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Ultrasonic bouts of a blind climbing rodent (*Typhlomys chapensis*): acoustic analysis

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ABSTRACT

The peculiar acoustic structure of ultrasonic bouts of blind climbing rodents *Typhlomys* might provide insight on their potential function. We examined 1481 bouts consisting of 1-6 pulses; 49.7% of them were single-pulse bouts. Bout duration and inter-bout interval depended on the number of pulses per bout, whereas period from start of a previous bout to start of the next bout was constant (80.0±2.9 ms). Ultrasonic pulses (540 pulses measured in a subset of 234 bouts) were short (0.68±0.15 ms) sweeps with fundamental frequency slopes from 127.3±6.3 kHz to 64.1±4.6 kHz and peak frequency at 93.3±7.4 kHz, emitted within bouts with inter-pulse periods of 13.03±3.01 ms. Single pulses and start pulses of multi-pulse bouts were lower in frequency than other pulses of the bouts. In contrast, pulse duration was independent on pulse position within bout. Pulses of *Typhlomys* were reminiscent of echolocation calls of *Murina* and *Myotis* bats, but higher in frequency, much shorter, fainter, displayed a convex contour of frequency modulation and only the fundamental frequency band without harmonics and were organized in bouts, that is not characteristic for bat echolocation. Most probably, *Typhlomys* uses their ultrasonic pulses for call-based orientation during locomotion, including climbing and jumping among bush branches.

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Introduction

In terrestrial mammals, ultrasonic pulses are used by insectivorous bats for capturing their mobile prey (Jones and Teeling 2006; Fenton 2013), whereas fruit bats use them as sonar signals for accurate landing or detection of medium-sized objects (Yovel et al. 2011). Ultrasonic bouts of small non-volant rodents, the blind Vietnamese pygmy dormice (*Typhlomys chapensis*), are intriguing to researchers as a potential ancestral state of bat echolocation (Panyutina et al. 2017; Thiagavel et al. 2018). It remains arguable whether bat echolocation evolved before, simultaneously or after developing the flying ability (Fenton et

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al. 1995; Speakman 2001; Schnitzler et al. 2003; Jones and Teeling 2006; Simmons et al. 2008; Maltby et al. 2010; Teeling et al. 2012).

At the same time, some animals use single audible calls and click trains for call-based orientation on the land, as e.g. shrews (Thomas and Jalili 2004; Siemers et al. 2009), and for hydrolocation (echo-ranging), as e.g. hippos *Hippopotamus amphibius* (Maust-Mohl et al. 2018). Examining the ultrasonic bouts of *Typhlomys* for their similar and different traits with calls of echolocating and echo-ranging species might highlight their potential function. However, the acoustic structure of ultrasonic bouts of *Typhlomys* was not before described in detail.

Early studies report ultrasonic clicks for shrews (Gould et al. 1964; Gould 1969; Buchler 1976; Tomasi 1979; Forsman and Malmquist 1988), tenrecs (Gould 1965) and rodents (Riley and Rosenzweig 1957; Bell et al. 1971; review: Thomas and Jalili 2004). However, more recent studies did not confirm ultrasonic vocalization for shrews (Thomas and Jalili 2004; Catania et al. 2008; Siemers et al. 2009; Volodin et al. 2015; Zaytseva et al. 2015). It has been proposed however that shrews instead use their sonic calls for echo-based orientation, e.g. twitters or audible clicks (Siemers et al. 2009; Volodin et al. 2015; Zaytseva et al. 2015).

In laboratory rats (Riede 2011; Brudzynski 2013) and mice (Arriaga and Jarvis 2013; Hammerschmidt et al. 2012; Hoffmann et al. 2012), no ultrasonic echolocation pulses have been described aside from the broadband, low-frequency to high-frequency range clicks in rats (Thomas and Jalili 2004). Probably, in the early behavioural experiments with vision-deprived rodents that reported the echo-based detection (Riley and Rosenzweig 1957; Bell et al. 1971; review: Thomas and Jalili 2004), the animals could use other cues for orientation aside from the echoes, e.g. smell or touch with vibrissae. Ultrasonic clicks were also not detected in many other species of rodents examined for their ultrasonic vocalization (Lepri et al. 1988; Holman et al. 1995; Kapusta et al. 1999; Wilson and Hare 2004; Kalcounis-Rueppell et al. 2006, 2010; Miller and Engstrom 2007; Nishiyama et al. 2011; Matrosova et al. 2012; Ter-Mikaelian et al. 2012; Murrant et al. 2013; Ancillotto et al. 2014; Campbell et al. 2014; Fernández-Vargas and Johnston 2015; Pasch et al. 2017; Riede et al. 2017; Zaytseva et al. 2017).

Recently, bouts of ultrasonic pulses reminiscent of the calls of echolocating bats were found in the Vietnamese pygmy dormouse (*Typhlomys chapensis* Osgood, 1932) (Panyutina et al. 2017). This species belongs to a separate family, Platacanthomyidae, of the order Rodentia (Abramov et al. 2014). *T. chapensis* inhabits subtropical forests of North Vietnam and Southern China. These small rodents (head-and-body length of 79–86 mm) are burrowing animals, mainly foraging for fruits, leaves, seeds, stems and insects (Smith 2008; Abramov et al. 2014; Cheng et al. 2017). This species is characterized by drastically reduced eyes, enlarged and unusually mobile ears, nocturnal activity and extremely fast locomotion over bush branches (Cheng et al. 2017; Panyutina et al. 2017). Because of the strongly reduced retina and optic nerve, this animal is incapable of object vision (Panyutina et al. 2017). Cheng et al. (2017) found a 1-bp deletion in the interphotoreceptor retinoid-binding protein gene which could be associated with a relaxed selection pressure on this visual gene. Ultrasonic pulses of *Typhlomys* are produced at significantly greater rates during locomotion compared to that in resting animals (Panyutina et al. 2017). In this study, we used acoustic recordings made during experiments with *T. chapensis* to conduct a detailed analysis of temporal and spectral

acoustic variables as a basis for a general discussion on the acoustics of echolocation sequences used by bats and whales.

