Acta Theriol
DOI 10.1007/s13364-011-0046-9

ORIGINAL PAPER

Species-specific and shared features in vocal repertoires of three Eurasian ground squirrels (genus *Spermophilus*)

Vera A. Matrosova · Irena Schneiderová · Ilya A. Volodin · Elena V. Volodina

Received: 16 March 2011 / Accepted: 27 May 2011

Abstract Along to alarm calls, Eurasian ground squirrels of the genus *Spermophilus* also produce other call types toward potential predators and rival conspecifics. Individually identified 50 speckled (*Spermophilus suslicus*), 18 European (*S. citellus*) and 59 yellow (*S. fulvus*) ground squirrels were examined for interspecies differences in their vocal repertoires. A separate sample of 116 (90 adult and 26 juvenile) *S. suslicus* was examined for presence of ultrasound in their alarm calls. In addition, all tonal calls in all the three species were checked for presence of nonlinear phenomena. Calls were elicited by approaching animals in live-traps or near burrows; some types of vocalizations were also recorded during handling. Eight call types, three tonal and five wideband ones, were described. Vocal repertoires were remarkably similar between species, excluding the alarm calls, which were species-specific. Alarm calls with ultrasonic components were found in two individuals of *S. suslicus*. Concerning nonlinear phenomena, biphonation in alarm calls of *S. suslicus*, frequency jumps and sidebands in screams of *S. citellus*, frequency jumps and subharmonics in screams of *S. fulvus* were found. Results are discussed with literature evidence on audible and ultrasonic vocalizations in ground squirrels.

Keywords Nonlinear phenomena · *Spermophilus citellus* · *Spermophilus fulvus* · *Spermophilus suslicus* · Vocal diversity · Ultrasound

Communicated by: Jan M. Wójcik

V. A. Matrosova (✉) · I. A. Volodin
Department of Vertebrate Zoology, Faculty of Biology,
Lomonosov Moscow State University,
Vorobievy Gory, 12/1,
Moscow 119991, Russia
e-mail: v.matrosova@gmail.com

V. A. Matrosova
Engelhardt Institute of Molecular Biology RAS,
Vavilov Str., 32,
Moscow 119991, Russia

I. Schneiderová
Department of Zoology, Faculty of Sciences, Charles University,
Viničná, 7,
Prague 2 128 44, Czech Republic

I. A. Volodin · E. V. Volodina
Scientific Research Department, Moscow Zoo,
B. Gruzinskaya, 1,
Moscow 123242, Russia

Introduction

Research of vocal communication of *Spermophilus* ground squirrels (Rodentia, Sciuridae) is strongly focused on alarm communication and in particular on nepotism and evolution of alarm communication (Sherman 1977; Blumstein 2007); ontogenesis (Matrosova et al. 2007; Swan and Hare 2008; Volodina et al. 2010), call similarity in close kin (Matrosova et al. 2008), cues to age, sex or individual identity (Leger et al. 1984; McCowan and Hooper 2002; Volodin 2005; Schneiderová and Policht 2010; Matrosova et al. 2011; Pollard and Blumstein 2011), stability of individual vocal signatures (Matrosova et al. 2009, 2010a, b), adaptations to propagation through the environment (Nikol'skii 1984; Wilson and Hare 2006) and relations between call structure and population density (Volodin et al. 2008). Alarm calls were shown to be species-specific (e.g., Nikol'skii 1979, 1984), and the alarm calls of interspecies hybrids, regularly met in sympatric areas (Ermakov et al. 2002), have

Published online: 09 June 2011

intermediate characteristics between parental species (e.g., Koeppl et al. 1978; Nikolśkii et al. 1984; Titov et al. 2005).

Most Eurasian *Spermophilus* species produce a single type of the alarm call (tonal, high-frequency) towards any predator, terrestrial or aerial (Nikolśkii 1979, 1984). Unlike some species of North American ground squirrels and also long-tailed ground squirrel *S. undulatus* produce two different types of alarm calls, the tonal high-frequency one (towards raptors), and the rhythmic wideband one (towards terrestrial predators) (California ground squirrel *S. beecheyi* (Owings and Leger 1980); Uinta ground squirrel *S. armatus* [Balph and Balph 1966]; Belding's ground squirrel *S. beldingi* [Turner 1973; Sherman 1977; Leger et al. 1984]; Richardson's ground squirrel *S. richardsonii* [Davis 1984]; arctic ground squirrel [Melchior 1971]; long-tailed ground squirrel [Nikolśkii 1984]). However, these different types of alarm calls may reflect the degree of threat and urgency of response rather than being referentially specific (Nikolśkii 1984; Macedonia and Evans 1993; Fichtel and Kappeler 2002; Digweed and Rendall 2009a, b).

Ultrasonic alarm call, with a high-amplitude tonal frequency band at 45 kHz, was reported only for Richardson's ground squirrel (Wilson and Hare 2004). This vocalization is produced with sudden exhalation concurrent with opening of the mouth, in the absence of audible sound excluding the faint sounds of rushing air, and function probably as a short-range alarm signal (Wilson and Hare 2006). Audible alarm calls of Richardson's ground squirrel are similar in the acoustic structure to alarm calls of speckled ground squirrel *S. suslicus* (Davis 1984; Volodin 2005). Similarly to Richardson's ground squirrel, some individual *S. suslicus* sometimes call through the widely open mouth, but in the absence of audible sound besides soft hissing (our unpublished observations). So we could reasonably expect to find ultrasonic alarms also in *S. suslicus*. At the same time, an attempt to find ultrasonic alarms in the European ground squirrel *S. citellus* in its natural colonies in Bulgaria was unsuccessful (Georgiev et al. 2004).

Previously nonlinear phenomena have not been investigated in alarm calls of any sciurid. A hypothesis has been proposed that nonlinear phenomena make alarm calls less predictable and thus more evocative to listeners, consequently preventing receivers from ignoring such calls (Fitch et al. 2002; Blumstein and Récapet 2009). Data supporting this hypothesis have been obtained with colonial ground-dwelling meerkats *Suricata suricatta*: in which subharmonics, naturally occurring in alarm calls, increase responsiveness of conspecifics (Townsend and Manser 2010). For non-alarm calls, nonlinear phenomena (deterministic chaos, subharmonics and biphonation) were reported as widely occurring in defensive screams of juvenile yellow-bellied marmots *Marmota flaviventris* (Blumstein et al. 2008).

According to the most recent revision of systematics, the genus *Spermophilus* can be classified in eight genera (*Notocitellus*, *Otospermophilus*, *Callospermophilus*, *Ictidomys*, *Poliocitellus*, *Xerospermophilus*, *Urocitellus* and *Spermophilus*; Helgen et al. 2009). Except for two species classified to the genus *Urocitellus,* all Eurasian ground squirrels were included into the genus *Spermophilus sensu stricto* ("Old World ground squirrels") with 14 species, formerly included in the nominate subgenus *Spermophilus*. Traditional subdivision into *Citellus, Colobotis* and *Urocitellus* was not supported by molecular data (Helgen et al. 2009).

Three object species of this study are speckled ground squirrel (*S. suslicus*), European ground squirrel (*S. citellus*) and yellow ground squirrel (*S. fulvus*), inhabiting the Middle and Eastern Europe (Nowak 1999; Helgen et al. 2009). The *S. suslicus* is relatively small-sized compared to other ground squirrels and is found in relatively closed habitats, covered with high grasses that block visibility during much of their aboveground activity season (Tchabovsky 2005; Volodin et al. 2008). The *S. citellus* is similar to *S. suslicus* by size and inhabits open steppe areas with a low grass cover (Kryštufek and Vohralík 2005). Unlike the former two species, *S. fulvus* is the largest species of the genus, inhabiting open steppe and desert habitats with patchy grasses (Kashkarov and Lein 1927; Tchabovsky 2005; Vasilieva et al. 2009).

In their structure, calls may be subdivided into two structural classes, of tonal and wideband calls. Tonal calls show signs of production from a vocal source (larynx with vocal folds): a tonal spectrum with the fundamental frequency and its harmonics, sometimes bearing nonlinear phenomena. Wideband call types lack the fundamental frequency and have an explosive wideband spectrum, revealing their production not with vocal folds but with another source, most probably vorticity in the vocal tract. For all the three species, only alarm calls have been described and analyzed in detail (*S. suslicus*: Nikolśkii 1979, 1984; Volodin 2005; Matrosova et al. 2007, 2009, 2011; Volodina et al. 2010; *S. citellus:* Nikolśkii 1979; Georgiev et al. 2004; Koshev and Pandourski 2008; Schneiderová and Policht 2010; *S. fulvus:* Nikolśkii 1979, 1984; Titov et al. 2005; Matrosova et al. 2007, 2010a, b; 2011). A pilot study of non-alarm vocalizations was done only for *S. suslicus* (Matrosova et al. 2006). Therefore, for all the three species, scarce or no data is available on vocalizations besides the alarm calls. The aims of this study were: (1) to study vocal diversity in *S. suslicus*, *S citellus* and *S fulvus* and to describe their vocal repertoires; (2) to examine vocalizations of all the three species for presence of nonlinear phenomena and (3) to check alarm calls of *S. suslicus* for presence of ultrasound.

