0.4}$. This has been shown for a wide range of mammals of different sizes, from rats to elephants (Fletcher, 2010).

According to this rule, there is a significant correlation between body size and peak frequency of squeaks of the

studied species (correlations with Spearman $R = -0.06$ were significant at $p < 0.05$) (Fig. 4). Root vole is knocked out of this pattern, since the peak frequency of its squeaks is higher than that of the lacustrine vole, which is smaller in size. But at the same time, the fundamental frequency of root vole's squeaks is significantly lower than all other studied species.

According to the discriminant analysis of squeaks from different species, the root vole also had the greatest value of the correct assignments, in comparison with other species. I can conclude that the root voles differ from other species with respect to the structure of their signals.

The root vole until recently was not included in the subgenus *Alexandromys*. The lacustrine voles were classified in the subgenus *Pallasinus*, as the closest relative of the root vole (Pavlinov, 2006). Now, the reed vole is considered to be the closest relative of lacustrine voles (Bannikova *et al.*, 2010), but according to craniometric indicators, lacustrine voles are similar to the Maximowicz's voles, which may be the result of convergent evolution (Lissovsy & Obolenskaya, 2011). Sounds of the root vole are similar, but still differ from those of the reed vole (Zorenko & Rutovskaya, 2006), which is consistent with the systematic constructions. The differences are in terms of a low fundamental frequency, and location of the peak frequency at 2–3 harmonics. According to my data, the sound signals of the lacustrine voles were indistinguishable from those of the Middendorff's voles. Therefore, I could conclude that the structure of the signal, as well as some craniological

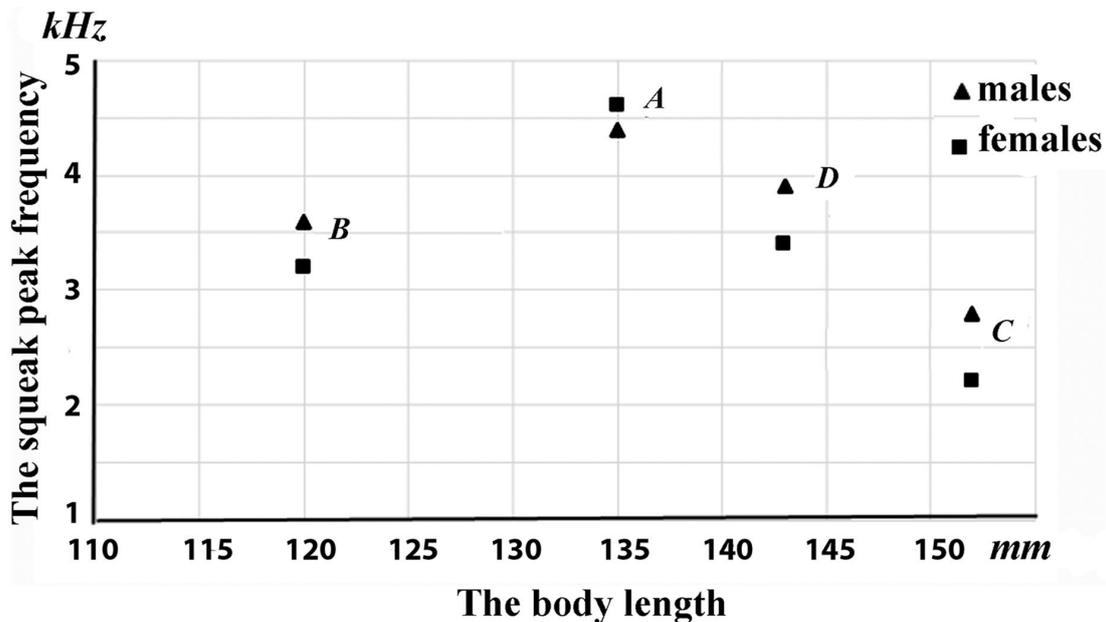


Fig. 4. Ratio of body size and peak frequency of squeaks, made by voles of subgenus *Alexandromys*: A — the root voles *M. oeconomus*; B — the lacustrine voles *M. limnophilus*; C — the Maximowicz's voles *M. maximowiczii*; D — the Middendorff's vole *M. middendorffii*. Spearman Rank Order Correlations ($R = -0.06$) are significant at $p < 0.05$.

signs, weakly reflect the phylogenetic relationships within the subgenus.