Materials and methods

Study site and subjects

Subjects were two captive adult males of the Vietnamese pygmy dormouse *T. chapensis* (thereafter *Typhlomys*) kept in Moscow Zoo (Moscow, Russia). These animals arrived at the zoo at a mature age 10 months before the start of experiments. These animals were live-trapped in a mountain tropical forest in North Vietnam, near Tram Ton Station of Hoang Lien National Park, West of Sa Pa Village, Lao Cai Province (22°21′N, 103°46′E) in autumn 2012, in the framework of a biodiversity survey carried out by the Joint Vietnam–Russian Tropical Research and Technological Centre. The animals were housed in separate cages in glass-and-wire-mesh cages 40 × 40 × 80 cm, with a bedding of mulch and enrichment of various shelters and tree branches. The animals were kept under a natural light regime and room temperature (24–26°C) and fed with small rodent chow and water *ad libitum*. Body mass was 20.1 g in male1 and 16.7 g in male2.

Experimental design

Experiments were carried out at the Scientific Department of Moscow Zoo on 15 and 23 July 2013. Both males were tested in both days, singly in a separate room without other animals in an experimental set-up representing a cage 30 × 50 × 100 cm with the back wall made of smooth plastic, the front and side walls made of glass and the rest walls of wire-mesh 10 × 10 mm. The cage contained many straight and branched dry branches of diameter 0.5–5 cm, the cage bottom was covered by a layer of mulch. During test trials, the cage was set vertically or horizontally (for more details of the testing procedure, see Panyutina et al. 2017).

In total, we conducted 13 test trials (7 with male1 and 6 with male2). During a test trial, an animal was released to the cage and was gently provoked to move over the branches with the experimenter's hand. A test trial lasted 2–12 min (mean ± SD = 4.8 ± 3.2 min), depending on the behaviour of the subject animal. All test trials were done between 14:00 and 18:00 at temperatures of 24–26°C; 11 trials at bright light of halogen lamps (2 kW t in total) and 2 trials at natural light from windows. All test trials were audio and video recorded with an ultrasonic recorder and two camcorders simultaneously; the recordings were synchronized by clicker signals. The parallel audio and video recordings at bright light were analysed in a previous study intended to examine how the animals combine the locomotion and the ultrasonic calls (Panyutina et al. 2017).

For audio recordings (sampling rate 768 kHz, 16 bit), we used a Pettersson D 1000X recorder with a built-in microphone (Pettersson Electronik AB, Uppsala, Sweden). During recordings, the distance from a hand-held microphone to a test animal varied between 10 and 50 cm. The microphone was oriented as far as possible close to the muzzle of a tested animal, because the sector for recording ultrasound is very narrow.

Each test trial was recorded as a wav-file. The total duration of audio recordings was 62 min (30 min from male1 and 32 min from male2).

For video recordings, we used simultaneously two camcorders: for the high-definition video (HD-video, 50 fps, shutter speed 1/1000 s, frame size 1920 × 1080 pixels, with soundtrack), we used a JVC GC-PX10 camcorder (Victor Company of Japan, Ltd., Yokohama, Japan) and for the high-speed (HS-video, 300 fps, shutter speed 1/2000 s, frame size 512 × 384 pixels, no soundtrack), we used a Casio EX-F1 camcorder (Casio Computer Co., Ltd., Tokyo, Japan).

Acoustic analysis

With Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany), all acoustic files were inspected for presence of ultrasound. For further acoustic analysis, we selected from all audio files 60 fragments of 0.44–6.2 s (mean ± SD = 2.16 ± 1.40 s) which contained many ultrasonic pulses with a high signal-to-noise ratio. The total duration of the 60 audio fragments was 129.4 s (45 fragments of total duration 89.5 s from male1 and 15 fragments of total duration 39.9 s from male2). Within fragments, we identified bouts of ultrasonic pulses, separated with intervals longer than the intervals between pulses within bouts (Figure 1, Supplementary Audio 1 and 2).

For each bout, we calculated the number of pulses per bout. On the screen with the standard marker cursor in the spectrogram window of Avisoft (sampling frequency 768 kHz, Hamming window, FFT 512 points, frame 50%, overlap 75%, frequency resolution 1500 Hz, time resolution 0.17 ms), we measured the duration of each bout (bout-dur), from the beginning of the start pulse to the end of the last pulse, and then the time interval to the next bout (bout-int), from the end of the last pulse of a previous bout to the beginning of the start pulse of the next bout. Also, we calculated the period between bouts (bout-period), as the sum of the duration of a bout and the interval to the next bout (Figure 1). Measurements were exported automatically to Microsoft Excel (Microsoft Corp., Redmond, WA, USA). In total, we analysed 1481 bouts (1035 from male1 and 446 from male2).