Materials and methods

Subjects, study sites and dates of work

Call recordings were made from adults and juveniles in natural colonies of the three study species of ground squirrels during their aboveground activity season from April to July. Adults were animals of their second season of life or older whereas juveniles were pups emerged from their natal burrows during the year of data collection. All individual *S. suslicus* and *S. fulvus* were microchip- (Bayer, Leverhusen, Germany) and dye marked (*p*-phenylenediamine; Rhodia, Paris, France) (as in Matrosova et al. 2007, 2009, 2010b). Individual *S. citellus* were also marked (900 Black, Palette, Schwarzkopf & Henkel, Düsseldorf, Germany), as in the study of Schneiderová and Policht (2010) and in Loděnice colony (see below), with microchips (Planet ID, Essen, Germany).

In the Moscow region location, Russia (54°47′N, 38°42′E), calls of 312 (230 adult and 82 juvenile) *S. suslicus* were recorded in 2003–2009. In the Lipetsk region location, Russia (52°37′N, 39°37′E), calls of 140 (96 adult and 44 juvenile) *S. suslicus* were recorded in 2010. At the Airfield Letňany location in Prague, Czech Republic (50°07′N, 14°31´E), calls of 40 (31 adult and nine juvenile) *S. citellus* were recorded in 2006–2008. In the meadow location in Loděnice, Czech Republic (49°59′N, 14° 09′E) calls of 40 (31 adult and nine juvenile) *S. citellus* were recorded in 2009. In the Saratov region location, Russia (50°43′N, 46°46′E), calls of 432 (107 adult and 325 juvenile) *S. fulvus* were recorded in 2005–2008.

Data collection

Calls of all *S. suslicus*, all *S. fulvus* and of *S. citellus* from the Loděnice location were emitted by animals sitting in wire-mesh traps or in hutches and calling toward a researcher. In the Airfield Letňany location, alarm calls of *S. citellus* were recorded when animals were free-ranging, and, after a recording session, each focal animal was captured with a loop, marked with black hair dye to avoid repeated recordings of the same individual, and released back. Because this mark is not permanent, we also used widely spaced sites of data collection to avoid repeated recordings from the same animals (Schneiderová and Policht 2010). In all the three species, some sound recordings were also made during the handling procedures and in one individual *S. citellus*, from the burrow during an aggressive encounter with a conspecific.

Each recording session lasted 4–6 min providing 30–40 calls per animal. In live-traps, the distance to the microphone was kept of 0.3 m for *S. suslicus* and of 1–2 m for *S. fulvus* and *S. citellus*. In freely running *S. citellus* the distance was 5–10 m. From live-traps, animals called either spontaneously or in response to additional stimulation (walking near the traps or movements of hand-held hat). Alarm calls elicited in live-traps in response to humans are similar to alarm calls from free-running animals (Matrosova et al. 2010b).

Calls of *S. suslicus*, with the exception of ultrasonic calls, and of *S. fulvus* were recorded using a Marantz PMD-222 (D & M Professional, Kanagawa, Japan) cassette recorder, AKG-C1000S (AKG-Acoustics, Vienna, Austria) cardioid electret condenser microphone, and type II chrome audiocassette EMTEC-CS II (EMTEC Consumer Media, Ludwigshafen, Germany) (frequency response 40 Hz–16 kHz on tape speed of4.75 mm/s). We also used a Marantz PMD-660 CF recorder and Sennheiser K6 ME-64 cardioid electret condenser microphone (Sennheiser Electronic, Wedemark, Germany) at 48 kHz sampling rate and 16 bit resolution. Calls of *S. citellus* were recorded using a Sony MZ-RH10 Hi-MD Walkman (Sony, Tokyo, Japan) digital recorder and RODE NTG-2 (Rode Microphones, Sydney, Australia) directional shotgun condenser or Audio-Technica ATR55 condenser microphones (44.1 kHz sampling rate, 16-bit resolution). To examine the alarm calls of *S. suslicus* for the presence of ultrasound, for 115 animals we made additional recordings of the calls with a Pettersson D 1000× with built-in microphones (Pettersson Electronik AB, Uppsala, Sweden) (192 kHz sampling rate, 24 bit resolution).

Call analysis

To describe vocal repertoires, we analyzed calls recorded in audible ranges of frequencies from 127 adult individuals of three species (Table 1). We took measurements from up to ten calls per animal per call type. We selected calls randomly among calls of good quality, i.e., not superimposed with wind, noise, or sounds animals make by hitting the live-trap. We measured all calls of good quality and then selected calls for analysis evenly among the measured calls in Excel. For *S. suslicus*, we analyzed in total 1,065 calls from 60 recording sessions, with one to four sessions per individual. For *S. citellus*, we analyzed in total 243 calls from 23 recording sessions, one to two sessions per individual. For *S. fulvus*, we analyzed in total 828 calls from 63 recording sessions, one to three sessions per individual. In addition, we examined alarm calls, recorded in the ultrasonic range from 116 (90 adult and 26 juvenile) individuals of *S. suslicus*, for presence of ultrasound.

All calls were analyzed spectrographically using Avisoft SASLab Pro (Avisoft Bioacoustics, Berlin, Germany). Calls of *S. suslicus* and *S. fulvus* and non-alarm calls of *S. citellus* were digitized at 24-kHz sampling frequency, 16-bit resolution. Alarm calls of *S. citellus* were digitized at 44.1 kHz, 16 bit resolution, to reveal better their spectral

Table 1 Call and animal samples used for describing the vocal repertoires of speckled (*S. suslicus*), European (*S. citellus*) and yellow (*S. fulvus*) ground squirrels

Species	Animals (males/females)	Number of calls of each call type (males/females)							
		Alarm call	Scream	Chatter	Grunt	Rapid grunt	Chirr	Snarl	Pant
S. suslicus	50	463	5	130	203	88	59	19	98
	25/25	228/235	3/2	69/61	124/79	64/24	25/34	3/16	74/24
S. citellus	18	90	35	8	26	74	6	17	16
	10/7/1[a]	46/44	20/15	1/0/7[a]	25/1	39/9/26[a]	2/4	13/4	10/6
S. fulvus	59	497	23	no calls	61	no calls	67	34	146
	27/32	247/250	7/16		34/27		31/36	9/25	69/77

[a] Calls of unsexed individual

features. All calls not bearing sound energy in lower parts of their spectra were high-pass filtered at 0.5 kHz to remove background noise. Spectrograms were created with Hamming window, FFT 512 or 1,024 points, frame 50% and overlap 96.87%. By spectrogram, we classified each call visually to one of eight types (alarm call, scream, chatter, grunt, rapid grunt, snarl, chirr, pant) according to the vocal traits described by Matrosova et al. (2006).

We identified notes (a single unit of vocalization, represented uninterrupted trace on the spectrogram) and bout of notes (series of a similar or different notes, separated from another bouts with interval longer that the duration of the bout). In each single note, we measured *note duration*. For call notes with clearly visible fundamental frequency (tonal call types), we measured *f0 st*, *f0 end*, *f0 max* and *f0 min* (Fig. 1a, Table 2). Additionally, for screams of *S. fulvus*, we measured two local peaks and one local depression of the *f0* (Fig. 2a). These additional measurements were taken to describe better the stereotypical "hat-like" frequency modulation (variable in other two species). For call notes without the evident fundamental frequency (wideband call types), we measured one to four most prominent *frequency peaks* in a mean power spectrum of a call (Fig. 1b, Table 2). For calls, representing a bout of notes, we also measured *bout duration* and *inter-note silence spaces* (Table 2). For the rhythmic call type (*chirr*), we measured the *pulse period* (Fig. 1b). Also, all tonal calls were checked for the presence of nonlinear phenomena in all the three species. Nonlinear phenomena in calls were registered as described by Wilden et al. (1998).

Descriptive statistics were calculated using STATISTICA, v. 6.0 (StatSoft, Tulsa, OK, USA). All means are given as mean ± SD.

