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ORIGINAL RESEARCH

Rutting calls of harem-holders, harem-candidates and peripheral male Siberian wapiti *Cervus canadensis sibiricus*: Acoustic correlates of stag quality and individual identity

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Abstract

This study investigates the effects of individuality and harem-holding status on the acoustic parameters of rutting calls (bugles) of 14 stags of Siberian wapiti *Cervus canadensis sibiricus*. The stags competed for mating with hinds in a large herd, free ranging inside a fenced area with complex landscape. We considered as harem-holders the stags, which kept a harem of 5 or more hinds for at least 2 days. Of the 15 days of observations enveloping the most active rutting period, during 3 days there was only one harem in the enclosure, during 9 days two harems, during 2 days three harems and during 1 day four harems. Stag bugles displayed both individual and status-related variation. Harem-holders compared with peripheral stags had shorter bugles with higher minimum fundamental frequency. After winning a harem and changing status from harem-candidate to harem-holder, stags shortened the duration of their bugles, lowered the beginning and maximum fundamental frequency and increased the minimum fundamental frequency. Significantly higher than the levels expected by chance, discriminant analysis classified 78.9% of bugles by the correct stag status and 53.2% of bugles by the correct individual callers. Different acoustic parameters encoded the status and individuality of the bugles. Status was encoded by the duration of the start and end parts and by the beginning and end fundamental frequencies. Individuality was encoded by the maximum fundamental frequency. We discuss that rutting calls of Siberian wapiti, although individualized, do not represent vocal signatures. However, these calls reliably mark stag harem-holding status.

Introduction

Among mammals, polygynous breeding systems are known for pinnipeds (Cassini, 1999; Krüger et al., 2014), artyodactyls (Blank, 2021), perissodactyls (Briefer et al., 2015), primates (Koda et al., 2018; Puts et al., 2016) and bats (Garg et al., 2018; Knörnschild et al., 2011). For males of these taxa, advertising male rank and current harem-holding status holds great importance. Sophisticated and exaggerated behavioural traits of male status (de la Peña et al., 2021) often include impressive acoustic signals (Reby & McComb, 2003a; Sanvito et al., 2007). Vocal individuality and acoustic traits associated with harem-holding status have not yet been investigated in greater detail for all species of polygynous ruminants, including representatives of the genus *Cervus elaphus sensu lato*, recently divided into three different species: red deer *Cervus elaphus*, hanglu *Cervus hanglu* and wapiti *Cervus canadensis* (Mackiewicz et al., 2022). Of these three *Cervus* species, harem-holding strategies were only studied for red deer (Clutton-Brock & Albon, 1979; Reby & McComb, 2003b). For other two species, patterns of harem-holding behaviour have yet to be studied.

During the mating season, male polygynous ruminants produce rutting calls for attracting females to harems and for deterring rival males. Among cervids, the most extensive studies of male rutting calls have been carried out for European red deer *Cervus elaphus* (Clutton-Brock & Albon, 1979; Reby & McComb, 2003b; Volodin et al., 2019), North American/Asian wapiti *C. canadensis* (Feighny et al., 2006; Golosova et al., 2017; Struhsaker, 1967; Volodin, Sibiryakova, et al., 2016) and European and Persian fallow deer *Dama dama* and *D. mesopotamica* (Charlton & Reby, 2011; Stachowicz et al., 2014; Vannoni & McElligott, 2008).

Among the acoustic features of male rank reflected in the rutting calls, large body size is of particular significance (Fitch & Hauser, 2003), correlating with male ability to compete for females (e.g. Birgersson & Ekvall, 1997) and often predetermining female choice for mating (Fitch & Hauser, 2003). Acoustic traits which potentially provide honest information about the caller's body size are call fundamental frequency (Garcia et al., 2017; Sibiryakova et al., 2021; Vannoni & McElligott, 2008) and vocal tract resonances (formants) (Charlton et al., 2009; Fitch, 1997; Reby & McComb, 2003b; Riede & Fitch, 1999; Sanvito et al., 2007; Vannoni & McElligott, 2008). In mammals, the larger the animal, the larger are the larynx and vocal folds and thereby the lower is the fundamental frequency (Titze et al., 2016). However, in mammals, the size of the larynx can evolve independently from the remaining body structures, making the fundamental frequency a less reliable indicator of body size (Fitch & Hauser, 2003; Riede & Brown, 2013), relative to formants which are always lower in animals with longer vocal tracts (Taylor & Reby, 2010). Thereby, the larger the animal, the longer is its vocal tract and the lower its call formants (Fitch & Hauser, 2003; Taylor & Reby, 2010).

Rutting calls of European red deer stags and wapiti stags are different in their acoustic structure (Frey & Riede, 2013). European red deer stags produce low-frequency roars with the maximum fundamental frequency ranging from 52 to 274 Hz across subspecies (Frey et al., 2012; Golosova et al., 2021; Kidjo et al., 2008; Reby & McComb, 2003b; Volodin et al., 2022), whereas North American/Asian wapiti mainly produce very high-frequency bugles with the maximum fundamental frequency ranging from 660 to 2824 Hz across subspecies (Feighny et al., 2006; Golosova et al., 2017; Nelson-Reinier & Clarke, 2023; Reby et al., 2016; Volodin et al., 2015). The low fundamental frequency of the roars of European red deer enables accenting the formants, including the lowest ones, which are clearly visible in spectrograms of the roars (Kidjo et al., 2008; Reby & McComb, 2003b; Volodin et al., 2019). However, the high-frequency bugles of North American/Asian wapiti do not reveal a clear formant structure (Feighny et al., 2006; Golosova et al., 2017; Titze & Riede, 2010), although they commonly contain the low fundamental frequency, approximately equal to the fundamental frequency of the roars of European red deer (Golosova et al., 2017; Reby et al., 2016). Paradoxically, these acoustical differences are not supported by respective anatomical differences in the length of the vocal folds: the vocal fold length of male European red deer (27–30 mm, Frey et al., 2012; Riede & Titze, 2008) is approximately the same as that of American wapiti *C. e. nelsoni* (30 mm, Riede & Titze, 2008).

