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Effects of free-ranging, semi-captive and captive management on the acoustics of male rutting calls in Siberian wapiti *Cervus elaphus sibiricus*

Olga S. Golosova¹ · Ilya A. Volodin^{1,2} · Inna L. Isaeva³ · Elena V. Volodina²

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Abstract In male European red deer *Cervus elaphus*, rutting calls that are responsible for male reproductive success are higher in fundamental frequency in captivity than in the wild. This study compares the acoustics of stag rutting calls among wild-living, semi-captive and captive stags within an Asian subspecies of *C. elaphus*, the Siberian wapiti *Cervus elaphus sibiricus*. Male Siberian wapiti rutting calls (bugles) were collected using automated recording systems in three populations (wild-living, semi-captive and captive), all originated from the Altai/Khakasian region of Central Siberia (Russia). Selected 435 bugles (145 per population) were analysed spectrographically for 14 variables of the bugle high (>1 kHz) fundamental frequency (g0) and scored for shape of g0 contour: trapeze, descending or saddle. Among bugles, 74.3% had the trapeze contour, 23.7% had the descending contour and 2.1% had the saddle contour. The additional low (<0.2 kHz) fundamental frequency (f0) was found in 76.1% of bugles, whereas deterministic chaos was found in 16.8% of bugles. Bugles of captive stags were shortest and highest in frequency. The captive

management selectively affected only bugles with the trapeze contour, whereas bugles with descending contour remained unaffected by variations of deer holding regime. Stag rutting bugles are subspecies-specific and may therefore serve as acoustic indicator of subspecies for the Siberian wapiti among other Asian and American subspecies of wapiti.

Keywords Red deer · Vocalization · Emotional arousal · Social effects · Between-population differences

Introduction

Vocalizations of ungulates represent potential indicators of animal welfare (Watts and Stookey 1999; Manteuffel et al. 2004; Briefer 2012; Briefer et al. 2015; Padilla de la Torre et al. 2015). Different management practices (free-ranging or farmed in enclosures of different sizes) affect social behaviour of red deer *Cervus elaphus*, primarily dispersion and local density (Coulson et al. 1997, 2004; Catchpole et al. 2004; Nussey et al. 2006; Robbins et al. 2016), as well as the acoustics of rutting vocalizations (Volodin et al. 2015a) and vocal activity (Volodin et al. 2016a). Although the Siberian wapiti *Cervus elaphus sibiricus* is the most important cervid species among farmed production animals of Russia, China and Kazakhstan that is intensively bred for velvet antlers (Lunitsin and Borisov 2012; Kim et al. 2015), welfare standards are not yet established for this subspecies. Studying basic vocal variation of rutting calls in wild-living and captive *C. e. sibiricus* provides important reference information, representing a start point, against which further research would compare vocal parameters recorded under conditions of poor or good welfare.

In red deer, rutting calls represent an important part of male courtship behaviour (Clutton-Brock et al. 1987, 2002; Frey

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✉ Ilya A. Volodin
volodinsvoc@gmail.com

¹ Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Vorobiev Gory, 1/12, Moscow 119234, Russia

² Scientific Research Department, Moscow Zoo, B. Gruzinskaya str., 1, Moscow 123242, Russia

³ Khakasskiy State Nature Reserve, Tsukanov str., 164, Abakan 655017, Russia

et al. 2012) and are responsible for male reproductive success (Reby and McComb 2003). During the rut, red deer stags vocalize to attract females and to compete with other stags for female harems (Clutton-Brock and Albon 1979). Rut vocal displays influence the dates of the ovulation in hinds, shifting them to earlier dates (McComb 1987) and help to prevent undesirable combats and energy costs for elucidating the rank of competitive males (Clutton-Brock and Albon 1979; Reby and McComb 2003; Reby et al. 2005) by advertising male quality (Bowyer and Kitchen 1987; Clutton-Brock and Albon 1979; Reby and McComb 2003).

Stags of the two related species, *Cervus elaphus* and *C. canadensis* produce their rutting calls in bouts that include from one to a few calls (Reby and McComb 2003; Kidjo et al. 2008; Frey et al. 2012). The longest and the most high-frequency calls are emitted via a widely opened mouth and represent the main calls in their bouts (Reby and McComb 2003; Frey et al. 2012).

In different parts of the large distribution area, stag rutting calls are different in the acoustic structure. The high-pitched rutting calls (bugles) with a high fundamental frequency g_0 (between 600 and 2500 Hz) are produced by Siberian wapiti *C. e. sibiricus*, Far-East wapiti *Cervus elaphus xanthopygus* and American wapiti *Cervus elaphus canadensis* = *C. canadensis* (Struhsaker 1968; Bowyer and Kitchen 1987; Feighny et al. 2006; Frey and Riede 2013; Volodin et al. 2013b, 2015b, 2016b; Reby et al. 2016). The low-pitched rutting calls (roars) with a low fundamental frequency f_0 (between 40 and 380 Hz) are produced by European subspecies of *C. elaphus* (Long et al. 1998; Reby and McComb 2003; Kidjo et al. 2008; Frey et al. 2012; Bocci et al. 2013; Passilongo et al. 2013; Della Libera et al. 2015; Sibiryakova et al. 2015; Volodin et al. 2015a).

Biphonic rutting calls, comprising both the high and low fundamental frequencies (respectively, g_0 and f_0) in their spectra, are produced by Central Asian subspecies *Cervus elaphus bactrianus* (Nikol'skii 1975; Nikol'skii et al. 1979; Volodin et al. 2013a) as well as by the Siberian and North American wapiti (Volodin et al. 2013b; Reby et al. 2016). Among ungulates, similarly wide ranges of fundamental frequencies are only known in bovids, domestic bulls *Bos taurus* (Hall et al. 1988; Volodin et al. 2017). For either cervids or bovids, mechanisms for producing the f_0 , g_0 and the biphonic calls, are still under debates (Riede and Titze 2008; Riede et al. 2010; Titze and Riede 2010; Frey and Riede 2013; Volodin et al. 2013a, b; Herbst 2014; Reby et al. 2016).