Ethical standards

During the course of our work, we adhered to the "Guidelines for the treatment of animals in behavioural research and teaching" (*Anim. Behav.*, 2006, 71:245–253) and to the laws of the Russian Federation and of the Czech Republic, the countries where the research was conducted. Research protocol # 2008-03 was approved by the Committee of bioethics of Lomonosov Moscow State University. Research protocol # 24773/2008-1001 was approved by the Animal

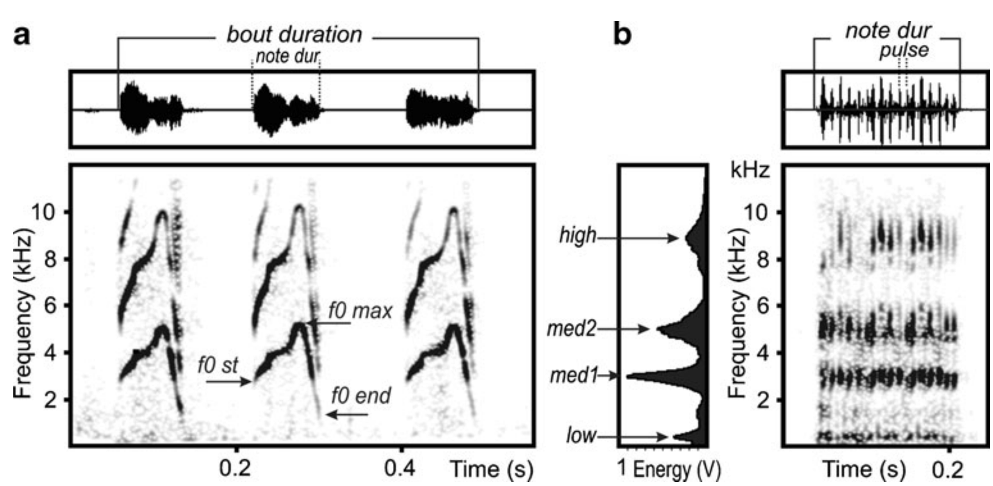

Fig. 1 Measured variables for a tonal call (**a**) and for a wideband call (**b**). *Low* low-frequency peak, *med* medium-frequency peaks, *high* high-frequency peak, *bout duration* duration of bout of notes, *note dur* duration of a call note, *pulse* pulse period. *Left*: power spectrum; *right*: spectrogram; *above*: waveform. The spectrogram parameters: sampling rate 24 kHz, FFT length 512 points, frame 50%, and overlap 93.75%

Table 2 Measured acoustic variables in speckled (*Spermophilus suslicus*), European (S. *citellus*) and yellow (*S. fulvus*) ground squirrels

Variable	Description
f0 st (kHz)	Fundamental frequency at the start of a note
f0 end (kHz)	Fundamental frequency at the end of a note
f0 max (kHz)	Maximum fundamental frequency of a note
f0 min (kHz)	Minimum fundamental frequency of a note
df (kHz)	Difference between the maximum and minimum fundamental frequencies of a note
High-frequency peak (kHz)	Most prominent frequency peak of a wideband call at 7–10 kHz
Medium-frequency peak(s) (kHz)	Most prominent peak (or two peaks in *chirr*s) of a wideband call between the high- and low-frequency peaks at 2–5 kHz
Low-frequency peak (kHz)	Most prominent frequency peak of a wideband call at 0–1 kHz
Note duration (ms)	Duration of a note
Bout duration (ms)	Duration of a bout of notes
Inter-note interval (ms)	Time period from the end of a previous note to the start of the next note

Care Committee of Faculty of Sciences, Charles University in Prague.

Results

In the three species, eight call types were found: three tonal and five wideband ones (Fig. 2, Tables 3 and 4). Acoustic structure of all call types excluding the alarm call was very stereotypic between species, i.e., was not species-specific (Fig. 2b–h).

Tonal calls

Alarm call

In all three species, alarm calls were the loudest and most common call types (Fig. 2a, Table 3). In *S. suslicus*,

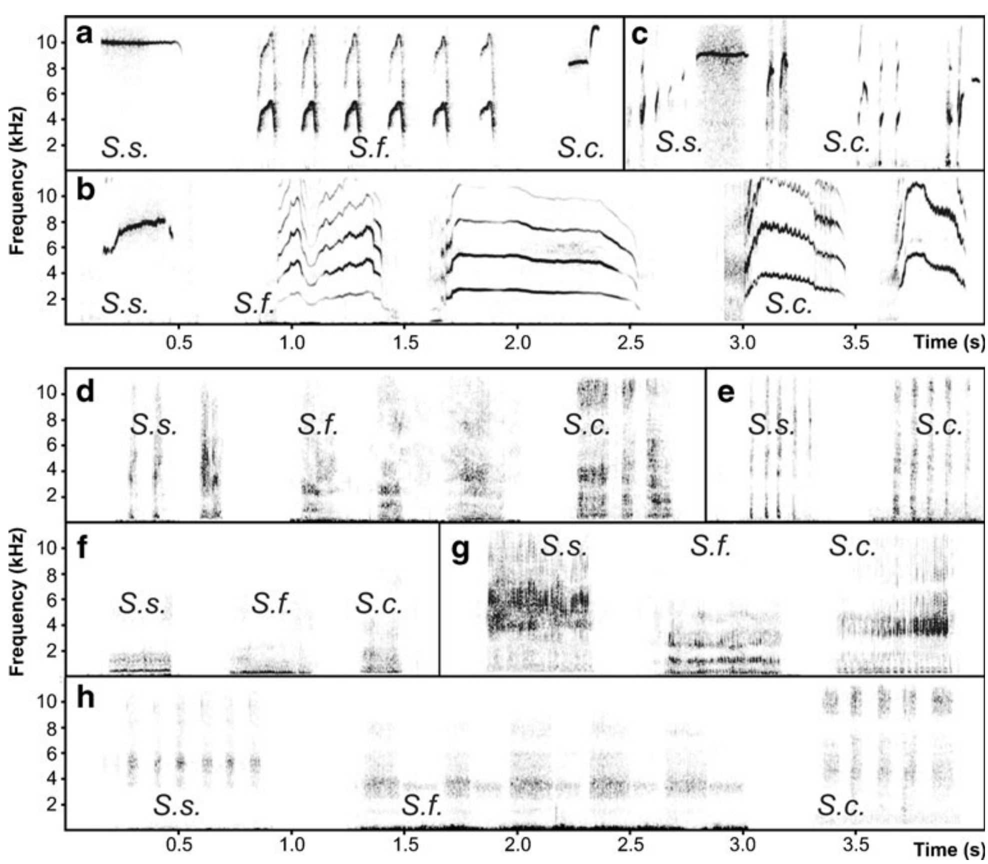

Fig. 2 Spectrogram illustrating tonal (**a**–**c**) and wideband (**d**–**h**) call types of three species of ground squirrels: *S.s.*, *Spermophilus suslicus*; *S.f.*, *S. fulvus*; *S. c.*, *S. citellus*. **a** alarm call, **b** scream, **c** chatter, **d** grunt, **e** rapid grunt, **f** snarl, **g** chirr, **h** pant. The spectrogram was created with sampling rate 24 kHz, FFT 512, frame 50%, overlap 87.5%. Audio files are available in the gallery at www.bioacoustica.org

Table 3 Values (mean ± SD; min–max) of variables for tonal call type notes of speckled (*S. suslicus*), European (*S. citellus*) and yellow (*S. fulvus*) ground squirrels