Rutting roars of European red deer stags advertise caller quality via the low formant frequencies: the lower the formant frequencies of the rutting calls, the higher is stag age and reproductive success (Reby et al., 2005; Reby & McComb, 2003b). A playback study showed that European red deer hinds prefer stag calls with low formants (Charlton et al., 2007); however, another study found a different pattern of responding, with hinds preferring stag roars with higher-frequency formants (Charlton et al., 2008). In fallow deer, high male rank is related to low formant frequencies and low minimum fundamental frequency of rutting groans (Briefer et al., 2010; Vannoni & McElligott, 2008).

The fundamental frequency (f0) of European red deer stag roars does not display a relationship with proxies (age and weight) of caller quality (Reby & McComb, 2003b). In contrast to the response to formant frequencies, red deer hinds do not show the differential responses to playbacks of stag calls with higher or lower f0 variants outside the rutting period (Charlton et al., 2008; McComb, 1991). However, hinds at the peak of their sexual receptivity may prefer stag calls with average subspecies-specific f0 compared to very low -frequency roars (Reby et al., 2010).

The general question of this study is about how vocal traits of stag rank are reflected in the high-frequency bugles of male wapiti (Feighny et al., 2006; Golosova et al., 2017; Reby et al., 2016). Unlike in male red and fallow deer, the low-frequency rutting calls of which reveal the formants (Taylor & Reby, 2010), the high-frequency rutting bugles of male wapiti with the, respectively, widely spaced harmonics of the high fundamental frequency (g0) do not accent the formants (Golosova et al., 2017; Reby et al., 2016; Volodin et al., 2015; Volodin, Sibiryakova, et al., 2016). Therefore, in wapiti stags, vocal cues to male harem status, determining stag mating success, are probably encoded in other acoustic variables.

Along with acoustic cues to harem-holding status, individual identity of stag rutting calls might also be important for attracting hinds to join the harem. However, previous studies have shown that rutting calls of male red and fallow deer display relatively low individual identity (Briefer et al., 2010; Reby et al., 1998, 2006; Vannoni & McElligott, 2008). The degree and role of vocal individuality is not yet fully understood in harem ruminants. Throughout a rutting period, individuality of male red and fallow deer rutting calls remains rather low, although above the chance level (Briefer et al., 2010; Reby et al., 1998, 2006; Vannoni & McElligott, 2007). In rutting fallow deer bucks, vocal cues of male quality prevail over the vocal cues of male identity (Briefer et al., 2010). However, red deer hinds may discriminate between the roars of their current harem-holder stag and those of neighbouring stags (Reby et al., 2001). For wapiti, the acoustic cues to male status and identity in the rutting bugles have yet to be studied. To date, in Siberian wapiti *C. canadensis sibiricus*, individuality has only been investigated in the contact calls of mothers and adolescents (Sibiryakova et al., 2018).

The Siberian wapiti inhabit the regions of Central Siberia of Russia and Kazakhstan (Fedosenko, 1980). Calendar dates of the rutting period in the Siberian wapiti are practically the same both in the wild (Volodin et al., 2013) and in semi-captive conditions (Rusin et al., 2021; Volodin, Volodina, et al., 2016). Furthermore, the general acoustic structure of male Siberian wapiti rutting bugles is very similar under captive, semi-captive and free-ranging conditions (Golosova et al., 2017; Volodin et al., 2013; Volodin, Sibiryakova, et al., 2016). The aim of this study was to determine the acoustic traits responsible for encoding individual identity and harem-holding status in the rutting bugles of free-ranging male Siberian wapiti, freely competing for matings with hinds in a large semi-captive herd.

Materials and methods

Ethical note

Animal care and all experimental procedures were in accordance with the 'Guidelines for the treatment of animals in behavioural research and teaching' [*Anim. Behav.*, 2020, 159, I–XI] and with the laws on animal welfare for scientific research of Russian Federation, where the study was conducted. The data collection protocol # 2011-36 was approved by the Committee of Bio-ethics of Lomonosov Moscow State University. In the deer facility, animal disturbance was kept at a minimum, and all data collection procedures were approved by the owners of this deer facility.

Study site, animals and dates

We recorded the rutting bugles of 14 individual Siberian wapiti stags from 20 September to 4 October 2018, during the most active rut period of this species (Rusin et al., 2021; Volodin, Volodina, et al., 2016). The recordings were conducted in a semi-captive population kept in a 70-ha enclosure located in the Kostroma region of Central Russia (58°24′ N, 43°15′ E). The enclosure consisted of two large and a few smaller sub-enclosures, joined for the entire duration of the rutting period: the gates between the sub-enclosures were permanently open and did not prevent animal transitions. The enclosure had a landscape with elevations and depressions of up to a few dozen metres, a small river, open territories and forested parts with small internal fields. This complex landscape prevented wapiti from visually spotting each other from a distance, and promoted high rutting vocal activity even when the animals were only tens of metres from each other, because they were separated by visual barriers.

Wapiti used the entire territory of the enclosure for grazing. In addition to grazing, the animals were fed once a day at about 17:00 with a small amount of barley and oat grain from one feeder. This food was provided by the farm keepers to accustom the animals to human presence. However, only about a half of the hinds and a few stags regularly visited the feeder.