The acoustics of individual ultrasonic pulses were measured in a subset of 234 bouts of highest quality (131 bouts of male1 and 103 bouts of male2). Of those 234 bouts, 80 bouts were 1-pulse bouts, 60 bouts were 2-pulse bouts, 50 bouts were 3-pulse bouts, 30 bouts were 4-pulse bouts and 14 bouts were 5-pulse bouts. As a preliminary visual inspection showed that below 10 kHz there was no signal, only noise, we applied a high-pass filter to ease analysis. After applying the high-pass filter at 10 kHz, we measured for each pulse the maximum fundamental frequency (fmax) and the minimum fundamental frequency (fmin) with the standard marker cursor in the spectrogram window of Avisoft (sampling frequency 768 kHz, Hamming window, FFT 512 points, frame 50%, overlap 93.75%, frequency resolution 1500 Hz, time resolution 0.04 ms) (Figure 1). Then, we calculated the depth of fundamental frequency modulation as df = fmax − fmin. Applying the automated parameter measuring option of Avisoft, we measured the pulse duration (dur), the duration to the maximum amplitude of the pulse in % of the entire pulse duration (distomax), the maximum amplitude frequency of a pulse (fpeak) and the bandwidth of the maximum amplitude frequency at distance −10 dB of maximum (bandw) (Figure 1). For bouts with more than one pulse, we additionally measured the period between pulses

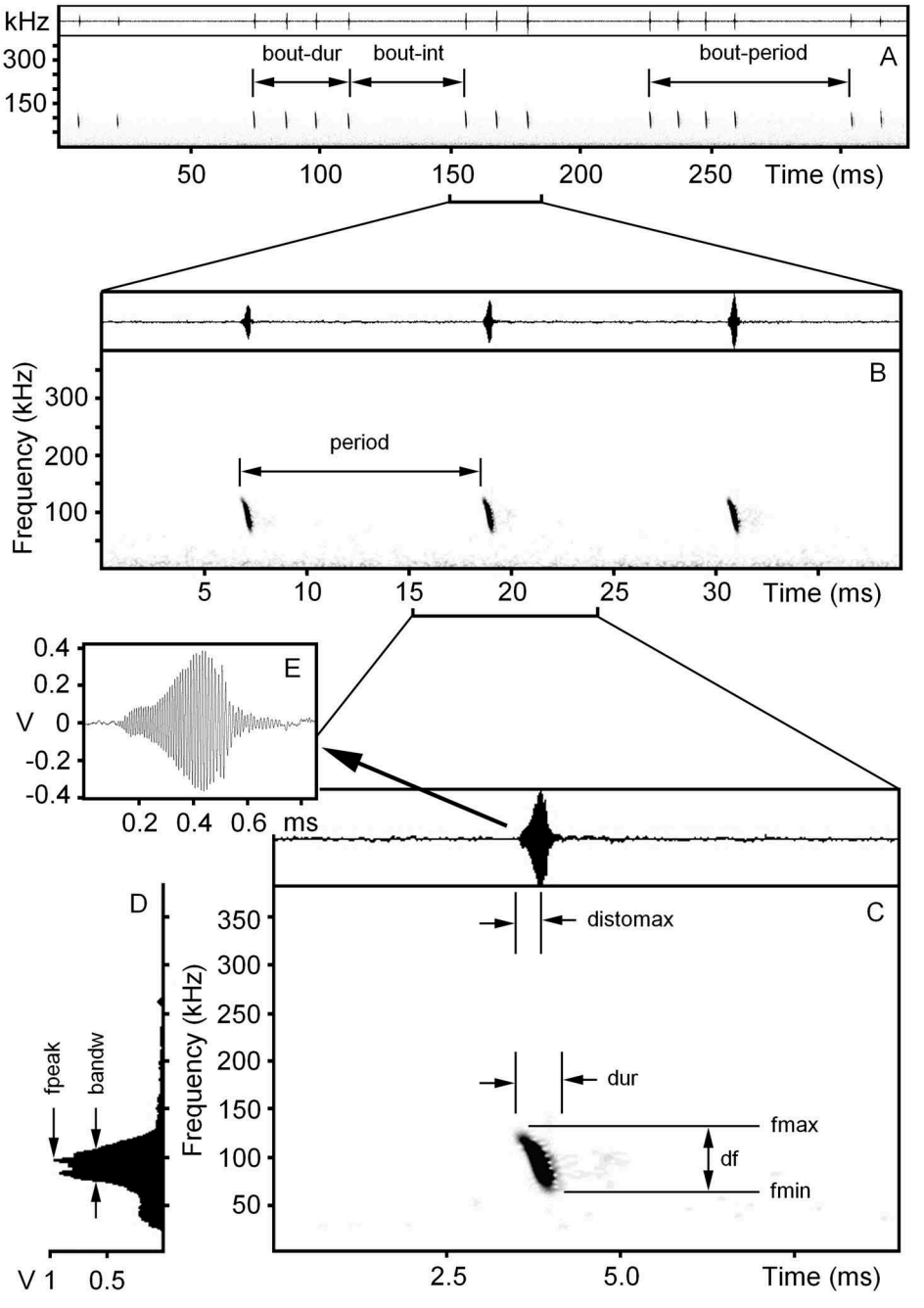


Figure 1. Spectrograms, waveforms and the power spectrum representing acoustic patterns and acoustic variables measured from individual ultrasonic pulses and pulse bouts of the Vietnamese pygmy dormouse *Typhlomys chapensis*. (A) Natural sequence of five ultrasonic bouts; bout-dur: the bout duration; bout-int: the interval to the next bout; bout-period: the period between bouts. (B) Expanded spectrogram of the three-pulse bout depicted on (A); period – the period between pulses. (C) and (D) Individual ultrasonic pulse; fmax: the maximum fundamental frequency; fmin: the minimum fundamental frequency; df: the depth of fundamental frequency modulation; dur: the pulse duration; distomax: the duration to the pulse maximum amplitude; fpeak: the maximum amplitude frequency; bandw: the bandwidth of the maximum amplitude frequency. (E) Expanded waveform of the pulse depicted on C.

(period), from the beginning of a pulse to the beginning of the next pulse (Figure 1). In total, we analysed 540 pulses (325 pulses from male1 and 215 pulses from male2).