Aside biphonation, rutting calls of both *C. elaphus* and *C. canadensis* may contain other kinds of nonlinear vocal phenomena: subharmonics, frequency jumps and deterministic chaos (Wilden et al. 1998). Accordingly to the degree of presence of deterministic chaos, roars of European red deer may be subdivided into common roars

with a clearly visible f_0 and its harmonics, and harsh roars, where f_0 is masked with deterministic chaos and/or subharmonics for most part of call duration (Reby and McComb 2003; Frey et al. 2012). Similarly, bugles of North American and Siberian wapiti may be subdivided into common bugles with a clearly visible g_0 and its harmonics, and harsh bugles, where g_0 is masked with deterministic chaos for most part of call duration (Feighny et al. 2006).

Variation of stag rutting calls has been thoroughly investigated across subspecies (Struhsaker 1968; Bowyer and Kitchen 1987; Reby and McComb 2003; Feighny et al. 2006; Kidjo et al. 2008; Frey et al. 2012; Bocci et al. 2013; Passilongo et al. 2013; Volodin et al. 2013a, 2015b, 2016b; Della Libera et al. 2015). Between populations within subspecies, a very low degree of variation may be inferred based on three studies of Iberian red deer *Cervus elaphus hispanicus* (Frey et al. 2012; Passilongo et al. 2013; Volodin et al. 2015a) compared to populations belonging to other subspecies of red deer (Reby and McComb 2003; Kidjo et al. 2008; Della Libera et al. 2015). In spite of the overall low between-population variation within the Iberian red deer, the fundamental frequency (f_0) was found higher in wild-living compared to farmed stags, probably as effect of elevated emotional arousal in captivity (Volodin et al. 2015a). For Siberian wapiti, while the overall vocal activity in rut period was found much lower for captive compared to semi-captive stags (Volodin et al. 2016a), the effects of captivity on the acoustics of rutting calls (bugles) were not yet investigated.

Siberian wapiti are large animals with withers height of stags up to 155 cm and stag body mass up to 416 kg (Fedosenko 1980). Wild Siberian wapiti inhabit mountain taiga to the south-east of Ural Mountains in Russia, Kazakhstan and China including Altai, Sayan Mountains, Lake Baikal region up to southern Yakutia (Stepanova 2010; Kuznetsova et al. 2012). Rutting calls of adult male Siberian wapiti are high-frequency bugles, with the maximum g_0 of 1.20–1.45 kHz, mean g_0 about 960 Hz, minimum g_0 about 0.3 kHz and duration about 3.03–3.07 s (Nikol'skii 2011; Volodin et al. 2013b, 2016b). On their natural breeding grounds in Siberia, the g_0 of stag rutting bugles of Siberian wapiti propagates by a distance of 1.5 km and can be qualitatively recorded by automated recording systems in radius of 1 km (Volodin et al. 2013b, 2016a). Some bugles of Siberian wapiti comprise an additional low (<0.2 kHz) fundamental frequency (f_0) (Nikol'skii 2011; Volodin et al. 2013b); however, the occurrence of f_0 in the bugles has not yet been studied to date. The purpose of this study was to compare the acoustics of Siberian wapiti stag rutting bugles for three populations that differed by deer management: wild-living, semi-captive and captive.

Materials and methods

Study sites and dates

Siberian wapiti stag rutting calls were collected with automated recording systems Song Meter SM2+ (Wildlife-Acoustics Inc., Maynard, MA, USA) in three study sites (three populations), differing by deer management (wild-living, semi-captive and captive), in rut periods of 2013 and 2015. All stags were pure Siberian wapiti originated from the same Altai/Khakasian region (Central Siberia, Russia).

Stags of the wild-living native population were recorded from 11 September to 10 October 2013 in the buffer zone of Khakasskiy State Nature Reserve, Republic of Khakasia (52° 07' N, 89° 32' E). This study site represented West Sayan Mountain taiga at altitude 1600–1700 m covered by forest of *Abies* sp. and *Pinus* sp. with large clearings. No supplementary food was provided. The population density in rut period 2011 comprised 0.00206 deer/ha (Kazakov 2012).

Stags of the semi-captive translocated population were recorded from 3 September to 11 November 2013 at Tver region (56° 30' N, 35° 27' E). This study site represented 5000-ha enclosed property covered by forest of *Abies* sp. and *Betula* sp. with large fields (former agriculture grounds). This population originated in 2006 from a few dozen Siberian wapiti translocated from Altai farms and in 2013 comprised approximately 400 animals. Supplementary food was only provided in winter, out of rut period. The population density in rut period of 2013 comprised 0.08 deer/ha.

Stags of the captive translocated population were recorded from 6 September to 30 October 2015 at Kostroma region (58° 24' N, 43° 15' E). This study site represented 70-ha enclosed property of former agricultural grounds with gardens and forest of *Populus* sp., *Pinus silvestris*, and *Salix* sp. This population originated in 2010 from a few dozen Siberian wapiti translocated from Altai farms and in 2015 comprised 140 animals, including 38 stags, 57 hinds and 45 calves. Supplementary food was provided every day, including rut period. The population density in rut period of 2015 comprised 2.0 deer/ha.

Data collection

Three stationary automated recording systems Song Meter SM2+ (one in each study site/population) were mounted on trees in places of most active rut at 2 m above the ground. Each recording system was equipped with two omnidirectional microphones, fixed horizontally at 180° to each other. The automated recording systems were set at maximum possible sensitivity, so potentially collected all stag rutting calls from the distance of about 1 km. The acoustic recording (22.05 kHz, 16 bit, stereo) was scheduled for 5 min/30 min (for wild-living stags) or 5 min/h (for semi-captive and captive

stags), respectively, 240 or 120 min in total per 24 h. Each 5-min recording was stored as wav-file. In total, during the respective rut periods, we collected 1267 5-min files (105.6 h of recording) for wild-living stags, 1680 5-min files (140 h of recording) for semi-captive stags and 1320 5-min files (110 h of recording) for captive stags.