The study herd originated in 2010–2012 from about one hundred pure Siberian wapiti, translocated from three different farms of the Altai/Khakasian region of Central Siberia (Russia) where the Siberian wapiti are native (Golosova et al., 2017; Rusin et al., 2021; Sibiryakova et al., 2018). In total, the study enclosure contained during the autumnal rutting season of 2018 22 adult stags (aged 5–10 years), 34 adult hinds (aged 2–10 years), 20 young stags (aged 2–4 years) and 18 calves aged under 1 year (born at the farm in the period from end of May to July 2018). During the data collection period, all stags, hinds and calves were free ranging in the enclosure and could freely interact without any barriers. All stags and hinds older than 1 year were tagged with individual Allflex (Palmerston North, New Zealand) plastic ear tags.

Audio recording

Behavioural observations and recording of stag rutting bugles were conducted by two researchers (IAV and EVV), working simultaneously but independently from each other in different parts of the enclosure and observing different individuals. Recordings were conducted on a daily basis, for 3 h after dawn from 06:00 to 09:00 and for two and half hours before dusk, from 16:00 to 18:30. The stags called towards hinds or rival stags but never vocalized toward calves or researchers. The researchers tried to approach the callers in order to be as close as possible without influencing the animals' behaviour, to obtain the highest quality recordings. The animals were habituated to human presence and reacted on them very weakly, or did not react at all even when the recording distance was as short as 20–30 m. As the animals actively moved, the recording distance could change during and between recordings. As a rule, most observations and audio recordings were made from a distance of 40–50 m.

We used the method of focal-animal sampling (Altmann, 1974), trying to record as many focal callers as possible each day and to collect approximately equal number of recordings from each focal caller during a day (during the morning and evening sessions of data collection). If the focal stag changed its status from harem-candidate to harem-holder or vice versa, it was selected as a primary focal animal during the given day.

The animals could be individually identified by their ear tags and, in addition, individual phenotypic traits. In all stags, the antlers were sawed out in June, when they were still in velvet. Observations of behaviour and identification of individual callers were made using the unaided eye or binoculars Olympus 8x21 DPC (Olympus Corp., Tokyo, Japan) over distances of up to 100 m. The following could cause issues with immediate identification: if the tagged ears were turned in or out, if animal position to microphone differed from the frontal and the tag was poorly visible or if the ear tags were covered in mud. Therefore, for precise identification of individual callers we took photos of the caller's head a few times during the recording using two Canon PowerShot SX50HS digital cameras (Canon USA, Melville, New York) and looked at these zoomed photos on the same day on a laptop. This enabled photoidentification by comparing the photos with referential photo gallery of all stags of the enclosure, prepared in advance. This comparison helped identify the focal callers where there were doubts about individual identification.

All audio recordings (48 kHz, 16-bit precision, mono) were collected using two solid state recorders Marantz PMD-660 (D&M Professional, Kanagawa, Japan) with Sennheiser K6-ME66 cardioid electret condenser microphones (Sennheiser electronic, Wedemark, Germany). For each recorded bugle, we commented by voice the caller's individual identity (ID) and the distance and orientation of the caller in relation to the microphone. Each recorded bugle was stored as a separate wav-file and documented in a pocked copybook, to identify the order of recordings for the subsequent detailed photo identification at the end of a day of recording. In total, we recorded 2100 audio files, each of which contained one, rarely two, bugles from an individually identified stag.

Samples of bugles

For spectrographic analysis, we selected non-overlapping bugles of a good signal-to-noise ratio, not broken with the wind and non-superimposed with alien noise or with calls of non-focal stags. The bugles were selected uniformly throughout the period of recording. In Siberian wapiti, most rutting calls are produced singly (Golosova et al., 2017) in contrast to European red deer, which produce multi-call bouts (Golosova et al., 2021; Kidjo et al., 2008; Volodin et al., 2019). Therefore, we included in the analyses single bugles. In total, we measured acoustic parameters from 398 bugles from the 14 stags.

From recordings of 6 (8–10 years old) harem stags, which had harems during data collection period, we created two samples of bugles. The first sample contained 20 bugles per individual, 120 bugles in total, recorded during 'hind-days held', when the callers had the status of 'harem-holders', following terminology by Reby and McComb (2003b). The second sample from the same 6 stags (20 bugles per individual from 5 stags and 18 bugles from the 6th stag, 118 bugles in total) was created from the bugles, recorded when the callers had not yet harems and were in the status of 'harem-candidates'. These two samples were used to estimate which parameters of bugles change with the change of stag status from 'harem-candidate' to 'harem-holder'.

From recordings of 8 (5–10 years old) rutting stags which did not have harems during the data collection period, we created the third sample of bugles, containing 20 bugles per individual, 160 bugles in total. These rutting stags, actively interested in the hinds, produced many bugles, tried to enter harems, sniffed the harem hinds but immediately retreated if they spotted the harem-holder approaching. Following the terminology by Struhsaker (1967), these rutting stags had 'peripheral' status.

Other 8 mature stags (5–10 years old) present in the enclosure were non-rutting stags which did not have harems and did not try to mate with hinds during the data collection period. These non-rutting stags either bugled rarely or did not vocalize at all and thus did not provide enough bugles for the analyses.

Acoustic analysis

Acoustic parameters were measured with Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany) and automatically exported to Microsoft Excel (Microsoft Corp., Redmond, WA, USA). Before the start of the acoustic analyses, we lowered the sampling rate of all audio files to 11 025 Hz for better frequency resolution and high-pass filtered them at 50 Hz to delete the low-frequency noise using Gauss filter. We measured the bugles with the following settings, providing 11 Hz frequency resolution and 5.8 ms time resolution: sampling frequency 11 025 Hz, Hamming window, FFT (Fast Fourier Transform) length 1024 points, frame 50%, and overlap 93.75%.