Statistics

Statistical analyses were carried out with STATISTICA, v. 8.0 (StatSoft, Inc., Tulsa, OK, USA). Means are given as mean ± SD. Significance levels were set at 0.05, and two-tailed probability values are reported. As the animal sample was too small for individual-based analyses (only two animals), we used in the statistical analyses pooled samples of bouts and pulses from both individuals (Leger and Didrichsons 1994). A Kolmogorov–Smirnov test showed that the distribution of all acoustic parameters of bouts and pulses did not depart from normality ($p > 0.05$), so we could apply parametrical tests. We used a one-way ANOVA with a Tukey HSD test to estimate the effect of the number of pulses per bout on bout acoustics. We used a nested design of ANOVA with a Tukey HSD test with number of pulses per bout nested within pulse position (first, second, third etc.) in bout to assess effect of these factors on pulse acoustics.

Results

Ultrasonic pulses of *Typhlomys* were organized in bouts (Figure 1). As 97.0% of measured intervals between bouts ($n = 1481$) were less than 0.3 s, we accepted that bouts belongs to the same series when intervals between them did not exceed 0.3 s and to different series when intervals between them were longer 0.3 s. For further analysis, we used intervals and periods, taken from bouts within series ($n = 1398$).

Bouts ($n = 1481$) consisted of 1–6 pulses (Table 1). Almost half of bouts consisted of only one pulse, and the percentage of multi-pulse bouts was inverse to the number of pulses per bout. Only 2 of the 1481 bouts consisted of 6 pulses, so we excluded them from the following statistical analyses.

ANOVA revealed effects of the number of pulses per bout on bout duration and inter-bout interval, but not on bout period ($n = 1398$ bouts). Bouts with more pulses were respectively longer. The longer were the bouts, the shorter were the inter-bout intervals, what resulted in nearly constant (80.0 ± 2.9 ms) period from the start of a

Table 1. Percentages of bouts with different numbers of pulses per bout, mean ± SD values of bout variables and one-way ANOVA results for comparison between bout variables.

		Bout variables		
Bouts	*N* bouts (percentage)	bout-dur (ms)	bout-int (ms)	bout-period (ms)
1-pulse bouts	721 (48.7)	0.9 ± 0.2^{a}	80.2 ± 36.9^{a}	81.1 ± 36.9
2-pulse bouts	399 (26.9)	16.1 ± 3.5^{b}	63.2 ± 22.2^{b}	79.2 ± 23.9
3-pulse bouts	229 (15.5)	27.1 ± 4.7^{c}	50.9 ± 12.4^{c}	78.0 ± 15.0
4-pulse bouts	109 (7.4)	35.2 ± 5.0^{d}	44.9 ± 11.4^{c}	80.1 ± 14.1
5-pulse bouts	21 (1.4)	42.3 ± 4.1^{e}	38.5 ± 5.8^{c}	80.8 ± 9.0
6-pulse bouts	2 (0.1)	66.45 ± 7.0		
ANOVA results	Total 1481	$F_{4,1474} = 6328.43$, $p < 0.001$	$F_{4,1393} = 75.74$, $p < 0.001$	$F_{4,1393} = 0.60$, $p = 0.66$

The same superscripts indicate which bouts did not differ significantly ($p > 0.05$, Tukey HSD test). Designations: bout-dur: the bout duration; bout-int: the interval to the next bout; bout-period: the period between bouts.

previous bout to the start of the next bout (Table 1, Figure 2). Bout period varied from 78 to 81 ms.

Ultrasonic pulses (n = 540) showed a descending pattern of frequency modulation, on average from 127 to 64 kHz, with fpeak at 93 kHz and bandw 34 kHz (Table 2, Figure 1). The decrease of the fundamental frequency was slow at pulse onset and accelerated to its end, what resulted in the convex profile of frequency modulation. Each pulse contained a few dozen of oscillation periods (Figure 1(e)). Pulse duration did not exceed 1 ms, pulse amplitude reached maximum in the middle of a pulse. The mean period to the next pulse for multi-pulse bouts was 13 ms (Table 2). The pulses contained only fundamental frequency band and no harmonics.

ANOVA did not reveal effects of the number of pulses per bout or pulse position (first, second, third etc.) in bout on pulse fmin, fpeak and bandw (Table 2, Figure 3). The fmax and depth of frequency modulation did not depend on the number of pulses per bout but were significantly lower in 1-pulse bouts and start pulses of multi-pulse bouts (n = 234; fmax = 125.5 ± 6.3 kHz and df = 61.6 ± 7.2 kHz) compared to all other pulses (n = 306; fmax = 128.6 ± 5.9 kHz and df = 64.5 ± 7.1 kHz), whereas all other pulses were undistinguishable (Table 2, Figure 3). Similarly, distomax did not depend on the number of pulses per bout but was significantly lower in 1-pulse bouts and in start pulses of multi-pulse bouts (n = 234; 49.6 ± 11.0%) compared to all other pulses