For acoustic analyses, we selected 435 stag rutting bugles (145 per study site/population) from 62 files for wild-living stags, 43 files for semi-captive stags and 72 files for captive stags. For the wild-living stags, we took all available bugles of good quality, whereas for the semi-captive and captive stags, we selected calls of good quality from different files along the rut period, to decrease potential pseudoreplication due to taking calls from the same individuals. All selected bugles were of good quality, not disrupted by wind or the calls of other animals, recorded with an appropriate level of recording and with signal-to-noise ratios sufficient for analysis of all acoustic variables measured in this study. The selected bugles were recorded when animals were in vicinity to the microphones; calls of poor quality recorded at far distance were not included in the acoustic analyses. Particular individuals could not be discriminated from the automated recordings, so the total number of recorded stags remained unknown.

Acoustic analyses

The acoustic variables were measured using Avisoft SASLab Pro software v. 5.2.07 (Avisoft Bioacoustics, Berlin, Germany). Before acoustic analysis, the bugles were downsampled to 11.025 kHz for better frequency resolution and high-pass filtered at 50 Hz to reduce the low-frequency background noise. Spectrograms were created with Hamming window, fast Fourier transform (FFT) 1024 points, frame 50% and overlap 93.75%, frequency resolution 10 Hz, temporal resolution 5.8 ms by using Avisoft. Measurements were exported automatically to Microsoft Excel (Microsoft Corp., Redmond, WA, USA).

Initial visual inspection of spectrograms revealed two clear and independently varying periodicities (fundamental frequencies). Following the study of North American wapiti (Reby et al. 2016), the lower periodical source is hereafter referred to as f_0 , and the higher periodical source is referred to as g_0 .

For each of the 435 bugles, we measured the same set of 14 g_0 -related acoustic variables: 4 temporal, 6 frequency and 4 power variables (Fig. 1). We measured the total duration of each bugle (duration), the duration from bugle onset to bugle plateau (dur_up), the duration of bugle plateau (dur_plat) and the duration from the end of bugle plateau to the end of the bugle (dur_down) manually on the screen with the standard marker cursor in the spectrogram window. Then, we performed measurements of the g_0 -related variables, the beginning ($g_0\text{beg}$), plateau ($g_0\text{plat}$), final ($g_0\text{end}$), maximum

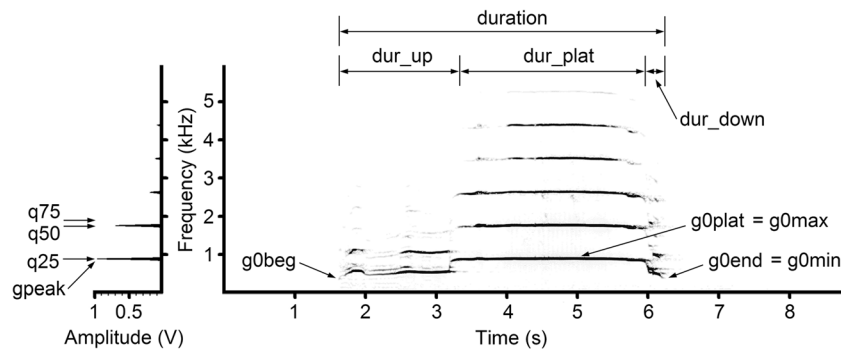


Fig. 1 Measured acoustic variables for rutting bugles of male Siberian wapiti. Spectrogram (*right*) and mean power spectrum of call plateau (*left*). Designations: *duration* bugle duration; *dur_up* bugle duration from onset to plateau; *dur_plat* plateau duration; *dur_down* duration from the end of bugle plateau to the end of the bugle; *g0beg* fundamental frequency at the onset of a call; *g0plat* fundamental frequency of call plateau; *g0end* fundamental frequency at the end of a

call; *g0max* maximum fundamental frequency; *g0min* minimum fundamental frequency; *gpeak* peak frequency of plateau; *q25* lower power quartile of plateau value; *q50* medium power quartile of plateau; *q75* upper power quartile of plateau value. The spectrogram was created at 11.025 kHz sampling frequency, fast Fourier transform (FFT) 1024, Hamming window, frame 50% and overlap 93.75%

(*g0max*) and minimum (*g0min*) fundamental frequencies manually on the screen with the reticule cursor. We also measured the *g0mean* by using the Praat DSP package (Boersma and Weenink 2013) following Reby and McComb (2003). The *g0* was tracked using a cross-correlation algorithm (to Pitch (cc) command in Praat), the time step in the analysis was 0.01 s; the lower and upper limits of the *g0* range were 100–2000 Hz. For the bugle plateau, we created the power spectrum in Avisoft, from which we automatically measured the peak frequency (*gpeak*) and the lower (*q25*), medium (*q50*) and upper (*q75*) quartiles, covering, respectively, 25, 50 and 75% of the energy of the call plateau spectrum (Fig. 1).

Each bugle was checked for presence/absence of the additional (low) fundamental frequency (*f0*) or its combinatory frequency bands resulting from interaction of *f0* and *g0* (Wilden et al. 1998; Frey et al. 2016; Reby et al. 2016). For calls, either containing *f0* or the linear combinations of *f0* with *g0*, we additionally measured two *f0*-related variables: the maximum (*f0max*) and minimum (*f0min*) manually on the screen with the reticule cursor (if the *f0* band was visible on the spectrogram) (Fig. 2), otherwise we measured the visible on the spectrogram linear combinatory bands of *g0* and *f0* and

then calculated the respective *f0max* and *f0min* (Volodin and Volodina 2002; Frey et al. 2016). In addition, in each bugle, we scored presence/absence of deterministic chaos (Fig. 2), responsible for appearance of harsh bugles (Wilden et al. 1998; Feighny et al. 2006). We scored the presence of *f0* and/or deterministic chaos only in cases where the total duration of the call portions bearing these nonlinear phenomena was over 10% of the total bugle duration.