Visual inspection of spectrograms revealed two different independently varying fundamental frequencies, the lower (f0) and the higher one (g0), following the terminology developed for the biphonic calls of North American wapiti (Reby et al., 2016) and Siberian wapiti (Golosova et al., 2017). For each of the 398 bugles, we measured the same set of 13 g0-related acoustic variables: 4 temporal, 5 frequency and 4 power variables, following Golosova et al. (2017) (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 measured the g0-related variables: the beginning (g0beg), plateau (g0plat), final (g0end), maximum (g0max) and minimum (g0min) fundamental frequencies, manually on the screen with the reticule cursor. 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 the presence/absence of the additional (low) fundamental frequency f0 (Fig. 2) or its combinatory frequency bands resulting from interaction of f0 and g0 (Golosova et al., 2017; Reby et al., 2016; Wilden et al., 1998). For calls either containing f0 or the linear combinations of f0 with g0, we additionally measured two f0-related variables: the maximum (f0max) and the minimum (f0min) manually on the screen with the reticule cursor over the visible f0 band on the spectrogram (Golosova et al., 2017). In addition, we scored each bugle for the presence/absence of deterministic chaos (Fig. 2), responsible for the appearance of harsh bugles (Feighny et al., 2006; Golosova et al., 2017; Wilden et al., 1998). 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 exceeded 10% of the total bugle duration (Golosova et al., 2017).

Statistical analyses

Statistical analyses were made with STATISTICA, v. 8.0 (StatSoft, Tulsa, OK, USA). In addition, permutation analysis was run with custom-made macros created in R (R Development Core Team., 2023). All means are given as mean ± SD. Significance levels were set at 0.05, and two-tailed probability values were reported. Distributions of 260 measured parameter values of 312 distributions did not depart from normality (Kolmogorov–Smirnov test, $P > 0.05$), so we could apply the parametrical tests (Dillon & Goldstein, 1984).

We used the nested two-way ANOVA with Tukey HSD (Honest Significantly Different) post hoc test with an individual nested within status (harem-holder, harem-candidate, peripheral) to estimate the effects of the factors 'individuality' and 'status' on the acoustic parameters of the bugles, with status and individual as fixed factors (to control for inclusion of more than one call from each individual). In ANOVA, we used all the three samples (of 160, 120 and 118 bugles, 398 bugles in total). We used Yates corrected χ^2 test to compare the proportions of bugles with deterministic chaos and the proportions of bugles with f0.

We used the standard procedure of Discriminant Function Analysis (DFA) to calculate the probability of classifying the bugles to the correct caller, using the samples of bugles from

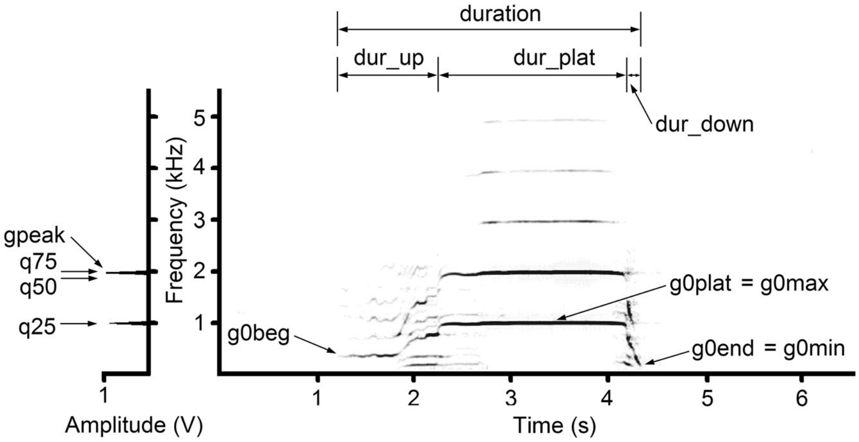

Figure 1 Measured acoustic variables for rutting bugles of male Siberian wapiti. Spectrogram (right) and mean power spectrum of call plateau (left). Designations: dur_down, duration from the end of bugle plateau to the end of the bugle; dur_plat, plateau duration; dur_up, duration from onset to plateau; duration, bugle duration; g0beg, fundamental frequency at the onset of a call; g0end, fundamental frequency at the end of a call; g0max, maximum fundamental frequency; g0min, minimum fundamental frequency; g0plat, fundamental frequency of call plateau; gpeak, peak frequency of plateau; q25, lower power quartile of plateau; q50, medium power quartile of plateau; q75, upper power quartile of plateau. The spectrogram was created at 11.025 kHz sampling frequency, Fast Fourier Transform (FFT) 1024, Hamming window, frame 50%, overlap 93.75%.

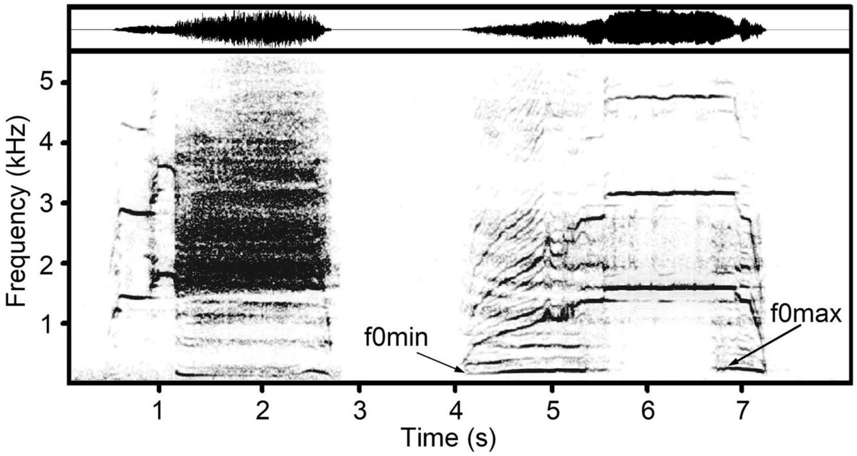

Figure 2 Wav-form (above) and spectrogram (below) of two rutting bugles of male Siberian wapiti. Left: bugle with deterministic chaos; right: bugle with additional low fundamental frequency f0. Designations: f0max, maximum low fundamental frequency; f0min, minimum low fundamental frequency. The spectrogram was created at 11.025 kHz sampling frequency, Fast Fourier Transform (FFT) 1024, Hamming window, frame 50%, overlap 93.75%.