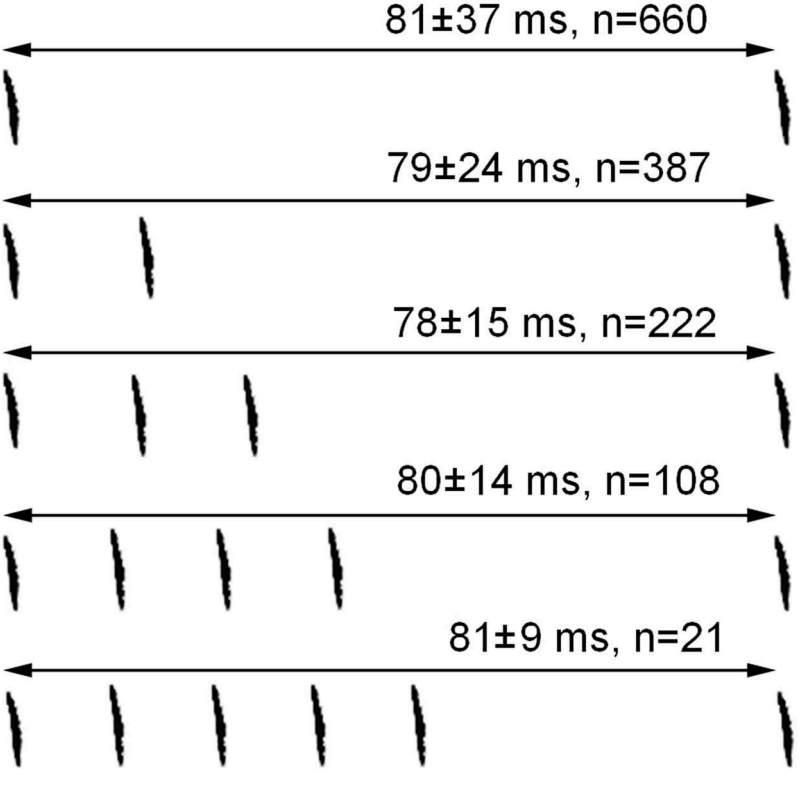


Figure 2. Constancy of bout period irrespective to the number of pulses per bout. The distance from a first pulse of previous bout to the first pulse of a subsequent bout remains always the same.

Table 2. Descriptive statistics (mean ± SD) for acoustic variables of ultrasonic pulses and a nested ANOVA results for comparison between the pulse variables depending on the number of pulses per bout and on pulse position in bout.

			ANOVA results	
Pulse variable	*N*	Mean ± SD	Number of pulses per bout	Pulse position in bout
fmax (kHz)	540	127.3 ± 6.3	$F_{10,\ 525} = 0.22$; $p = 0.99$	**$F_{4,\ 525} = 7.17$; $p < 0.001$**
fmin (kHz)	540	64.1 ± 4.6	$F_{10,\ 525} = 1.68$; $p = 0.08$	$F_{4,\ 525} = 1.38$; $p = 0.24$
df (kHz)	540	63.2 ± 7.3	$F_{10,\ 525} = 0.80$; $p = 0.63$	**$F_{4,\ 525} = 5.37$; $p < 0.001$**
dur (ms)	540	0.68 ± 0.15	**$F_{10,\ 525} = 1.96$; $p < 0.05$**	$F_{4,\ 525} = 0.87$; $p = 0.48$
distomax (%)	540	51.7 ± 11.1	$F_{10,\ 525} = 1.15$; $p = 0.32$	**$F_{4,\ 525} = 3.00$; $p < 0.05$**
fpeak (kHz)	540	93.3 ± 7.4	$F_{10,\ 525} = 1.29$; $p = 0.23$	$F_{4,\ 525} = 0.72$; $p = 0.58$
bandw (kHz)	540	33.6 ± 9.7	$F_{10,\ 525} = 0.87$; $p = 0.56$	$F_{4,\ 525} = 1.23$; $p = 0.28$
period (ms)	306	13.03 ± 3.01	**$F_{6,\ 296} = 15.18$; $p < 0.001$**	**$F_{3,\ 296} = 3.26$; $p < 0.05$**

Significant differences are given in bold. Designations: *N*: number of pulses; fmax: maximum fundamental frequency; fmin: minimum fundamental frequency; df: depth of fundamental frequency modulation; dur: pulse duration; distomax: the duration to the pulse maximum amplitude; fpeak: the maximum amplitude frequency of a pulse; bandw: the bandwidth of the maximum amplitude frequency at distance −10 dB of maximum; period: the inter-pulse period.