The subgenus *Alexandromys* had diverged from the subgenus *Microtus* in the Early Pleistocene about 1.9 million years ago (Abramson *et al.*, 2009). Later, it was divided to subgenera *Alexandromys* and *Pallasinus* at approximately 1.2 million years ago (Bannikova *et al.*, 2010). The sexual behavior in the subgenus *Alexandromys* developed independently of the subgenus *Microtus*: a number of specific behavioral patterns during between-sex encounters, typical for this subgenus (Zorenko, 1990), hip glands and marking of the substrate with their secretion have appeared (Quay, 1968; Aksenova, 1973). Less active physiological stimulation in sexual behavior in the voles of this subgenus probably required more active behavioral stimulation, which promoted synchronization of the sexual behavior of the pair, including the development of singing. Singing is more common in voles of subgenus *Alexandromys* than in common and social voles (subgenus *Microtus*). Less than 30% ($n = 65$) of males of this species exhibit singing during sexual behavior (Zorenko, 2013). Singing of males is probably derived from low-intensity squeaks (Zorenko & Rutovskaya, 2006).

The different size of acoustic repertoire can be explained by the various social structures of species and their mating systems (Zorenko, 1990). For example, the males of bank voles (*Myodes*) do not sing (Rutovskaya, 1998). The social structure of its populations constitutes a single-group a hierarchical structure and the females mate with any male (Chistova, 2002). On the contrary, the short-tailed vole (*Microtus agrestis* Linnaeus, 1761) is a territorial species (Viitala, 1977), and males must overcome the territorial aggression of the female for successful reproduction. The social voles (subgenus *Sumeriomys*) begin to reproduce after a pair is formed. The specific behavior (walz, singing) may co-ordinate the sexual behavior (Zorenko, 2013).

Most of the adult root voles lead a sedentary lifestyle, observed by tag recapture (Karaseva, 1957; Karaseva & Ilenko, 1957) and radio-tracking studies (Gliwicz 1997). Animals dig burrows under the roots of bushes (Flint *et al.*, 1970). The female sites are usually isolated from each other, whereas the male territories overlap each other, as well as the territories of multiple breeding females (Gliwicz, 1997). Therefore, the main reproduction strategy of the root vole is promiscuity or polygyny (Tast, 1966). However, as the population density declines, the root vole can form monogamous breeding pairs (Viitala, 1994). In winter, the root vole can form aggregations of up to 10 individuals (Frank & Zimmermann, 1956), who are often of the same sex (Tast, 1966). This is possible, since voles are relatively tolerant of each other. In an experimental setting, more than 50% of the interactions between voles were neutral, and aggression among unfamiliar pairs accounted for 33.33% of the total interactions (Ivankina, 1974). Singing was registered more often in this species than in the voles of subgenus *Microtus*. But is not an obligatory element of sexual behavior: about 50–60% ($n = 17$) of

the root vole males sing during encounter with females (Zorenko, 1990).

Far more acoustically active are reed voles, in which 70% ($n = 27$) of males sang at every meeting with females, regardless of their physiological state (Zorenko & Rutovskaya, 2006). The lifestyle of this species is family-colonial; all burrows of one colony are interconnected by a network of paths gnawed in the grass (Dymin, 1974; Kostenko, 1984). According to the results of pairwise planting, it can be noted that the breeding male is friendly towards members of its own group, including grown offspring, but is aggressive towards unfamiliar voles. In their behavior ritualized patterns predominate, rather than direct aggression (Zorenko & Rutovskaya, 2006).

The Middendorf's voles also form colonies (Flerov, 1933). They dig shallow burrows in dry places, often in hummocks and bushes, with well-marked trails between the nests (Mezenniy, 1975). According to Zorenko (1990), up to 100% of males actively sing, but in our experiments Middendorf's vole males did not sing toward unfamiliar females and the only record of their singing was from the already-mated pair.

Males of other studied species also actively sing in inter-sexual relations, but we little known about the spatial distribution and social structure of these species. The lacustrine voles do not form colonies (Smith & Xie, 2008). The Maximowicz's voles form mosaic settlements, in open, moistened and bushy places, which form strips stretched along the flood plain (Meyer *et al.*, 1996; Vojta, 2002). Voles live in families in shallow burrows (Nekipelov, 1936). The spatial organization and social structure of these species have not been studied.

Conclusions

The vocal repertoire of the voles from several species of the subgenus *Alexandromys* in captivity includes only two signals, squeaks and singing. Singing is a typical signal for voles of the subgenus and males often produced songs during encounters with the females, yet, singing is not an obligatory pattern of behavior, during mating. It is likely that the intensity of the use of singing depends on the social structure of the species. The social structure varies across these species, but it has been poorly studied.

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