Statistical analyses

Statistical analyses were made with STATISTICA, v. 8.0 (StatSoft, Tulsa, OK, USA); all means are given as mean \pm SD. Significance levels were set at 0.05, and two-tailed probability values were reported. The values of acoustic variables (*gpeak*, *q25*, *q50*, *q75*), not satisfying the criteria of normality with Kolmogorov–Smirnov test, were log-transformed to be introduced into parametric tests. We used a two-way factorial ANOVA with a Tukey honestly significant difference (HSD) test to estimate the effects of factor “population” and factor “contour” (contour of *g0* fundamental frequency, Fig. 2) on bugle acoustics. We used Yates corrected

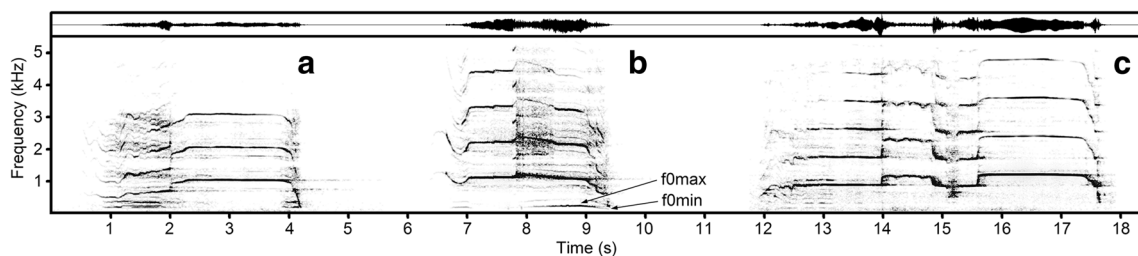


Fig. 2 Classifying rutting bugles of Siberian wapiti by contours of the high fundamental frequency *g0*: **a** trapeze bugle, **b** descending bugle, **c** saddle bugle. An additional (low) fundamental frequency *f0* is visible at the beginning of each of the three bugles and at the end of the first and of the second bugles. A short fragment of deterministic chaos is visible at the middle of the third bugle. Designations: *f0max* maximum low

fundamental frequency *f0*; *f0min* minimum low fundamental frequency *f0*. The spectrogram was created at 11.025 kHz sampling frequency, fast Fourier transform (FFT) 1024, Hamming window, frame 50% and overlap 93.75%. The audio file of these calls is available as Supplementary Audio S1

χ^2 test to compare the proportions of bugles with different contours of g0, the proportions of bugles with deterministic chaos and the proportions of bugles with f0, between populations.

Results

Of the total of measured 435 main bugles (145 bugles per population), 335 (81.6%) were produced singly (as single-call bouts); other 80 bugles (18.4%) were the longest calls in bouts that contained a few short calls (from 1 to 16) in addition to the main bugle. On average, bouts contained 1.42 ± 1.25 bugles per bout.

The g0max of the bugles varied from 0.52 to 2.56 kHz (mean 1.36 ± 0.29 kHz) and the g0min varied from 0.12 to 0.99 kHz (mean 0.41 ± 0.18 kHz) (Table 1). Duration of the main bugles varied from 0.83 to 5.95 s (mean 3.12 ± 0.70 s). Each bugle displayed a well-expressed plateau of g0; the plateau duration comprised 1.63 ± 0.77 s, thus covering the most part of total call duration (Table 1). The plateau of g0 was commonly found in bugle central part; in 66.9% of bugles g0plat coincided with g0max. Along plateau, g0plat varied weakly, so the plateau was nearly horizontal in 380 bugles, whereas 55 bugles displayed small elevations along $21.2 \pm 13.8\%$ of plateau duration.

All the 435 bugles were classified to one of g0 contours, trapeze, descending or saddle (Fig. 2). In the trapeze bugles, g0 contour initially rose, then reached a plateau and afterwards fell rapidly towards the end of a call. In the descending bugles, the rising phase was lacking so that the bugle started with the high frequency corresponding to g0 plateau. In saddle bugles,

a prominent descent of g0 followed with its rise. In saddle bugles, plateau could be reached before or after descent of g0. Among the total of 435 bugles, 323 (74.3%) comprised the trapeze bugles, 103 (23.7%) comprised the descending bugles and 9 (2.1%) comprised the saddle bugles.

In captive population, percentage of trapeze bugles (84.8%) was higher compared to either semi-captive (71.0%) or wild-living (66.9%) population ($\chi^2 = 7.24$, $p = 0.007$ and $\chi^2 = 11.77$, $p < 0.001$, respectively), whereas percentage of descending bugles was lower in captive (13.1%) compared to either semi-captive or wild-living population ($\chi^2 = 11.68$, $p < 0.001$ and $\chi^2 = 8.51$, $p = 0.004$, respectively). Percentages of descending bugles did not differ between wild-living (30.4%) and semi-captive populations (27.6%) ($\chi^2 = 0.15$, $p = 0.70$). Saddle bugles were rare in any population, comprising in wild-living population 2.8% of bugles, in semi-captive population 1.4% of bugles and in captive population 2.1% of bugles.

The additional (low) fundamental frequency (f0) or its linear combinatory frequency bands were found in 331 (76.1%) of 435 bugles. Bugle average f0min was 0.18 ± 0.08 kHz and bugle average f0max was 0.21 ± 0.10 kHz. Percent of bugles with f0 did not differ between captive (86.9%) and wild-living (79.3%) populations ($\chi^2 = 2.46$, $p = 0.12$), but was significantly lower in semi-captive population (62.1%, $\chi^2 = 22.23$, $p < 0.001$ and $\chi^2 = 9.59$, $p = 0.002$, respectively).