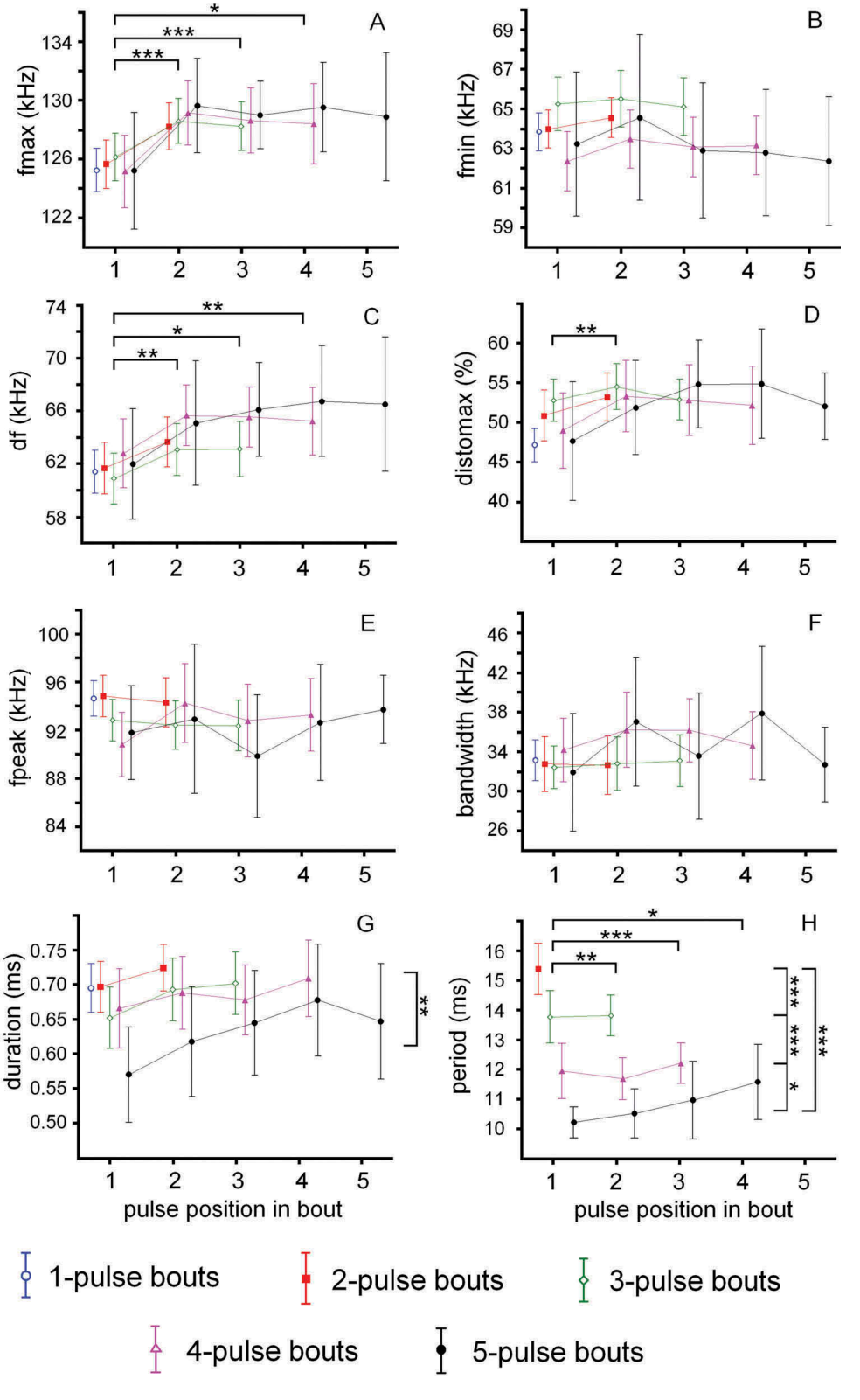
(n = 306; 53.3 ± 10.9%), whereas all other pulses were undistinguishable (Table 2, Figure 3).

In contrast, pulse duration was independent on pulse position in bout but was significantly longer in pulses of 2-pulse bouts (n = 120; 0.71 ± 0.14 ms) compared to pulses of 5-pulse bouts (n = 70; 0.63 ± 0.14 ms) (Table 2, Figure 3). The effect of the number of pulses per bout on inter-pulse period was much stronger compared to the effect of pulse position in bout (Table 2). The longest inter-pulse period was found in 2-pulse bouts (n = 60; 15.39 ± 3.37 ms), and the period steadily shortened with the increase of number of pulses per bout. The inter-pulse period comprised 13.80 ± 2.75 ms (n = 100) in 3-pulse bouts, 11.95 ± 2.08 ms (n = 90) in 4-pulse bouts and 10.83 ± 1.81 ms (n = 56) in 5-pulse bouts; differences were significant for all comparisons (Figure 3). In the multi-pulse bouts, the significantly longer inter-pulse periods occurred after the start pulses (n = 154; 13.73 ± 3.39 ms) than after pulses in any other position (n = 152; 12.31 ± 2.36 ms); the inter-pulse periods after the non-start pulses were undistinguishable (Figure 3).

In addition to the bouts of ultrasonic pulses, we detected a few other *Typhlomys* ultrasonic calls (less than 10 calls in total), representing short high-frequency squeaks (80–100 kHz) with a broken contour of fundamental frequency. These calls were excluded from the analyses.

Discussion

The detailed acoustic analysis revealed an unusual organization of *Typhlomys* ultrasonic bouts, where the period from the start of a previous bout to the start of the next bout was constant regardless of the number of pulses per bout (Figure 2). At the same time, the period between pulses shortened with an increase of the number of pulses per bout. Both single pulses and start pulses of multi-pulse bouts were lower in maximum fundamental frequency and less deeply modulated compared to other pulses that were undistinguishable from each other. Duration, minimum fundamental frequency, peak frequency and bandwidth were not affected by pulse position within bout.


A
fmax (kHz)
B
fmin (kHz)
C
df (kHz)
D
distomax (%)
E
fpeak (kHz)
F
bandwidth (kHz)
G
duration (ms)
H
period (ms)
pulse position in bout
pulse position in bout
1-pulse bouts
2-pulse bouts
3-pulse bouts
4-pulse bouts
5-pulse bouts

In bats, echolocation calls are very variable in their acoustic structure (Fenton and Bell 1981; Jones and Teeling 2006; Surlykke and Kalko 2008; Fenton 2013). The *Typhlomys* pulse frequency range (from 127 to 64 kHz) fits to the upper part of frequency range of bat echolocation calls (Fenton and Bell 1981; Fenton 2013; Jakobsen et al. 2013b; Thiagavel et al. 2017). Compared to *Typhlomys* with a body mass of 15–20 g (this study), bats that produce similar calling frequencies as *Typhlomys* are either smaller (3–9 g) or are of similar size (9–15 g): trident bats *Cloeotis percivali* (Fenton and Bell 1981; Thiagavel et al. 2017), roundleaf bats of genus *Hipposideros* (Fenton and Bell 1981; Pavey et al. 2001; Taylor et al. 2005), Ussuri tube-nosed bats *Murina ussuriensis* (Fukui et al. 2004), lesser horseshoe bats *Rhinolophus hipposideros* (Parsons and Jones 2000; Obrist et al. 2004) and soprano pipistrelle *Pipistrellus pygmaeus* (Jakobsen et al. 2013b). We found that peak frequency of ultrasonic pulses of *Typhlomys* (93 kHz) was higher than in vespertilionid bats of comparable size, thus fitting approximately to a bat weighing 4–5 g (Thiagavel et al. 2017).