Variable	Species	Call type		
		Alarm Call	Scream	Chatter
Note duration (ms)	*S. suslicus*	241±62; 77–435	214±78; 131–317	22±9; 8–59
	S. citellus	70±10; 49–87[a] 48±18; 12–89[b]	385±84; 228–581	27±8; 17–45
	S. fulvus	76±11; 52–113	530±176; 288–912	–
f0 start (kHz)	*S. suslicus*	9.46±0.80; 6.18–11.8	4.46±1.16; 3.42–5.74	6.41±1.5; 3.45–10.59
	S. citellus	8.18±0.42; 7.06–8.95 [a] 11.08±1.18; 8.18–13.6 [b]	2.75±0.47; 2.15–4.31	3.38±0.39; 2.85–4.4
	S. fulvus	2.29±0.35; 1.17–3.75	1.94±0.41; 1.12–2.6	–
f0 max (kHz)	*S. suslicus*	9.66±0.75; 6.42–11.8	5.77±1.68; 4.19–8.08	–
	S. citellus	8.79±0.45; 7.83–9.64[a] 13.66±1.2; 11.28–15.76[b]	2.42±0.39; 1.59–3.37	3.22±0.64; 1.96–4.4
	S. fulvus	5.34±0.39; 4.31–6.32	3.85±1.39; 1.96–6.09	–
f0 end (kHz)	*S. suslicus*	9.17±0.97; 6.02–11.8	4.11±1.68; 2.62–6.75	7.1±1.64; 1.81–11.03
	S. citellus	8.29±0.4; 7.23–8.95[a] 12.9±1.06; 10.93–14.98[b]	2.81±0.75; 1.59–4.92	4.08±1.29; 1.96–6.32
	S. fulvus	1.78±0.24; 1.03–2.69	1.78±0.6; 1.0–2.92	–
df (kHz)	*S. suslicus*	0.61±0.6; 0.08–4.83	1.88±0.63; 0.91–2.39	1.1±0.81; 0.01–4.31
	S. citellus	0.89±0.1; 0.69–1.21[a] 2.9±1.14; 0.77–7.06[b]	3.9±0.75; 2.44–5.25	1.43±0.78; 0.47–3.19
	S. fulvus	3.56±0.38; 2.34–4.55	2.17±1.08; 0.75–4.71	–
Inter-note interval (ms)	*S. suslicus*	–	–	41±31; 4–176
	S. citellus	5±4; 0–20	–	49±15; 21–61
	S. fulvus	138±27; 148–374	–	–

The number of notes for *chatter* was 190 for *S. suslicus* and 13 for *S. citellus*; the samples of notes for *alarm call* and *scream* are given in Table 1

[a] First note of the *S. citellus* alarm call

[b] Second note of the *S. citellus* alarm call

alarm calls were single notes, weakly modulated in frequency, slightly decreasing in frequency to the end of the call, and produced in prolonged series with regular intervals. Occasionally (less than in 1% of individuals) alarm calls were complicated with nonlinear phenomena (subharmonics or biphonation) (Fig. 3). In *S. citellus*, alarm calls composed of two distinctive notes of total duration 126±20 ms, sometimes the first or second note was missing. The two notes could follow one after another without any silence space or were separated by inter-note interval up to 19.6 ms. The first note was modulated weakly in frequency, while the second note was modulated stronger (Fig. 2a). The frequency modulation of the second note was usually ascending and could be slightly descending to the end. In *S. fulvus*, alarm calls were bouts of 1–16 (more often three) notes, strongly modulated in frequency. The alarm call bouts, in their order, occurred either singly or were produced in long series with regular intervals, strongly exceeding the duration of bouts.

In all three species, the alarm calls were emitted towards potential predators, mainly humans (Slobodchikoff et al. 1991; Shekarova et al. 2008) and raptors: common buzzards (*Buteo buteo*), marsh hawks (*Circus cyaneus*), common kestrels (*Falco tinnunculus*), black kites (*Milvus migrans*), and towards terrestrial predators: dogs (*Canis familiaris*), domestic cats (*Felis catus*), red foxes (*Vulpes vulpes*) or harmless animals: European hares (*Lepus europaeus*) and cows (*Bos taurus*). Also, animals produced alarm calls during capturing, handling, encounters with conspecifics or without evident reasons. When emitting the alarm calls, free-running animals either pressed a body to the ground staying on four legs, or stayed on hind legs. The mouth openings, exhalatory movements and occasionally tail flipping were observed. In live-traps, animals decreased their

Table 4 Values (mean ± SD; min–max) of variables for wideband call types of speckled (*S. suslicus*), European (*S. citellus*) and yellow (*S. fulvus*) ground squirrels

Variable	Species	Call type				
		Grunt	Rapid grunt	Chirr	Snarl	Pant
Duration (ms)	*S. suslicus*	84±47; 22–240	32±10; 12–75	123±56; 37–260	183±72; 73–353	42±17; 13–99
	S. citellus	212±75; 117–434	45±25; 13–122	302±142; 94–506	188±76; 90–345	55±17; 30–93
	S. fulvus	110±43; 39–259	–	244±86; 94–546	249±84; 136–527	199±66; 93–371
Inter-note interval (ms)	*S. suslicus*	–	47±19; 12–150	–	–	66±28; 22–147
	S. citellus	–	90±36; 44–178	–	–	107±26; 72–152
	S. fulvus	–	–	–	–	199±55; 85–350
High-frequency peak (kHz)	*S. suslicus*	–	–	8.38±1.36; 3.1–10.33	–	9.29±0.79; 7.14–11.19
	S. citellus	–	–	8.0±1.22; 6.89–10.27	–	10.2±0.27; 9.79–10.87
	S. fulvus	–	–	3.2±1.14; 1.96–6.32	–	7.59±1.13; 4.66–10.85
Medium-frequency peak (kHz)	*S. suslicus*	4.25±0.76; 2.9–6.28	4.51±0.75; 2.43–6.89	3.46±0.72; 1.55–4.78 5.22±0.85; 3.1–7.06	–	5.13±0.30; 4.45–6.37
	S. citellus	4.13±0.72; 1.78–5.39	4.52±0.76; 2.43–6.89	4.5±0.61; 3.52–5.34	–	4.23±0.69; 2.85–4.87
	S. fulvus	2.75±1.24; 0.89–5.62	–	1.43±0.55; 0.65–2.85	–	3.49±0.86; 1.28–5.85
Low-frequency Peak (kHz)	*S. suslicus*	0.43±0.12; 0.3–1.12	0.48±0.23; 0.32–1.82	0.44±0.09; 0.3–0.8	0.37±0.05; 0.35–0.43	–
	S. citellus	1.27±0.68; 0.42–2.15	0.8±0.57; 0.32–2.06	1.1±1.0; 0.28–2.67	0.4±0.12; 0.28–0.79	–
	S. fulvus	0.28±0.06; 0.18–0.51	–	0.31±0.14; 0.14–0.89	0.28±0.07; 0.23–0.56	–

The number of notes for *rapid grunts* was 279 for *S. suslicus* and 74 for *S. citellus*; the samples of notes for other call types are given in Table 1

movemental activity after start of calling and froze, producing a series of calls with approximately equal inter-call intervals.

Ultrasound in S. suslicus alarm calls

Besides typical alarm calls in two of 115 individuals we registered the ultrasound. In one juvenile male *S. suslicus,* we found that seven of 60 elicited alarm calls contained a tonal ultrasound component alongside the audible fundamental frequency *f0* (Fig. 4b). The *f0* band was 9.4 kHz, corresponding to *f0 max* of this species (Table 3), whereas the ultrasound frequency band *g0* was 84 kHz. At the spectrogram, combinatory frequency bands (*g0-f0* ca. 74.7 kHz and *g0-2f0* ca. 65.5 kHz), arising as a result of interaction between the ultrasonic and the audible fundamental frequency bands, are visible (Fig. 4b). Such acoustic structure means that this call is biphonic, as it contains two unrelated fundamental frequencies, produced with two sound sources (Wilden et al. 1998).

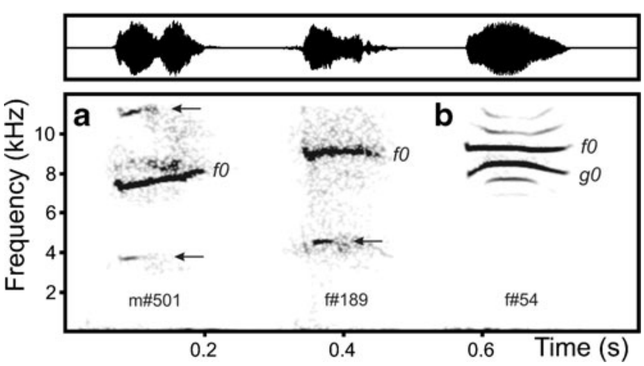

Fig. 3 Spectrogram (*below*) and waveform (*above*) illustrating nonlinear phenomena in alarm calls of *S. suslicus*. **a** Subharmonics (*marked with arrows*) are additional frequency bands of 1/2 of the fundamental frequency. **b** Biphonation is recognizable by presence in a call spectrum of two non-related fundamental frequencies (*f0* and *g0*) and by appearance of additional frequency bands, representing their linear combinations (Wilden et al. 1998). The spectrogram was created with sampling rate 24 kHz, FFT 512, frame 50%, overlap 93.75%

In addition, in one adult female, we recorded 75 calls, all with a wideband ultrasonic component (Fig. 4c). They were of comparable duration to the typical alarm calls, and were also emitted at intensive exhalations. Distinct from typical alarm calls, the alarm calls with a wideband ultrasonic component were much softer and sounded like hissing.