Deterministic chaos was found in 73 (16.8%) of 435 bugles. Percent of bugles with deterministic chaos did not differ between wild-living (22.8%) and semi-captive (22.8%) populations, but was significantly lower (4.8%) in captive population ($\chi^2 = 18.13$,

Table 1 Values (mean \pm SD) of acoustic variables of Siberian wapiti stag rutting bugles recorded in three populations and displaying three different contours of g0

Acoustic variable	Total (n = 435)	Population			Contour		
		Wild-living (n = 145)	Semi-captive (n = 145)	Captive (n = 145)	Trapeze (n = 323)	Descending (n = 103)	Saddle (n = 9)
duration (s)	3.12 ± 0.70	3.29 ± 0.85	3.14 ± 0.65	2.93 ± 0.51	3.11 ± 0.69	3.10 ± 0.67	3.92 ± 0.90
dur_up (s)	0.97 ± 0.57	1.02 ± 0.63	0.83 ± 0.52	1.04 ± 0.53	1.02 ± 0.55	0.76 ± 0.54	1.29 ± 1.08
dur_plat (s)	1.63 ± 0.77	1.70 ± 0.92	1.83 ± 0.74	1.34 ± 0.52	1.58 ± 0.76	1.78 ± 0.78	1.34 ± 0.75
dur_down (s)	0.53 ± 0.44	0.57 ± 0.51	0.47 ± 0.39	0.55 ± 0.40	0.50 ± 0.39	0.54 ± 0.48	1.34 ± 0.92
g0beg (kHz)	0.82 ± 0.37	0.81 ± 0.46	0.92 ± 0.31	0.72 ± 0.30	0.70 ± 0.31	1.15 ± 0.33	1.05 ± 0.34
g0plat (kHz)	1.28 ± 0.29	1.22 ± 0.35	1.25 ± 0.22	1.37 ± 0.26	1.32 ± 0.28	1.16 ± 0.28	1.32 ± 0.18
g0end (kHz)	0.43 ± 0.21	0.38 ± 0.20	0.50 ± 0.15	0.42 ± 0.25	0.42 ± 0.21	0.46 ± 0.21	0.54 ± 0.25
g0max (kHz)	1.36 ± 0.29	1.30 ± 0.36	1.32 ± 0.23	1.45 ± 0.22	1.37 ± 0.28	1.31 ± 0.30	1.46 ± 0.21
g0min (kHz)	0.41 ± 0.18	0.35 ± 0.17	0.49 ± 0.15	0.37 ± 0.19	0.39 ± 0.17	0.46 ± 0.20	0.46 ± 0.15
g0mean (kHz)	1.12 ± 0.23	1.04 ± 0.30	1.12 ± 0.16	1.19 ± 0.19	1.13 ± 0.23	1.08 ± 0.25	1.15 ± 0.16
gpeak (kHz)	1.35 ± 0.47	1.24 ± 0.47	1.38 ± 0.52	1.42 ± 0.40	1.37 ± 0.46	1.24 ± 0.48	1.59 ± 0.60
q25 (kHz)	1.00 ± 0.32	0.81 ± 0.27	1.09 ± 0.21	1.11 ± 0.36	1.02 ± 0.32	0.94 ± 0.29	1.03 ± 0.27
q50 (kHz)	1.41 ± 0.37	1.28 ± 0.33	1.46 ± 0.39	1.49 ± 0.35	1.44 ± 0.37	1.29 ± 0.34	1.54 ± 0.40
q75 (kHz)	2.24 ± 0.63	2.17 ± 0.68	2.38 ± 0.55	2.17 ± 0.62	2.23 ± 0.62	2.26 ± 0.63	2.28 ± 0.67

duration bugle duration; *dur_up* bugle duration from onset to plateau; *dur_plat* plateau duration; *dur_down* duration from the end of bugle plateau to the end of the bugle; *g0beg* beginning value of g0; *g0plat* plateau value of g0; *g0end* final value of g0; *g0max* maximum value of g0; *g0min* minimum value of g0; *g0mean* mean value of g0; *gpeak* peak frequency of plateau; *q25* lower power quartile of plateau value; *q50* medium power quartile of plateau; *q75* upper power quartile of plateau value

$p < 0.001$ in both cases). Percent of trapeze bugles with deterministic chaos was lower in captive (4.1%) compared to either semi-captive (26.2%) or wild-living (28.9%) population ($\chi^2 = 20.84$, $p < 0.001$ and $\chi^2 = 24.25$, $p < 0.001$, respectively). Percent of descending bugles with deterministic chaos comprised 11.4% in wild-living, 15.0% in semi-captive and 10.5% in captive population (differences are non-significant).

To compare the effects of factors population and g0 contour on bugle acoustics, we included in analysis only bugles with trapeze and descending contours and excluded bugles with saddle contours, as their number was too small ($n = 9$, 2.1% of all bugles) for statistic comparisons. Factor population had significant effect on all the 14 acoustic variables of bugles, for the exception of g0plat (Table 2). The g0 contour had significant effect on dur_up, g0beg, g0plat, g0min, gpeak and q50. Conjoint effect of both factors was found on dur_plat, dur_down and g0beg (Table 2). Effect of population was stronger than the effect of g0 contour (Table 2). However, for dur_up, g0plat and especially for g0beg, effect of g0 contour was stronger than the effect of population (Table 2), due to different shapes of the trapeze and descending contours (Fig. 2).

Comparison of values of acoustic variables between trapeze and descending bugles and between populations, showed that trapeze bugles were longer in wild-living than in captive population (Fig. 3). For trapeze bugles, duration did not differ between semi-captive and wild-living or between semi-captive and captive populations (Fig. 3). For descending bugles, differences in duration (longer for wild-living population) did not reach threshold of significance. Within population, this variable did not differ between contours (Fig. 3).

The dur_plat for trapeze bugles was similar between wild-living and semi-captive populations and was the shortest in

captive population (Fig. 3). For descending bugles, dur_plat was longer for semi-captive than for wild-living population (Fig. 3). Within population, this variable did not differ between contours (Fig. 3).

The g0beg was lower for trapeze than for descending bugles in any population (Fig. 3), due to difference between contour shapes (Fig. 2). For trapeze bugles, g0beg was higher in semi-captive than in any other population (Fig. 3). For descending bugles, this variable did not differ between populations.

The g0plat was higher in trapeze than in descending bugles in captive population (Fig. 3), due to difference between contour shapes (Fig. 2). For trapeze bugles, g0plat was higher in captive than in any other population. For descending bugles, this variable did not differ between populations (Fig. 3).