Ultrasonic pulses of *Typhlomys* were strongly reminiscent of *Murina* and *Myotis* bat FM (frequency modulated) ultrasonic echolocation calls (Figure 4). For example, in two *Murina* species, the maximum fundamental frequency ranges of 105–113 kHz, the minimum of 44–51 kHz, the peak frequency of 51–87 kHz and call duration 1.7–1.8 ms (Obrist et al. 2004). In nine *Myotis* species, the maximum fundamental frequency ranges of 74–121 kHz, the minimum of 14–42 kHz, the peak frequency of 37–73 kHz and call duration of 2.2–6.0 ms (Parsons and Jones 2000; Russo and Jones 2002; Obrist et al. 2004). As *Myotis* calls are increasing in frequency and decreasing in duration at approaching prey (Siemers and Schnitzler 2004), they reach the frequency range of *Typhlomys* ultrasonic pulses but still remain much longer in duration. Thus, compared to *Murina* bats (Fukui et al. 2004) and *Myotis* bats (Parsons and Jones 2000; Russo and Jones 2002; Obrist et al. 2004), the *Typhlomys* calls were higher in frequency and shorter in duration (Figure 4).

Another remarkable distinction from bat FM ultrasonic echolocation calls was the convex contour of frequency modulation, with a slower decrease of fundamental frequency at the beginning than at the end of a call in *Typhlomys*. Contrastingly, for bats, a concave contour of frequency modulation is more characteristic, whereas a convex contour occurs very rarely (Parsons and Jones 2000; Obrist et al. 2004).

This study confirmed previous findings (Panyutina et al. 2017) that ultrasonic pulses of *Typhlomys* practically lack harmonics. In the FM calls of bats including *Myotis*, which are similar in structure to the *Typhlomys* calls, harmonics are well visible (Obrist et al. 2004; Siemers and Schnitzler 2004) and play an important role for distinguishing echoes from the own FM calls (Hiryu et al. 2010; BatesAkre et al. 2011; Fenton et al. 2011).

Figure 3. Values (mean ± 2SE) of pulse variables depending on the number of pulses per bout and pulse position in bout. (a) Maximum fundamental frequency, (b) minimum fundamental frequency, (c) depth of fundamental frequency modulation, (d) the duration to the pulse maximum amplitude, (e) the maximum amplitude frequency of the pulse, (f) the bandwidth of the maximum amplitude frequency at distance −10 dB of maximum, (g) pulse duration, (h) the inter-pulse period. Results for comparison of acoustic variables between pulses (two-way ANOVA with Tukey HSD test) are given with brackets, where ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.

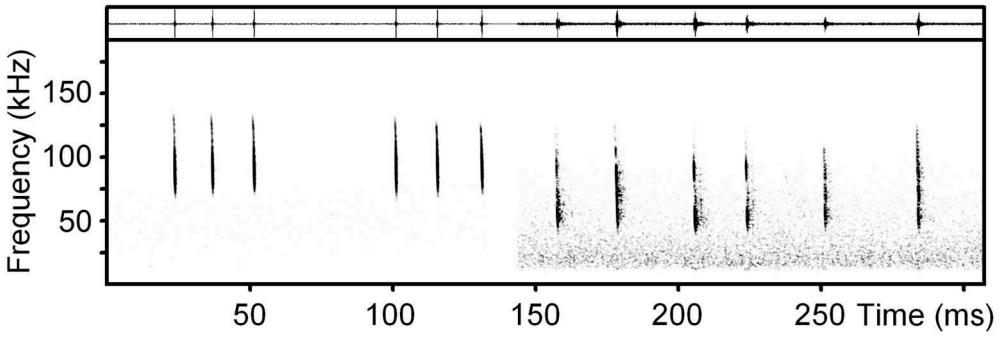


Figure 4. Spectrogram (below) and waveform (above) illustrating similar acoustic patterns between the Vietnamese pygmy dormouse *Typhlomys chapensis* (two three-pulse ultrasonic bouts) and the Hilgendorf's tube-nosed bat *Murina hilgendorfi* ultrasonic calls (six ultrasonic pulses). The ultrasonic echolocation calls of Hilgendorf's tube-nosed bat were recorded in Moscow Zoo using an automated recording device SongMeter SM2BAT+ (384 kHz, 16 bit), established for one night on a top of a wire-mesh indoor enclosure, containing a group of nine individual bats (six males, three females). The bats originated from Barsukovskaya cave, Novosibirsk region, Russia (54°22′N, 83°57′E). The spectrogram was created with a Hamming window, 384 kHz sampling rate, FFT 1024 points, frame 50% and overlap 93.75%. A .wav file of the calls is available in Supplementary Audio 3.

In addition, the similarity of *Typhlomys* ultrasonic pulses with FM bat calls suggests their production in the larynx (Suthers and Fattu 1982; Harrison 1995; Mergell et al. 1999; Suthers 2004). Production with tongue clicks (Egyptian fruit bats *Rousettus aegyptiacus*, Yovel et al. 2011; shrews, Gould 1969; Zaytseva et al. 2015) or another non-laryngeal mechanism (odontocetes, Cranford et al. 1996, 2011; Madsen et al. 2013; Ridgway et al. 2015) is less probable. In bats, the echolocation pulses are produced with vocal membranes on the vocal folds (Suthers and Fattu 1982; Harrison 1995; Mergell et al. 1999; Suthers 2004). Further research investigating the anatomy of the vocal apparatus could reveal or reject the presence of vocal fold membranes in *Typhlomys*. However, the lack of harmonics in *Typhlomys* ultrasonic pulses points to a different mechanism of sound production, e.g. the so-called edge-tone mechanism found in some other rodents (Riede 2011, 2013; Riede et al. 2017).