the peripheral rutting stags (160 bugles) and bugles from harem-candidates (118 bugles). To estimate stability of vocal individuality with change of stag status from harem-candidate to harem-holder, we conducted cross-validation of bugles recorded from 6 stags when they already became harem-holders (120 bugles) using discriminant functions, created for bugles from the peripheral rutting stags and bugles from harem-candidates (278 bugles). We conducted another DFA to calculate the probability of classifying the bugles to the correct status using samples of bugles from the peripheral rutting stags (160 bugles) and harem-holders (120 bugles). In both DFAs we included 10 of 13 measured acoustic parameters: dur_up, dur_plat, dur_down, g0beg, g0end, g0max, gpeak, q25, q50 and q75. Duration was excluded from DFA analyses, because this parameter is a sum of the values dur_up, dur_plat and dur_down. The g0plat and g0min were excluded from the analyses because they were highly correlated with g0max and g0end, respectively.

We used Wilks' Lambda, to estimate the impact of each acoustic parameter in the DFA. For validating the DFA results, we calculated the values of probability of correctly classifying the bugles to individuals, by applying the permutation test for probability of incorrect classification in the DFA (Solow, 1990), with macros created in R. Random values were calculated from DFA on 1000 randomized permutations of datasets (Mundry & Sommer, 2007; Solow, 1990). For each distribution obtained with permutations, we noted whether the observed value exceeded 95% (950 values), 99% (990 values) or 99.9% (999 values) within the distributions (Mundry & Sommer, 2007; Solow, 1990). If the observed value exceeded 95%, 99% or 99.9% values within the distribution, we established that the observed value differed significantly from the random value with a probability of $P < 0.05$, $P < 0.01$ or $P < 0.001$, respectively (Briefer et al., 2010; Chelysheva et al., 2023; Solow, 1990).

Results

Timing of harem-holding

We considered it harem holding when the stags kept spatial proximity during at minimum 2 days with a group of hinds (of 5 or more), controlled hinds during their transitions and deterred rival stags. In cases when the stag temporally controlled a group of hinds for 1 day but then lost the control over them, we did not consider it a harem-holder. During the data collection period (15 days), the harem stags held their harems on average for 5.2 days (2, 4, 4, 4, 6 and 11 days in six different individuals). During 3 days, there was only one harem in the enclosure, during 9 days two harems, during 2 days three harems and during 1 day four harems.

Acoustic variation of bugles

The g0max of the bugles varied from 0.78 to 2.93 kHz (mean 1.56 ± 0.36 kHz) and the g0min varied from 0.12 to 1.18 kHz (mean 0.35 ± 0.19 kHz) (Table 1). Duration of the bugles varied from 1.37 to 5.67 s (mean 3.91 ± 0.61 s). Each bugle displayed a well-expressed plateau of g0; the plateau duration varied from 0.36 to 3.00 s (mean 1.34 ± 0.49 s), thus covering the most of total call duration (Table 1).

The bugles displayed both individual and status-related variation (Table 1, Fig. 3). Two-way ANOVA showed that the factor ‘individuality’ affected all of the 13 acoustic parameters, whereas the factor ‘status’ did not affect dur_plat or q25. Bugles of harem-holders ($n = 120$) compared to bugles of peripheral stags ($n = 160$) had shorter duration, shorter dur_up and dur_down, higher g0end and g0min, and higher gpeak, q50 and q75, but g0plat and g0max did not differ between these samples of bugles (Table 1). After winning a harem and changing status from harem-candidate to harem-holder, stags shortened the duration of their bugles as indicated by shortening of dur_up and dur_down, lowered g0beg, g0plat and g0max, increased g0end and g0min; however, they did not change gpeak and quartiles (apart from q75 which increased) (Table 1). Bugles of harem-candidates ($n = 118$) differed from the bugles of peripheral stags ($n = 160$) by a shorter dur_down and gpeak and all parameters of g0 (Table 1).

The f0 was found in 374 (94.0%) of the 398 bugles: in 90.6% of the 160 bugles of the peripheral stags, in 95% of the 120 bugles of harem-holders and in 97.5% of the 118 bugles of harem-candidates. Percent of bugles with f0 was higher in harem-candidates than in harem-holders ($\chi^2 = 4.17$, $P < 0.05$).

Bugle average f0max was 0.23 ± 0.04 kHz and bugle average f0min was 0.11 ± 0.03 kHz. The f0max did not differ between stags with different status (range: from 0.22 to 0.23 kHz). The f0min was the highest in the peripheral stags (0.12 ± 0.03 kHz) compared to harem-holders or harem-candidates (0.10 ± 0.03 kHz in both cases).