For trapeze bugles, g0end was higher in semi-captive than in wild-living population. For descending bugles, this variable was significantly higher in semi-captive than in captive population (Fig. 3). Within population, this variable did not differ between contours (Fig. 3).

For trapeze bugles, g0mean was higher in captive than in wild-living population; however, this variable did not differ between semi-captive and wild-living, or between semi-captive and captive populations (Fig. 3). For descending bugles, this variable did not differ between populations. Within population, g0mean did not differ between contours (Fig. 3).

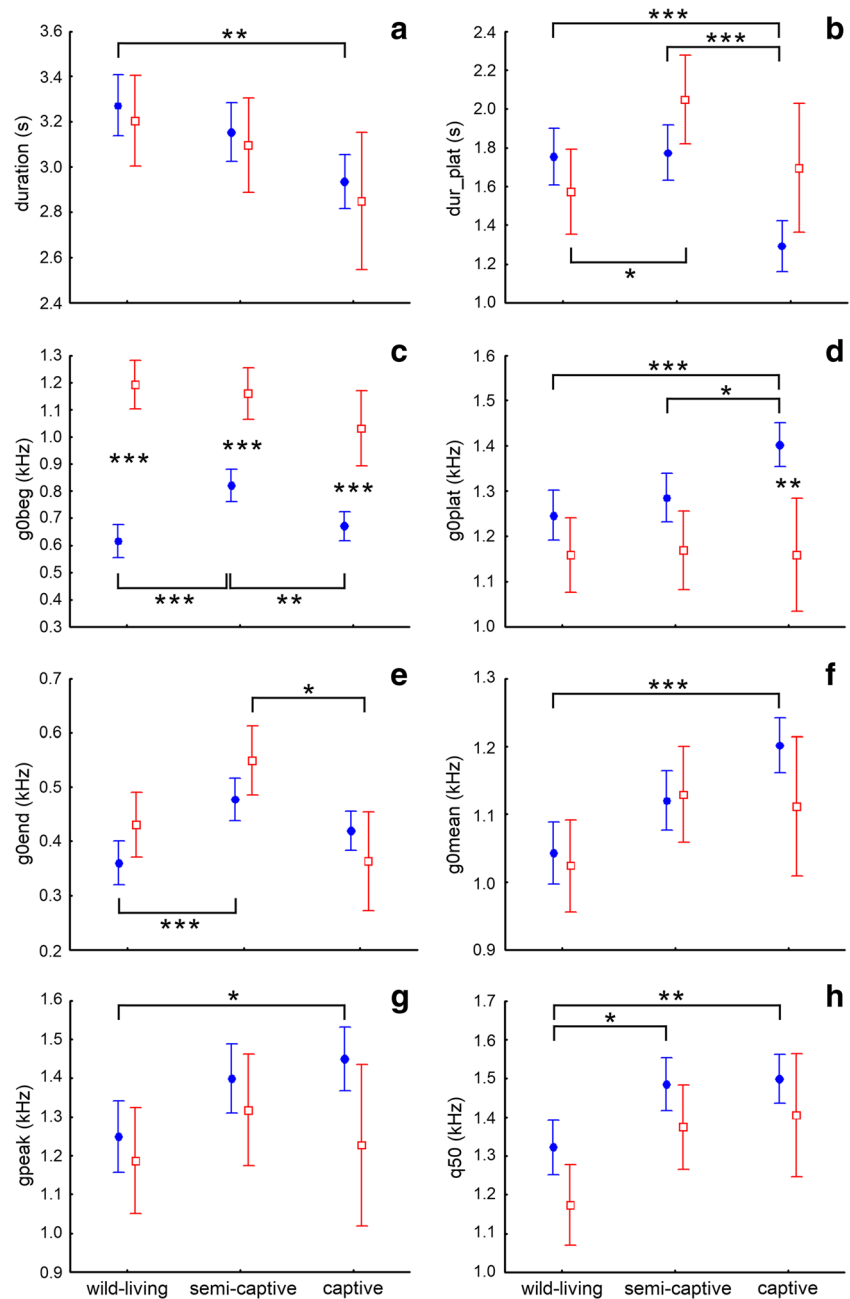
For trapeze bugles, gpeak was higher in captive compared to wild-living population; however, this variable did not differ between wild-living and semi-captive, or between semi-captive and captive populations (Fig. 3). For descending bugles, this variable did not differ between populations. Within population, this variable did not differ between contours (Fig. 3).

Table 2 Results of two-way factorial ANOVA for the influence of the factors contour and population and their conjoint effects on the acoustics of Siberian wapiti rutting bugles. Only bugles with trapeze and descending contours were included in analysis