Another distinction from bat calls is that *Typhlomys* pulses are very faint. This estimation is imprecise, as it was not supported by direct measurements of sound pressure level and comes from the observation that *Typhlomys* ultrasonic pulses could not be heard using a bat detector. In addition, these pulses could only be recorded at close distance (10–50 cm) to the calling individual and at high recording levels. At the same time, in bats, the echolocation calls are very intense, comprising in many species 100–110 dB SPL (Sound Pressure Level) and even over 130 dB SPL in 10 cm from the mouth (Holderied and Von Helversen 2003; Surlykke and Kalko 2008; Fenton 2013; Jakobsen et al. 2013a). Consistently, bat FM echolocation calls may be more intensive because they are produced through the widely opened mouth (Neuweiler 2003), whereas no mouth opening was visible on our high resolution videos of calling *Typhlomys* analysed in the study by Panyutina et al. (2017). So, *Typhlomys* apparently produces its ultrasonic pulses through the nose. Further studies are necessary to

measure the sound pressure level of *Typhlomys* ultrasonic pulses and to confirm the nasal emission and to examine the hearing abilities of *Typhlomys*.

The high-frequency hearing limit (the highest frequency audible at 60 dB SPL) is higher in echolocating bats and whales than in non-echolocating mammals with comparable functional interaural distance (Heffner et al. 2001; Heffner and Heffner 2008). Hearing abilities of *Typhlomys* have not yet been investigated, but similar-sized rodents, domestic mice *Mus musculus*, are known to display a high-frequency hearing limit of 92 kHz (Heffner and Masterton 1980; Heffner and Heffner 2010). So, we assume that *Typhlomys* can hear higher frequencies than the mice which lack the ultrasonic pulses in their vocal repertoire (Arriaga and Jarvis 2013; Hammerschmidt et al. 2012; Hoffmann et al. 2012). In this case, *Typhlomys* would be capable of hearing echoes of own ultrasonic pulses and use them for call-based orientation.

The most remarkable trait of *Typhlomys* ultrasonic pulses was their organization in bouts of more than one pulse, following each other with a constant period of 80 ms. This period might reflect the respiratory rate of *Typhlomys*. Consistently, rodents produce ultrasonic trills consisting of a few short calls within a single expiration (Riede 2013). Whereas *Typhlomys* produce bouts of uniform pulses emitted with a constant bout-to-bout period (this study), sequences of echolocation calls of bats and whales are rarely produced in bouts and both the call-to-call period and call structure change during the phase of approaching prey (Kalko 1995; Kalko et al. 1998; Holderied et al. 2005; Fenton 2013; Ratcliffe et al. 2013; Wisniewska et al. 2014; Ridgway et al. 2015). During the approach phase towards the prey, these flying and swimming mammals produce so-called buzzes, rapid pulse sequences resulting from a shortening of the inter-pulse periods (Kalko 1995; Kalko et al. 1998; Fenton 2013; Ratcliffe et al. 2013; Wisniewska et al. 2014; Ridgway et al. 2015).

There is some evidence of ultrasonic multi-pulse bouts in whales (Li et al. 2005; Lammers and Castellote 2009; Finfer et al. 2012); however, their function still remains unclear. At the same time, audible (below 10 kHz) multi-click (from 3 to 56 clicks) trains of hippopotamus *H. amphibius* (Barklow 1997; Maust-Mohl et al. 2015) function for echo-ranging when searching for food in murky waters where visibility is poor (Maust-Mohl et al. 2015, 2018). This is reminiscent of *Typhlomys* which is permanently facing the situation in which vision cannot be used for orientation. Similar to ultrasonic bouts of *Typhlomys*, the audible underwater trains produced by hippos also lacked the terminal buzz phase. Distinctive to *Typhlomys*, hippos never produced individual clicks (Maust-Mohl et al. 2018).

It seems probable that *Typhlomys* uses the ultrasonic pulses only for orientation, at least in our experiments. The pulses have a low intensity compared to the high-intensity calls of bats, so they could only allow an estimation of the distance to branches that are very close to the calling animal (Panyutina et al. 2017). So, these pulses are probably inapplicable for detecting and catching prey, distinctive to echolocation calls of bats and whales (Kalko 1995; Fenton 2013; Berta et al. 2014). Whereas bats and whales shorten intervals between pulses at approaching to prey (Kalko 1995; Fenton 2013), *Typhlomys* evidently uses a different way of adjusting their spatial location. Compared to bats, the speed of *Typhlomys* locomotion is not so high. Therefore, they do not need to vary strongly the period between the ultrasonic pulses. At locomotion, they increase the use

of multi-pulse bouts relative to single pulses without shortening the intervals between bouts (Panyutina et al. 2017).

Bouts and pulses of *Typhlomys* also differ from ultrasonic calls of species, using them as cryptic anti-predator alarms. These animals are Sunda colugos *Galeopterus variegatus* (Miard et al. 2018) and two ground squirrel species of the genus *Spermophilus* (Wilson and Hare 2004, 2006; Matrosova et al. 2012). Unlike *Typhlomys*, in these species, the ultrasonic calls display an inverse U-shaped contour of frequency modulation.

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Data accessibility

Audio files supporting this article have been uploaded as supplementary material.

Disclosure statement

No potential conflict of interest was reported by the authors.

Ethics

For all experiments, we adhered to the 'Guidelines for the treatment of animals in behavioural research and teaching' (2006, Animal Behaviour, 71, 245–253). This study was approved by the Committee of Bio-ethics of Lomonosov Moscow State University (research protocol 2011-36).

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