Scream

In all three species, screams were prolonged, penetrating notes, high in amplitude and deeply modulated in frequency (Fig 2b; Table 3). In *S. suslicus*, screams were high-amplitude calls, deeply modulated in frequency, of comparable duration to the alarm call. In *S. citellus*, contour of frequency modulation of screams was three-part, with the first part ascending in frequency, the second part with relatively constant frequency and the third part descending in frequency. The relative durations of these three parts were variable. All screams contained a secondary saw-like

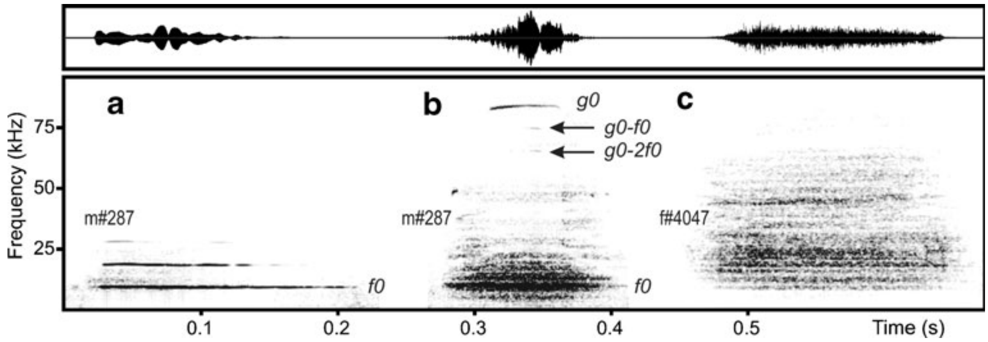

Fig. 4 Spectrogram (*below*) and waveform (*above*) illustrating ultrasound in alarm calls of speckled ground squirrels (*S. suslicus*). **a** The typical alarm call; **b** the alarm call with an audible frequency band *f0*, the ultrasonic frequency band *g0* and the combinatory frequency bands *g0–f0* and *g0–2f0* (*marked with arrows*); **c** the alarm call with a wideband ultrasonic component. The spectrogram was created with sampling rate 192 kHz, FFT 512, frame 100%, overlap 75%

frequency modulation. In *S. fulvus*, scream was the longest call type, typically with "hat-like" frequency modulation, with two local peaks, of 3.93±1.43 and 3.89±1.45 kHz, respectively, and with one local depression of 3.58±1.47 kHz in between. Besides, 12 of 23 screams contained a secondary saw-like frequency modulation. Screams could be pure or containing subharmonics (in three of six individual *S. fulvus*, producing the given call type, Fig. 5a), frequency jumps (in three of six *S. fulvus* and in one of four *S. citellus*, producing the given call type, Fig. 5b,c), and sidebands (in all four individual *S. citellus*, producing the given call type, Fig. 5d).

Emission of screams was related to defensive behaviour, with attempts to bite a researcher at handling. Occasionally we observed that juvenile screams attracted attention of conspecifics (who crawled out of burrows, observed and approached a trapped juvenile).

Chatter

Chatters were bouts of low-amplitude short notes, slightly modulated in frequency, and either followed or not followed by an alarm call (Fig. 2c, Table 3). In *S. suslicus*, chatters were single notes (83 of 130 chatters) or bouts of two to five notes (47 of 130), with an average bout duration 94±42 ms. Each next note in a bout was higher in frequency compared to the preceding one; so the overall run of frequency of a sequence is always ascending. In 101 from 130 bouts chatters were followed by an alarm call. In *S. citellus*, chatters were single notes (six of eight) or bouts of

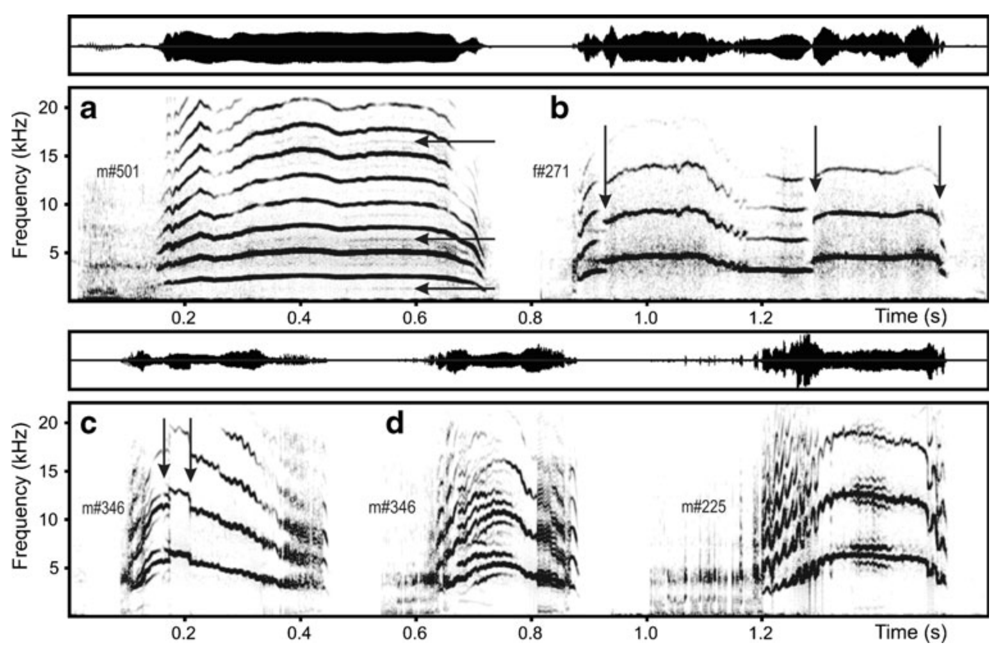

Fig. 5 Spectrogram (*below*) and waveform (*above*) of screams containing nonlinear phenomena: **a** subharmonics and **b** frequency jumps in the screams of *S. fulvus* (marked by arrows); **c** frequency jumps and **d** sidebands in screams of *S. citellus*. The spectrogram was created with sampling rate 44.1 kHz, FFT 512, frame 50%, overlap 87.5%

two to four notes (two of eight), sometimes followed by an alarm call (one of eight). In these cases, the alarm call contained only the first note. Bout duration was 235±44 ms. In *S. fulvus*, this call type was not found.

Chatter was associated with high movemental activity of a caller (often produced by a frightened caller rushing over the live-trap). Besides, chatter occurred during encounters between conspecifics and during handling.

Wideband calls

Grunt

Grunts were variable in structure, low-amplitude notes, produced singly or in irregular series with variable inter-call intervals (Fig. 2d, Table 4). The low- and medium-frequency peaks were most prominent in all three species. Grunts were often produced in interspersion with other call types. There were no notable differences in patterns of grunts between species.

Grunts were produced by animals at high arousal, at capture and during handling, and were associated with enhanced vocalization and movements, and with attempts to bite a researcher. Rather often, a caller fell on its back or attacked a trap wall on side of the microphone.

Rapid grunt

Low-amplitude bouts of short notes, separated with short inter-note intervals (Fig. 2e, Table 4). Like in grunt, the low- and medium-frequency peaks were most prominent. In *S. suslicus,* bouts consisted of two to seven notes (more often three), bout duration was 203±97 ms. In *S. citellus*, *rapid grunts* were produced in bouts of duration 550±222 ms consisting of two to ten notes (more often six). In *S. fulvus*, this call type was not found. Grunt and rapid grunt have similar patterns of power peaks, but differ noticeably by their temporal parameters, what results in strong differences in sounding between them.

Similarly to grunt, rapid grunt was commonly produced at rushes of the caller, provoked with hand-held hat movements over the live-trap. Soft quality was probably due to the call production with semi-closed mouth. Besides, rapid grunts were produced by two *S. citellus*, encountered in a burrow after getting frightened by an approaching human.

Snarl

Long single notes, with the low-frequency peak most prominent, in all three species (Fig. 2f, Table 4).

Snarl was rare call, so it was difficult to judge about its functioning. The call was produced with the closed or semi-closed mouth and was not attended with active movements but occasionally with wire mesh gnawing.