Deterministic chaos was found in 124 (31.2%) of the 398 bugles. Percent of bugles with deterministic chaos did not differ between the sample of 120 bugles from harem-holders (35.8%) and the sample of 118 bugles from harem-candidates (38.1%), but it was significantly lower (22.5%) in the sample of 160 bugles from peripheral stags ($\chi^2 = 5.38$, $P < 0.05$ and $\chi^2 = 6.79$, $P < 0.01$, respectively).

DFA for classifying bugles to individuals and status

For excluding the influence of stag status on DFA, we used the sample of bugles from peripheral stags ($n = 160$ bugles) and the sample of bugles from harem-candidates ($n = 118$ bugles), that is, the two sets of samples where the stags were not harem-holders. The DFA included 10 measured acoustic parameters (dur_up, dur_plat, dur_down, g0beg, g0end, g0max, gpeak, q25, q50 and q75). The average value of correct classification of the bugles to individuals with DFA was 53.2%, which was significantly higher than the level expected by chance as 19.9 ± 2.0%, min = 12.9%, max = 26.7% (permutation test, 1000 permutations, $P < 0.001$) (Table 2). In the order of decreasing importance, g0max, g0end and g0beg were mainly responsible for the discrimination of individuals by their bugles. However, among individuals, the value of correct assignment of the bugles varied from 15% to 95% and did not exceed the maximum value of the DFA chance level 26.7% for 2 individuals (Table 2). Although the average value of correct classification exceeded the chance value, only 12 individuals could be reliably recognized by their bugles. The average value of correct assignment of bugles to an individual was higher for harem-candidates (60.9%) compared to peripheral stags (47.5%) (Table 2).

We compared the stability of vocal individuality between harem-candidates and harem-holders. We conducted cross-validation of the sample of bugles from harem-holders ($n = 120$ bugles) using discriminant functions, created for the total sample of bugles from peripheral stags and harem-candidates ($n = 278$ bugles) (Table 2). The cross-validation revealed a strong decrease in assignment of the bugles to correct callers. The average value of correct assignment to individuals decreased from 60.9% to 36.7%. The value of correct assignment of bugles varied among harem-holders from 10% to 80% and did not exceed the maximum value of the DFA chance level of 26.7% for 3 of 6 individuals (Table 2). Thus, individualistic traits of the bugles were not retained with the change of individual stag status from a harem-candidate to a harem-holder.

We also conducted DFA for classifying the bugles to correct status, using the samples from peripheral stags (160 bugles) and harem-holders (120 bugles). The DFA included the same 10 measured acoustic parameters (dur_up, dur_plat, dur_down,

Table 1 Values (mean ± SD) of bugle parameters and the results of the nested two-way ANOVA for individual and status-related differences

		Bugles by status			ANOVA	
Acoustic parameter	All bugles ($n = 398$)	Peripheral stags ($n = 160$)	Harem-holders ($n = 120$)	Harem-candidates ($n = 118$)	Status differences	Individual differences
duration (s)	3.91 ± 0.61	3.14 ± 0.64^{a}	2.59 ± 0.49^{b}	2.93 ± 0.54^{c}	$F_{2,378} = 36.90$; $P < 0.001$	$F_{17,378} = 4.87$; $P < 0.001$
dur_up (s)	1.05 ± 0.52	1.10 ± 0.52^{a}	0.91 ± 0.55^{b}	1.12 ± 0.48^{a}	$F_{2,378} = 7.65$; $P < 0.001$	$F_{17,378} = 6.81$; $P < 0.001$
dur_plat (s)	1.34 ± 0.49	1.32 ± 0.52	1.37 ± 0.43	1.35 ± 0.53	$F_{2,378} = 0.50$; $P = 0.61$	$F_{17,378} = 6.23$; $P < 0.001$
dur_down (s)	0.52 ± 0.46	0.72 ± 0.57^{a}	0.31 ± 0.25^{b}	0.46 ± 0.32^{c}	$F_{2,378} = 37.56$; $P < 0.001$	$F_{17,378} = 3.59$; $P < 0.001$
g0beg (kHz)	0.63 ± 0.30	0.56 ± 0.29^{a}	0.63 ± 0.27^{b}	0.72 ± 0.32^{c}	$F_{2,378} = 14.00$; $P < 0.001$	$F_{17,378} = 13.35$; $P < 0.001$
g0plat (kHz)	1.50 ± 0.35	1.46 ± 0.32^{a}	1.46 ± 0.35^{a}	1.60 ± 0.37^{b}	$F_{2,378} = 14.01$; $P < 0.001$	$F_{17,378} = 25.60$; $P < 0.001$
g0end (kHz)	0.38 ± 0.22	0.31 ± 0.16^{a}	0.45 ± 0.26^{b}	0.40 ± 0.21^{c}	$F_{2,378} = 30.59$; $P < 0.001$	$F_{17,378} = 17.75$; $P < 0.001$
g0max (kHz)	1.56 ± 0.36	1.51 ± 0.32^{a}	1.55 ± 0.36^{a}	1.65 ± 0.41^{b}	$F_{2,378} = 11.23$; $P < 0.001$	$F_{17,378} = 28.65$; $P < 0.001$
g0min (kHz)	0.35 ± 0.19	0.29 ± 0.14^{a}	0.42 ± 0.23^{b}	0.37 ± 0.19^{c}	$F_{2,378} = 32.33$; $P < 0.001$	$F_{17,378} = 18.86$; $P < 0.001$
gpeak (kHz)	1.61 ± 0.54	1.51 ± 0.47^{a}	1.71 ± 0.62^{b}	1.66 ± 0.50^{b}	$F_{2,378} = 7.76$; $P < 0.001$	$F_{17,378} = 9.28$; $P < 0.001$
q25 (kHz)	1.38 ± 0.30	1.40 ± 0.31	1.34 ± 0.31	1.41 ± 0.28	$F_{2,378} = 1.90$; $P = 0.15$	$F_{17,378} = 11.92$; $P < 0.001$
q50 (kHz)	1.71 ± 0.46	1.62 ± 0.43^{a}	1.78 ± 0.51^{b}	1.74 ± 0.44^{b}	$F_{2,378} = 6.26$; $P < 0.001$	$F_{17,378} = 8.72$; $P < 0.001$
q75 (kHz)	2.30 ± 0.57	2.19 ± 0.56^{a}	2.45 ± 0.53^{b}	2.30 ± 0.58^{a}	$F_{1,266} = 11.11$; $P < 0.001$	$F_{17,378} = 12.14$; $P < 0.001$