Acoustic variable	Factor		
	Population	Contour	Population and Contour
duration	<i>$F_{2,420} = 5.65$; $p = 0.004$</i>	$F_{1,420} = 0.78$; $p = 0.38$	$F_{2,420} = 0.01$; $p = 0.99$
dur_up	$F_{2,420} = 4.17$; $p = 0.02$	<i>$F_{1,420} = 14.78$; $p < 0.001$</i>	$F_{2,420} = 0.46$; $p = 0.63$
dur_plat	<i>$F_{2,420} = 7.35$; $p < 0.001$</i>	$F_{1,420} = 3.54$; $p = 0.06$	$F_{2,420} = 4.40$; $p = 0.02$
dur_down	<i>$F_{2,420} = 5.01$; $p = 0.007$</i>	$F_{1,420} = 0.06$; $p = 0.81$	<i>$F_{2,420} = 9.01$; $p < 0.001$</i>
g0beg	<i>$F_{2,420} = 4.87$; $p = 0.008$</i>	<i>$F_{1,420} = 135.92$; $p < 0.001$</i>	<i>$F_{2,420} = 5.12$; $p = 0.01$</i>
g0plat	$F_{2,420} = 1.70$; $p = 0.18$	<i>$F_{1,420} = 20.16$; $p < 0.001$</i>	$F_{2,420} = 1.78$; $p = 0.17$
g0end	<i>$F_{2,420} = 12.41$; $p < 0.001$</i>	$F_{1,420} = 1.39$; $p = 0.24$	$F_{2,420} = 2.52$; $p = 0.08$
g0max	$F_{2,420} = 3.84$; $p = 0.02$	$F_{1,420} = 1.18$; $p = 0.28$	$F_{2,420} = 2.26$; $p = 0.11$
g0min	<i>$F_{2,420} = 21.59$; $p < 0.001$</i>	$F_{1,420} = 7.31$; $p = 0.01$	$F_{2,420} = 2.25$; $p = 0.11$
g0mean	<i>$F_{2,420} = 7.83$; $p < 0.001$</i>	$F_{1,420} = 1.50$; $p = 0.22$	$F_{2,420} = 1.00$; $p = 0.37$
gpeak	$F_{2,420} = 3.06$; $p = 0.05$	$F_{1,420} = 4.91$; $p = 0.03$	$F_{2,420} = 0.70$; $p = 0.50$
q25	<i>$F_{2,420} = 34.18$; $p < 0.001$</i>	$F_{1,420} = 2.57$; $p = 0.11$	$F_{2,420} = 1.22$; $p = 0.30$
q50	<i>$F_{2,420} = 10.69$; $p < 0.001$</i>	$F_{1,420} = 7.80$; $p = 0.01$	$F_{2,420} = 0.16$; $p = 0.86$
q75	<i>$F_{2,420} = 4.94$; $p = 0.008$</i>	$F_{1,420} = 0.00$; $p = 0.99$	$F_{2,420} = 0.19$; $p = 0.82$

Significant differences are given in italics

Fig. 3 Comparison of values of acoustic variables for Siberian wapiti stag rutting bugles with trapeze (*solid circles*) and descending (*empty squares*) contours of g0 for three populations (wild-living, semi-captive, captive). Designations: **a** bugle duration; **b** plateau duration; **c** beginning value of g0; **d** g0 plateau value; **e** final value of g0; **f** mean value of g0; **g** peak frequency of plateau; **h** medium power quartile of plateau. *Circles* and *squares* show averages, whiskers show 95% confidence intervals. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, Tukey post hoc test



For trapeze bugles, q50 was lower in wild-living than in any other population (Fig. 3). For descending bugles, this variable did not differ between populations. Within population, this variable did not differ between contours (Fig. 3).

Between-population differences depended on g0 contour; they were strong in trapeze bugles but practically lacked in descending bugles (Figs. 3, 4). Comparison of fundamental frequency (g0) contours of bugles between populations revealed that trapeze bugles had the shortest duration and dur_plat and the highest g0plat in captive population (Fig. 4). At the same time, trapeze bugles had the highest g0beg in semi-captive population. In contrast to trapeze bugles, no noticeable between-population difference was found (Fig. 4).

Discussion

This study presents first direct comparison of stag rutting calls (bugles) between-populations within subspecies of *C. elaphus*, *C. e. sibiricus*. Bugle acoustics were very similar between the three study populations of Siberian wapiti, wild-living, semi-captive and captive. Nevertheless, between-population acoustic differences were found in bugle duration, high fundamental frequency (g0) and proportion of bugles with trapeze, descending and saddle contours. Factor population had stronger effect on bugle acoustics than factor contour of g0 (trapeze vs. descending). Bugles of captive stags were the shortest and highest

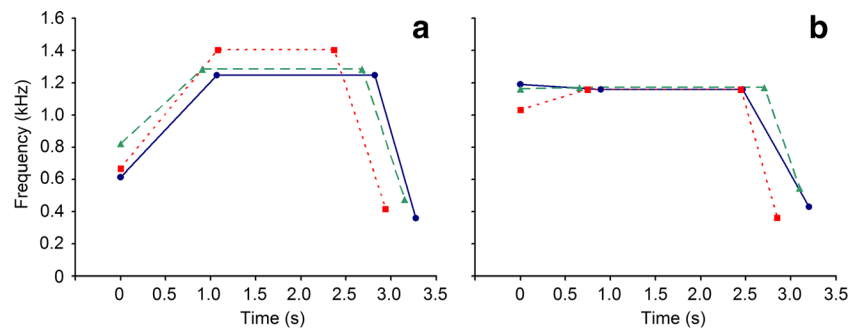


Fig. 4 Between-population differences in values of g_0 -related variables between **a** trapeze and **b** descending contours of Siberian wapiti stag rutting bugles. *Solid lines* indicate wild-living population, *dashed lines* indicate semi-captive population and *dotted lines* indicates captive

population. *Circles, triangles and squares* label positions of g_0beg , g_0plat and g_0end in wild-living, semi-captive and captive population, respectively. For designations of variables see Table 1

in frequency; bugles of wild-living stags were the longest and lowest in frequency; whereas bugles of semi-captive stags were intermediate in their characteristics. These between-population differences depended on shape of contour of g_0 , being substantially more prominent for bugles with trapeze contour than for bugles with descending contour (Figs. 3, 4).

Bugles of Siberian wapiti of this study were very similar in the acoustics to those of bugles of Siberian wapiti, reported earlier (Nikol'skii et al. 1979; Volodin et al. 2013b, 2016b). They were comparable in duration although a few higher in fundamental frequency than in stag bugles recorded in the same wild-living population of Khakasia in another (2012) rutting period (duration = 3.07 s, g_0max = 1.23 kHz, g_0min = 0.29 kHz; Volodin et al. 2013b), or than in stag bugles of captive Siberian wapiti from zoos and the same captive population of Kostroma farm (duration = 3.04 s, g_0max = 1.20 kHz, g_0min = 0.30 kHz; Volodin et al. 2016b). As in this study, bouts containing a single long bugle occurred much more frequently than bouts containing a few short bugles along to the long main bugle (Nikol'skii et al. 1979; Volodin et al. 2013b).