Chirr

The high-amplitude single pulsed notes (Fig. 2g, Table 4), produced through the widely opened mouth, with visible pulsation of the tongue (V. Matrosova, personal observations). In *S. suslicus,* pulse period was 10.8±1.7 ms (*N*=59). Four frequency peaks were well expressed: the low-, the high- and the two medium-frequency peaks, of 3.46±0.72 and 5.22±0.85 kHz, respectively. In *S. citellus*, chirr was poorly distinguished from grunt, because of irregular pulsation. Pulse period was 21.7±6.5 ms (*N*=4). The medium-frequency peak and sometimes low-frequency peak were well expressed in *S. citellus*. In *S. fulvus*, pulse period was 14.6±1.4 ms (*N*=67). The low-, the high- and the medium-frequency peaks were well expressed.

Chirr attended aggressive behaviour of captured animals in response to movements of hand-held hat. Callers could fall to their backs or actively gnawed the wire mesh. Call amplitude increased at shorter distance to the frightening stimulus.

Pant

Low-amplitude short notes at exhalations, produced in semi-regular series. A single wideband call type where the note low-frequency peaks were missing, whereas the medium- and high-frequency peaks were prominent, in all the three species (Fig. 2h, Table 4).

*Pant*s were evidently produced by animals when they were tired of loud calling in live-traps. Sometimes pants were interspersed with other call types, mainly with grunts or rapid grunts.

Transitional calls

In all species, we observed many calls, showing traits of two different types. Transitions could be observed between almost any of the call types, but were mostly found between grunt, rapid grunt, pant, chirr, alarm call and chatter and vice versa.

Discussion

Shared and species-specific acoustic features

The most intriguing finding in our study is that most call types were remarkably similar in structure between species, with the exception of alarm calls which were strongly species-specific (Fig. 2). The obtained data are consistent with the earlier findings of strong species-specific differences in the structure of alarm calls in Eurasian species of ground squirrels and increasing differences with greater distance between geographical populations (Nikoĺskii 1979, 1984; Nikoĺskii and Rumyantsev 2004). It is unclear, why the alarm calls were species-specific and the non-alarm calls were similar in different species. Some parallels can be found in bats Madeira pipistrelle *Pipistrellus maderensis* and Kuhl's pipistrelle *P. kuhlii*, the structure of social calls was very similar between species, whereas echolocation calls were markedly different (Russo et al. 2009). It seems that both alarm and non-alarm calls are used in communication both with predators and with conspecifics. People were surrogate predators in current research, and all call types were recorded towards them. Also, in the Lipetsk region location, we observed many chases and fights between *S. suslicus*, always attended with calls, sounding similar to non-alarm calls described in this study.

In spite of the between-species differences in ecology and biology, *S. suslicus*, *S. citellus* and *S. fulvus* shared the same set of six (first two species all the eight) agonistic vocalizations toward potential predators. We did not find any one single call type characteristic of only one single species. In *S. fulvus*, we failed to find one tonal and one wideband call type of the set of the eight call types. It seems that both chatter and rapid grunt represented modified alarm call and grunt, "broken" into short separate elements. As *S. fulvus* do not show a tendency to broken their calls, it is most probable that these two call types do not exist in *S. fulvus* rather than were not found by our group.

Stronger similarity in vocal sets between *S. suslicus* and *S. citellus* could be due to their closer phylogenetic relatedness compared to *S. fulvus* (Helgen et al. 2009). The occurrence of call types did not depend on sex or age (our unpublished data).

Mainly, the alarm call functions to avoid predation (review by Blumstein 2007). Functions of other call types could not be stated unambiguously, however based on recording context, we propose that under natural conditions they are produced either when the source of danger is in immediate vicinity of a caller or during encounters of conspecifics. Further study of vocal and social behaviour alongside with detailed acoustic analysis and playback experiments is necessary to clear up the functions of different agonistic vocalizations in ground squirrels.

Comparison with related species

It is reasonable to expect, based on the remarkable similarity in non-alarm agonistic vocalizations of the three species, that a similar organization of vocal repertoires may be found in related species. Indeed, some call types described in this study, were found in closely related genera of ground squirrels (Table 5). Nevertheless, the literature-based comparison of vocal repertoires between species is complicated because different call types are named differently or vice versa, the same terms are applied to structurally different call types. This problem arises even at comparison of different evidences on the same species. For example, *trill* of the Belding's ground squirrel described by Robinson (1981) is the same vocalization as *churr* described by Turner (1973) in the same species. So far, no common terminology for call types has been established for ground squirrels, although conspicuous similarities in some vocalizations of several species indicate that they may represent the same vocalization. Therefore, synonyms of the same call types should be taken into consideration when data of different authors are used for between-species comparisons.

For the alarm call (Table 5), the comparison is further complicated because of existence of structurally different types of alarm calls in some North American species of ground squirrels (i.e., Balph and Balph 1966; Melchior 1971; Turner 1973; Sherman 1985). Analysis of the data found in the literature, containing both description and spectrograms of different calls of ground squirrels, has allowed observers to establish four groups of alarm calls, which vary in their acoustic structure (Table 5). Three of them include alarm calls of tonal structure: single-note weakly modulated (whistles, to this group, the alarm calls of *S. suslicus* and *S. citellus* can be assigned), bouts of one-to-few modulated notes (*chirps*) and multiple-note bouts, different in the degree of modulation (trills, churrs, to this group, the alarm calls of *S. fulvus* can be assigned). The alarm calls from these groups are mostly (but not always) related to the context of mobbing of raptors. The fourth group of alarm calls includes bouts of many short wideband notes (chatter). This kind of the alarm calls attends the appearance of terrestrial predators and has no evident analogues among Eurasian species of ground squirrels.

Similar-to-scream call type has been reported for at least two species of ground squirrels and for pups of yellow-bellied marmots (Blumstein et al. 2008). This vocalization attends situations of extreme danger, when an animal was in human hands or in teeth of a predator (Table 5). Vocalization similar to chatter was reported for another ground squirrel species. The "grunt" was reported for a few species of ground squirrels under the term "growl". However, the term growl is not perfectly correct, because this call type does not contain the low-frequency rhythmic component. Vocalizations similar to rapid grunt were reported for two species of ground squirrels; however, the detailed comparison is complicated because of the poor quality of spectrogram provided as illustrations. No comparative data is available on snarl, chirr and pant. Snarl and pant both are

Table 5 Comparison of described in Eurasian ground squirrel call types with literature data on vocal repertoires in North American ground squirrels

Vocalization	Synonyms	Species	Spectral characteristics	Behavioural context
Alarm call	Churr	*S. armatus*[1,5] *S. columbianus*[2,5] *S. elegans*[5] *S. richardsonii*[5] *S. variegatus*[6]	Bouts of several tonal notes, usually of decreasing intensity, with *f0* varying according to species of 2–8 kHz. Duration of notes is also variable according to species. First note usually differs from the following ones in its frequency and duration.	Attends encounters of terrestrial predators. Also produced during agonistic interactions and in the context of post-copulatory mate guarding (*S. beldingi*).
	Trill	*S. beldingi*[7,12] *S. lateralis*[4] *S. saturatus*[4]		
	Chirp	*S. armatus*[1,5] *S. columbianus*[2,5,8] *S. beldingi*[7,12] *S. elegans*[5] *S. richardsonii*[3,5]	Produced singly or in bouts of 2–3 notes; consists of high-frequency, mostly tonal, frequency-modulated notes (in *S. beecheyi* can contain wideband component); variable in duration and usually decreasing in *f0* (although increasing in *S. beecheyi*); varying according to species of 3–7 kHz. Sometimes it may immediately precede a churr call.	Attends encounters of aerial and terrestrial predators. Also produced during agonistic interactions and in the context of post-copulatory mate guarding (*S. columbianus*).
	Chat	*S. beecheyi*[11]		
	Whistle	*S. beecheyi*[11] *S. beldingi*[7] *S. columbianus*[5] *S. richardsonii*[3,5] *S. parryii*[9,10] *S. variegatus*[6]	Single-note tonal call with slight frequency modulation and *f0* varying between species of 2–8 kHz. Duration is variable and usually longer those of chirp (within the vocal repertoire of a species). Sometimes it may immediately precede a churr call.	Attends encounters of aerial and terrestrial predator and agonistic interactions with conspecifics.
	Chatter	*S. beecheyi*[11] *S. parryii*[9,10]	Bouts of several short, mostly wideband, notes (ranging in *f0* of ca. 2–8 kHz).	Attends encounters of terrestrial predators and agonistic chases of conspecifics.
Ultrasonic alarm call	Whisper call	*S. richardsonii*[13]	Single-note tonal call with slight frequency modulation and *f0* ca. 50 kHz. Duration ca. 225 ms.	Short-range alarm call.
Scream	Squawk Squeal	*S. armatus*[1] *S. columbianus*[2] *S. richardsonii*[5]	Highly variable in the structure, *f0* and duration; tonal call.	Produced when the caller is attacked by a conspecific or by a predator and during handling.
Chatter	Squeal	*S. armatus*[1]	Short tonal calls. Highly variable in structure, *f0* and duration.	Produced by animals attacked by a predator.
Grunt	Growl	*S. armatus*[5] *S. columbianus*[5] *S. elegans*[5] *S. variegatus*[6]	Wideband calls with energy mainly concentrated within one or two bands, first band between 0 and 2 kHz and the second one between 4 and 6 kHz.	Attends chasing a conspecific and during handling. Associated with treating behaviour.
	Squawk	*S. columbianus*[2]		
Rapid grunt	Growl	*S. variegatus*[6]	One wideband note in the range of 0–5 kHz followed by many notes in the range of 0–1.2 kHz.	Attends agonistic encounters with conspecifics.