Individual was nested within status (peripheral, harem-holder, harem-candidate). Designations: dur_down, duration from the end of bugle plateau to the end of the bugle; dur_plat, plateau duration; dur_up, duration from onset to plateau; duration, bugle duration; g0beg, beginning value of g0; g0end, end value of g0; g0max, maximum value of g0; g0min, minimum value of g0; g0plat, g0 plateau value; gpeak, peak frequency of plateau; q25, lower power quartile of plateau; q50, medium power quartile of plateau; q75, upper power quartile of plateau. Different superscripts (^{a,b,c}) indicate statistically different values (Tukey post hoc, $P < 0.05$).

g0beg, g0end, g0max, gpeak, q25, q50 and q75). The DFA for status showed the average value of correct assignment of bugles of 78.9% (88.1% for peripheral stags and 66.7% for harem-holders), which was significantly higher than the level expected by chance as 55.9 ± 2.7%, min = 47.3%, max = 66.3% (permutation test, 1000 permutations, $P < 0.001$). In the order of decreasing importance, dur_down, g0end and q75 were mainly responsible for the discrimination of status from the bugles. As the values of correct assignment of the bugles to peripheral stags and to harem-holders exceeded the maximum value of the DFA chance level, the bugles provided reliable cues to stag status.

Discussion

Status and individuality of stag rutting calls

This study showed that acoustic traits of Siberian wapiti rutting bugles encode both stag harem status and stag individuality. We also found that different acoustic parameters encoded status and individuality. Traits of stag status were related to the duration of the start and end part of their bugles and with the beginning and end fundamental frequencies (g0) of the bugles. At the same time, traits of individuality were related to bugle g0max. This is different from European fallow deer bucks, in which individuality and quality features can be encoded in the same components of their rutting calls (Briefer et al., 2010).

Acoustic features associated with harem-holding status in male Siberian wapiti included shortened duration of the beginning and the end parts of their rutting bugles and high g0min and g0end. These features discriminate between harem-holders and peripheral stags and arose in the harem-holders when they changed their status from harem-candidates to harem-holders (Table 1). In contrast to Siberian wapiti, duration traits do not encode male status neither in the roars of red deer stags nor in the groans of fallow deer bucks (Briefer et al., 2010; Reby & McComb, 2003b; Vannoni & McElligott, 2008). For rutting red deer stags, the most reliable traits of male quality are the low formant frequencies of the roars, but the fundamental frequency does not display a relationship with stag harem/mating status (Reby & McComb, 2003b). In rutting Eurasian fallow deer bucks, the low f0min of the groans is the acoustic trait