This study, in the first time, describes three contours of fundamental frequency (g_0) in calls of Siberian wapiti. The different contours of g_0 are also characteristic for bugles of other subspecies of wapiti. Both trapeze and descending contours of fundamental frequency are also presented in Far-East wapiti (Volodin et al. 2015b), and the trapeze contour is presented in North American wapiti (Bowyer and Kitchen 1987; Feighny et al. 2006; Reby et al. 2016). Further study should compare the occurrence of rutting calls with different contours not only between different wild-living and captive populations of Siberian wapiti but also between different subspecies of wapiti.

In this study, population management strongly affected the maximum fundamental frequency and duration of bugles. Captive Siberian wapiti stags produced higher-frequency although shorter-duration bugles compared to either wild-living or semi-captive stags. However, differences in fundamental frequency were found only in trapeze bugles, whereas, the

fundamental frequency of the descending bugles did not differ between populations (Fig. 4). A crowd of males and females on a relatively small territory of the farm evokes elevated emotional arousal, what resulted in increase of fundamental frequency of bugles in captive males (Manteuffel et al. 2004; Briefer 2012). In addition, a better physical condition of well-fed farmed stags due to availability of supplementary food could also be responsible for the higher-frequency bugles of captive males. Similar data on the higher-frequency rutting calls in farmed red deer compared to the natural populations were earlier obtained for Iberian red deer (Volodin et al. 2015a).

Furthermore, the high animal density during breeding season is not typical for the Siberian wapiti, as wild-living animals in nature during the rut walk in small harem groups of one stag and 2–4 hinds (Fedosenko 1980). Captive management, especially in small enclosures, might destroy the characteristic for this subspecies structure of harem groups, by forcing males to permanently compete with each other, by using also the vocal displays. For instance, rutting males of the Scottish red deer *Cervus elaphus scoticus*, vocalize more often when they hear rutting calls of other males (Clutton-Brock and Albon 1979). In sika deer *Cervus nippon*, the number of calls of harem-holding males positively correlates with distance to other males (Bartoš et al. 2003). In fallow deer *Dama dama*, a close vicinity of hinds and vocalizing males during the rut also resulted in increase of fundamental frequency of male rutting calls (Charlton and Reby 2011). Aside effect of captivity on g_0 , the higher fundamental frequency might result from elevated testosterone levels, as was reported for singing male white-handed gibbons *Hylobates lar* (Barelli et al. 2013).

In this study, we found that the second low fundamental frequency (f_0) represented a characteristic trait for rutting bugles of Siberian wapiti, being presented in as much as 76% of bugles. At the same time, another nonlinear phenomenon, the deterministic chaos (Wilden et al. 1998) occurred much more rarely, in only 17% of the bugles. Previously, the occurrence of the low fundamental frequency in bugles was not analysed,

although it was known for both Siberian (Nikol'skii 2011; Volodin et al. 2013b) and for American wapiti (Feighny et al. 2006; Reby et al. 2016). The f_0 values in Siberian wapiti of this study were very close to the values reported for either biphonic rutting bugles of American wapiti (average maximum $f_0 = 0.19$ kHz, Reby et al. 2016) or for the biphonic bugles of domestic bulls *B. taurus* (average maximum $f_0 = 0.22$ kHz, Volodin et al. 2017).

Acoustic structures of rutting bugles are very similar across populations of Siberian wapiti and at the same time do not overlap with bugles of other wapiti (Fig. 5). American wapiti produce bugles with a very high fundamental frequency g_0 (>2.0 kHz), whereas the duration of the bugles is not so much long (2.4–2.8 s) (Feighny et al. 2006; Reby et al. 2016). In Far-East wapiti, the maximum fundamental frequency of the rutting bugles is much lower (0.66 kHz), however the duration is much longer (3.4 s) (Volodin et al. 2015b). Similarly, in Iberian red deer, stag roars from four populations were found very close in values of acoustic variables, but very distinctive from roars of other subspecies of red deer (Volodin et al. 2015a). Therefore, stag rutting bugles are subspecies-specific and may serve as acoustic indicator of subspecies for Siberian wapiti among other Asian and American subspecies of wapiti (Fig. 5).

In this study, we used automated recording systems for collecting rutting bugles of Siberian wapiti. This allowed to cover the entire rut period without disturbing the animals and provided uniform collection of data throughout the rut period. The automated recording systems work autonomously by predetermined schedule during day and night and day after day (Volodin et al. 2016a). However, this method of data collection only allows collecting calls of individually unidentified animals (although see Sibiryakova et al. 2017).

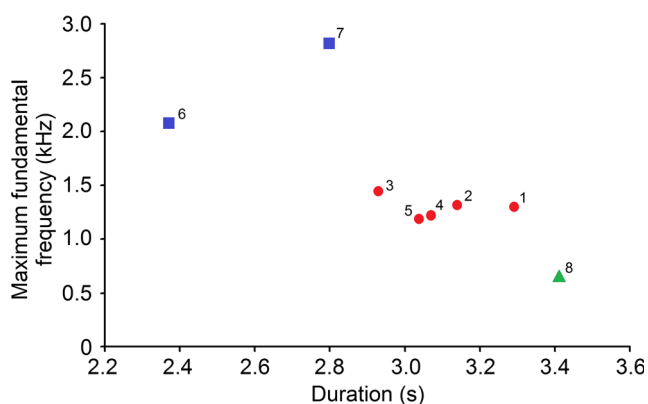


Fig. 5 Maximum fundamental frequency and duration of wapiti stag rutting bugles across subspecies: red circles indicate Siberian wapiti *C. e. sibiricus*; green triangle indicates Far-East wapiti *C. e. xanthopygus*; blue squares indicate American wapiti *C. canadensis*. Based on: 1 this study, wild-living population; 2 this study, semi-captive population; 3 this study, captive population; 4 Volodin et al. 2013b; 5 Volodin et al. 2016b; 6 Feighny et al. 2006; 7 Reby et al. 2016; 8 Volodin et al. 2015b

Nevertheless, for comparison the acoustics between populations or between subspecies, the use of automated recording systems throughout the rut provides valid and easily obtainable data.

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