Comparisons are based on structural and situational similarity

[1] Balph and Balph 1966; [2] Betts 1976; [3] Davis 1984; [4] Eiler and Banack 2004; [5] Koeppl et al. 1978; [6] Krenz 1977; [7] Leger et al. 1984; [8] Manno et al. 2007; [9] Melchior 1971; [10] Nikoĺskii 1984; [11] Owings and Virginia 1978; [12] Robinson 1981; [13] Wilson and Hare 2004, 2006

very low intensity, which is what probably complicates their revealing in unrestrained ground squirrels. The structure of chirr, for the exclusion of its rhythmic component and long duration, is similar to that of grunts (synonym, occurring in the literature: *growl*). This can result in imprecise distinction between these call types, showing in addition many intermediate forms.

Nonlinear phenomena

Scarce data is available on the use of nonlinear phenomena in vocalizations of ground-dwelling sciurids. The most spectacular example is represented by pup screams in yellow-bellied marmots (Blumstein et al. 2008) produced during handling procedures after capturing in live-traps. Besides deterministic chaos, 55% marmot screams contained subharmonics and 13% contained biphonation. In ground squirrels in the current study, the context of the acoustic structure of screams was similar to those for pup screams in yellow-bellied marmots (Fig. 4). Consistently, these screams contained nonlinear phenomena, subharmonics, frequency jumps and sidebands, probably resulting from the state of high arousal of animals emitting screams. Their probable function may be to discourage a predator with dissonant loud calls (Owren and Rendall 1997), unlike appealing to parents for defense, as in marmot pups (Blumstein et al. 2008).

In alarm calls, the nonlinear phenomena were observed very rarely. They were found only in three individual *S. suslicus* of 435. Alarm calls of *S. citellus* contain two parts, probably produced from two different sound sources (Nikolśkii 1979, 1984; Schneiderová and Policht 2010). A similar kind of alarm calls was found in some Eurasian species of ground squirrels (Asia Minor ground squirrel *S. xanthoprymnus*, Caucasian mountain ground squirrel *S. musicus*, little ground squirrel *S. pygmaeus*, Alashan ground squirrel *S. alashanicus*, *S. citellus*, Taurus ground squirrels *S. taurensis*). However, in *S. citellus* we did not find any one single call, where the frequency bands of the first and second notes overlapped in time at least on the small part of the call, and did not find signs of interaction between frequency bands of the first and second notes. We can conclude that nonlinear phenomena rarely occur in vocalizations of ground squirrels and further study is necessary to investigate their role in acoustic communication.

Ultrasound

While about 50% of mammalian species produce ultrasounds (Gould 1983), among ground-dwelling sciurids, the ultrasound has been reported only for the *S. richardsonii* (Wilson and Hare 2004, 2006). Accordingly to our results for *S. suslicus*, this species uses the ultrasound extremely rarely. We registered the ultrasound only in two of 115 individuals (i.e., not more than in 1–2% individuals). Probably because of its rare occurrence, the ultrasound was not found in *S. citellus*, for which only 41 recordings were made from free-ranging unmarked individuals (Georgiev et al. 2004). We also observed and videotaped one individual of this species calling through with widely opened mouth without audible sounds (I. Schneiderová, personal observation). Thus, we can also expect to find ultrasound alarms in the *S. citellus*.

The ultrasound found in *S. suslicus* was in the higher-frequency range (ca. 84 kHz) than expected based on the evidence for *S. richardsonii* (ca. 48 kHz; Wilson and Hare 2004). We also found in *S. suslicus* two variants of ultrasound: the tonal one, containing alongside the fundamental frequency the second high fundamental frequency, and the noisy “whisper” (Fig. 4). It is probable that *S. richardsonii* produce biphonic calls as well, although Wilson and Hare (2004, 2006) have always been recording calls using either a system limited to ultrasound alone or audible frequencies alone. Despite the lack of recordings, it is readily apparent in observing *S. richardsonii* in the field that calls are seldom discretely audible or ultrasonic, but rather form a continuum between those extremes (J.F. Hare, personal communication). Given the rare occurrence and poor propagation of the very high-frequency ultrasound, the functioning of ultrasound alarms as specific “cryptic” call to warn nearby conspecifics of potential danger (Wilson and Hare 2006), it is hardly probable for *S. suslicus*. A more probable function may be the enhanced structural variability of alarm calls to prevent habituation to such stimuli.

Acknowledgments We thank S.A. Shilova, A.V. Tchabovsky, L.E. Savinetskaya, O.N. Shekarova, A.F. Babitsky, S.V. Pivanova, N.A. Vasilieva, J. Matějů and P. Schnitzerová for help with data collection and to V. Vohralík and R. Frey for help with literature. We are sincerely grateful to the two anonymous reviewers for very constructive comments. This study was supported by the Russian Foundation for Basic Research, grant 09-04-00416 (for VAM, IAV, EVV), and by the Ministry of Education, Youth and Sports of the Czech Republic (project No. 0021620828) and the Ministry of the Environment of the Czech Republic (project No. SP/2d4/61/08) (for IS).

Conflict of interest The authors do not have any conflict of interest. All funding sources are declared in the Acknowledgements.

References

Balph DM, Balph DF (1966) Sound communication of Uinta ground squirrels. J Mammal 47:440–450

Betts BJ (1976) Behaviour in a population of Columbian ground squirrels, *Spermophilus columbianus columbianus*. Anim Behav 24:652–680

Blumstein DT (2007) The evolution of alarm communication in rodents: structure, function, and the puzzle of apparently altruistic calling in rodents. In: Wolff JO, Sherman PW (eds) Rodent societies. Univ. Chicago Press, Chicago, pp 317–327

Blumstein DT, Récapet C (2009) The sound of arousal: the addition of novel non-linearities increases responsiveness in marmot alarm calls. Ethology 115:1074–1081

Blumstein DT, Richardson DT, Cooley L, Winternitz J, Daniel JC (2008) The structure, meaning and function of yellow-bellied marmot pup screams. Anim Behav 76:1055–1064

Davis LS (1984) Alarm calling in Richardson's ground squirrels (*Spermophilus richardsonii*). Z Tierpsychol 66:152–164

Digweed SM, Rendall D (2009a) Predator-associated vocalizations in North American red squirrels, *Tamiasciurus hudsonicus*: are alarm calls predator specific? Anim Behav 78:1135–1144

Digweed SM, Rendall D (2009b) Predator-associated vocalizations in North American red squirrels (Tamiasciurus hudsonicus): To whom are alarm calls addressed and how do they function? Ethology 115:1190–1199

Eiler KC, Banack SA (2004) Variability in the alarm call of golden-mantled ground squirrels (*Spermophilus lateralis* and *S. saturatus*). J Mammal 85:43–50

Ermakov OA, Surin VL, Titov SV, Tagiev AF, Luk'yanenko AV, Formozov NA (2002) A molecular genetic study of hybridization in four species of ground squirrels (*Spermophilus*: Rodentia, Sciuridae). Russ J Genet 38(7):796–809

Fichtel C, Kappeler PM (2002) Anti-predator behavior of group-living Malagasy primates: mixed evidence for a referential alarm call system. Behav Ecol Sociobiol 51:262–275

Fitch WT, Neubauer J, Herzel H (2002) Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production. Anim Behav 63:407–418

Georgiev A, Keppler S, Haas H (2004) A preliminary investigation into the alarm-calling behaviour of European sousliks (*Spermophilus citellus*). In: Behavioural Ecology excursion to Bulgaria. Project report on the European Souslik Working Group. http://www.geocities.com/thesousliks

Gould E (1983) Mechanisms of mammalian auditory communication. In: Eisenberg JF, Kleiman DG (eds) Advances in the study of mammalian behaviour. Special Publication. American Society of Mammalogists, Shippensburg, pp 265–342

Helgen KM, Cole FR, Helgen LE, Wilson DE (2009) Generic revision in the holarctic ground squirrel genus *Spermophilus*. J Mammal 90:270–305

Kashkarov D, Lein L (1927) The yellow ground squirrel of Turkestan, *Cynomys fulvus oxianus* Thomas. Ecology 8:63–72

Koeppl JW, Hoffman RS, Nadler CF (1978) Pattern analysis of acoustical behavior in four species of ground squirrels. J Mammal 59:677–696

Koshev Y, Pandourski I (2008) Structure and variability of alarm calls of European ground squirrel (Rodentia: *Spermophilus citellus* L. 1766) from Western Bulgaria. Acta Zool Bulg 60:99–105

Krenz MC (1977) Vocalization of the rock squirrel *Spermophilus variegatus*. Dissertation, Texas Tech University, Lubbock, TX

Kryštufek B, Vohralík V (2005) Mammals of Turkey and Cyprus. Rodentia: I. Sciuridae, Dipodidae, Gliridae, Arvicolinae. University of Primorska, Koper

Leger DW, Berney-Key SD, Sherman PW (1984) Vocalizations of Belding's ground squirrels (*Spermophilus beldingi*). Anim Behav 32:753–764

Macedonia JME, Evans CS (1993) Variation among mammalian alarm call systems and the problem of meaning in animal signals. Ethology 93:177–197

Manno TG, Nesterova AP, Debarbieri LM, Kennedy SE, Wright KS, Dobson FS (2007) Why do male Columbian ground squirrels give a mating call? Anim Behav 74:1319–1327

Matrosova VA, Volodin IA, Volodina EV (2006) The diversity of calls produced by live-trapped speckled ground squirrels *Spermophilus suslicus* (Rodentia, Sciuridae). Bull Moscow Soc Naturalists 111:84–87 [In Russian]

Matrosova VA, Volodin IA, Volodina EV, Babitsky AF (2007) Pups crying bass: vocal adaptation for avoidance of age-dependent predation risk in ground squirrels? Behav Ecol Sociobiol 62:181–191

Matrosova VA, Volodin IA, Volodina EV (2008) Does kinship affect the alarm call structure in the yellow ground squirrel *Spermophilus fulvus*? Lynx (Praha) ns 39:295–303

Matrosova VA, Volodin IA, Volodina EV (2009) Short-term and long-term individuality in speckled ground squirrel alarm calls. J Mammal 90:158–166

Matrosova VA, Volodin IA, Volodina EV, Vasilieva NA (2010a) Stability of acoustic individuality in the alarm calls of wild yellow ground squirrels *Spermophilus fulvus* and contrasting calls from trapped and free-ranging callers. Naturwissenschaften 97:707–715

Matrosova VA, Volodin IA, Volodina EV, Vasilieva NA, Kochetkova AA (2010b) Between-year stability of individual alarm calls in the yellow ground squirrel *Spermophilus fulvus*. J Mammal 91:620–627

Matrosova VA, Blumstein DT, Volodin IA, Volodina EV (2011) The potential to encode sex, age and individual identity in the alarm calls of three species of Marmotinae. Naturwissenschaften 98:181–192

McCowan B, Hooper SL (2002) Individual acoustic variation in Belding's ground squirrel alarm chirps in the High Sierra Nevada. J Acoust Soc Am 111:1157–1160

Melchior HR (1971) Characteristics of arctic ground squirrel alarm calls. Oecologia 7:184–190

Nikol'skii AA (1979) Species specifity of alarm call in sousliks (*Citellus*, Sciuridae) of Eurasia. Zool Zh 58:1183–1194 [In Russian]

Nikol'skii AA (1984) Zvukovye signaly mlekopitajushchih v evolucionnom processe [Sound signals of mammals in evolution]. Nauka, Moscow [in Russian]

Nikol'skii AA, Rumyantsev VYu (2004) Variability of alarm call in ground squirrels of Major group (Rodentia, Sciuridae, *Spermophilus*) as a model of geographic species formation. Zool Zh 83:1008–1017 [In Russian]

Nikol'skii AA, Denisov VP, Stojko TG, Formozov NA (1984) The alarm call in F_1 hybrids *Citellus pygmaeus* x *C. suslica* (Sciuridae, Rodentia). Zool Zh 63:1216–1225 [In Russian]

Nowak RM (1999) Walker's mammals of the world, 6th edn. John Hopkins Univ. Press, Baltimore

Owings DH, Leger DW (1980) Chatter vocalizations of California ground squirrels: predator- and social-role specifity. Z Tierpsychol 54:163–184

Owings DH, Virginia RA (1978) Alarm calls of California ground squirrels (*Spermophilus beecheyi*). Z Tierpsychol 46:58–70

Owren MJ, Rendall D (1997) An affect-conditioning model of nonhuman primate vocal signals. In: Owings DH, Beecher MD, Thompson NS (eds) Perspectives in ethology, vol. 12. Plenum, New York, pp 299–346

Pollard KA, Blumstein DT (2011) Social group size predicts the evolution of individuality. Curr Biol 21:413–417

Robinson SR (1981) Alarm communication in Belding's ground squirrels. Z Tierpsychol 56:150–168

Russo D, Teixeira S, Cistrone L, Jesus J, Teixeira D, Freitas T, Jones G (2009) Social calls are subject to stabilizing selection in insular bats. J Biogeogr 36:2212–2221

Schneiderová I, Policht R (2010) Alarm calls of the European ground squirrel *Spermophilus citellus* and the Taurus ground squirrel *S. taurensis* encode information about caller identity. Bioacoustics 20:29–43

Shekarova ON, Neronov VV, Savinetskaya LE (2008) Speckled ground squirrel (*Spermophilus suslicus*): current distribution, population dynamics and conservation. Lynx (Praha) ns 39:317–322

Sherman PW (1977) Nepotism and the evolution of alarm calls. Science 197:1246–1253

Sherman PW (1985) Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation? Behav Ecol Sociobiol 17:313–323

Slobodchikoff CN, Kiriazis J, Fischer C, Creef E (1991) Semantic information distinguishing individual predators in the alarm calls of Gunnison's prairie dogs. Anim Behav 42:713–719

Swan DC, Hare JF (2008) Signaler and receiver ages do not affect responses to Richardson's ground squirrel alarm calls. J Mammal 89:889–894

Tchabovsky AV (2005) Sociality of ground squirrels: effect of body size and habitat type. Bull Moscow Soc Nat Explorers, Dept of Biology 110(4):80–88 [In Russian]

Titov SV, Ermakov OA, Surin VL, Formozov AN, Kasatkin MV, Shilova SA, Shmyrov AA (2005) Molecular genetic and bioacoustic diagnostics russet (*Spermophilus major* Pallas, 1778) and yellow (*S. fulvus* Lichtenstein, 1823) ground squirrels from mixed colony. Bull Moscow Soc Naturalists 110:72–77 [In Russian]

Townsend SW, Manser MB (2010) The function of nonlinear phenomena in meerkat alarm calls. Biol Lett. doi:10.1098/rsbl.2010.0537

Turner LW (1973) Vocal and escape responses of *Spermophilus beldingi* to predators. J Mammal 54:990–993

Vasilieva NA, Savinetskaya LE, Tchabovsky AV (2009) Large body size and short period of activity do not impede fast growth in the long-teeth ground squirrel (*Spermophilus fulvus*). Zool Zh 88:339–343 [In Russian]

Volodin IA (2005) Individuality of alarm calls in the spotted suslik (*Spermophilus suslicus*, Rodentia, Sciuridae). Zool Zh 84:228–235 [In Russian]

Volodin IA, Volodina EV, Matrosova VA, Savinetskaya LE, Shekarova ON, Voytsik VA (2008) Population density does not affect the alarm call characteristics in the speckled ground squirrel (*Spermophilus suslicus*). Lynx (Praha), ns 39(2):333–342

Volodina EV, Matrosova VA, Volodin IA (2010) An unusual effect of maturation on the alarm call fundamental frequency in two species of ground squirrels. Bioacoustics 20:87–98

Wilden I, Herzel H, Peters G, Tembrock G (1998) Subharmonics, biphonation, and deterministic chaos in mammal vocalization. Bioacoustics 9:171–196

Wilson DR, Hare JF (2004) Ground squirrel uses ultrasonic alarms. Nature 430:523

Wilson DR, Hare JF (2006) The adaptive utility of Richardson's ground squirrel (*Spermophilus richardsonii*) short-range ultrasonic alarm signals. Can J Zool 84:1322–1330