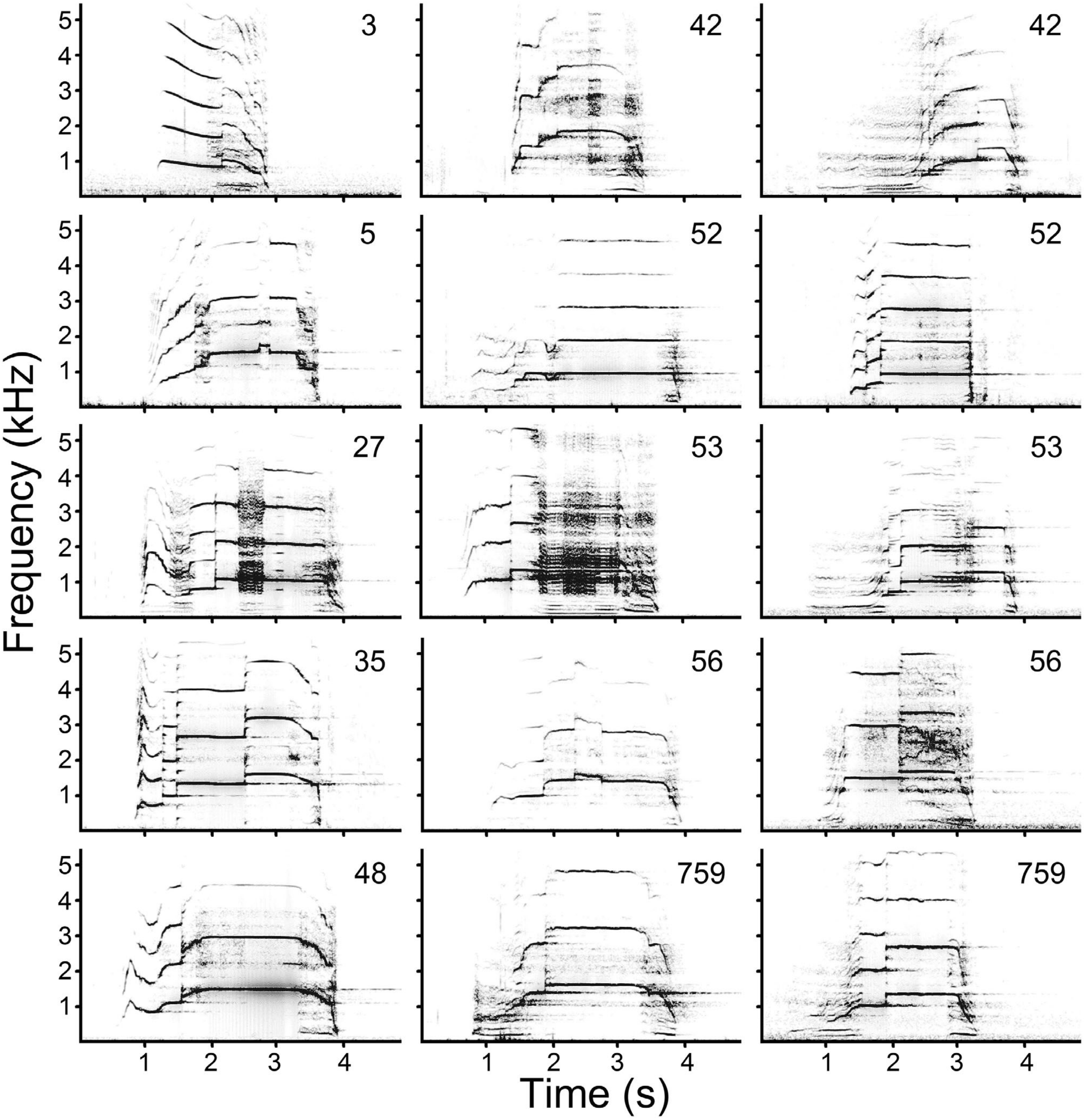

Figure 3 Spectrograms illustrating individual and status-related variation of rutting bugles of male Siberian wapiti. The numbers indicate individual stags. The left column contains the bugles from peripheral stags; the middle column contains the bugles from harem-candidate stags; the right column contains the bugles from the same stags as in the middle column, when they changed their status from harem-candidates to harem-holders. The spectrogram was created at 11.025 kHz sampling frequency, Fast Fourier Transform (FFT) 1024, Hamming window, frame 50%, overlap 93.75%.

labelling the high-ranking bucks (Briefer et al., 2010; Vannoni & McElligott, 2008). In contrast, in Siberian wapiti in this study, the higher g0min of the bugles marked the higher-ranking stags, which were able to hold harems.

Traits of acoustic individuality are related to g0max of the bugles, which, as a rule, in Siberian wapiti is equal to the fundamental frequency of bugle plateau (Golosova et al., 2017; this study). After a stag has won a harem and changed status

Table 2 Assignment of bugles to a predicted individual stag caller with DFA and cross-validations

Stag ID	Status	*n* bugles	*n* correctly assigned bugles, DFA	% correctly assigned bugles, DFA	% correctly assigned bugles, cross-validation
stag 3	P	20	10	50.0	
stag 5	P	20	3	15.0	
stag 27	P	20	19	95.0	
stag 35	P	20	7	35.0	
stag 36	H	20	12	60.0	80.0
stag 42	H	18	10	55.6	25.0
stag 48	P	20	11	55.0	
stag 52	H	20	11	55.0	10.0
stag 53	H	20	11	55.0	25.0
stag 56	H	20	12	60.0	45.0
stag 57	P	20	11	55.0	
stag 637	P	20	11	55.0	
stag 759	H	20	16	80.0	35.0
stag 787	P	20	4	20.0	
Total		278	145	53.2	36.7

The DFA was conducted based on the total sample of bugles from the peripheral rutting stags (160 bugles) and harem-candidates (118 bugles). Cross-validation of bugles of harem-holders (120 bugles) was conducted using discriminant functions created for bugles from the peripheral rutting stags and bugles from harem-candidates (278 bugles). Designations: H, harem-candidates/harem-holder; *n*, number of bugles; P, peripheral stags.

from harem-candidate to harem-holder, the acoustic parameters of its rutting calls also change and the bugles do not retain their individualistic traits, although g0max remains unchanged (Tables 1 and 2). In the bugles of Siberian wapiti in this study, individuality was not high, although significantly higher than the chance level and reliably discriminated the bugles of 12 out of 14 stags from the total sample (Table 2).

Vocal identity across sex and age classes

Our results confirmed a common rule that male rutting calls of artiodactyls are not strongly individualistic and display from average to low level of individual distinctiveness. For example, classifying 147 rutting groans of 4 fallow deer bucks using neural network showed 87.9% correct assignment to individuals (Reby et al., 1998). Furthermore, classifying 153 rutting groans from 16 fallow deer bucks using DFA provided 36.6% correct assignment to individuals (Vannoni & McElligott, 2007), and classifying 305 rutting groans from 14 fallow deer bucks, recorded during 3 rutting seasons using DFA, showed 38.7% average value of correct assignment to individuals (Briefer et al., 2010). Cross-validation of the groans recorded in the following years by discriminant functions created based on the calls of the previous years showed the decrease of the average value of correct assignment to individual to 21.6% (Briefer et al., 2010). However, classifying bouts of rutting roars and separate roars from 7 red deer stags using the hidden Markov model computed on the cepstral coefficients provided 93.4% correct assignment to individual; cross-validation values varied from 58.1% to 84.9% depending on the number of bouts used for training (Reby et al., 2006).

Compared with relatively poor and instable acoustic cues to individual identity in the rutting bugles of male Siberian wapiti, the contact calls of hinds and adolescent Siberian wapiti from the same herd display well-expressed individualistic traits. For example, DFA based on acoustic variables of 134 oral contact calls of 9 hinds and 129 calls of 9 adolescents accurately classified to individual 92.5% of hind calls and 96.9% of adolescent calls (Sibiryakova et al., 2018). As in stag bugles in this study, the g0max in the contact calls of Siberian wapiti hinds and adolescents was among the parameters mainly contributing to vocal individuality (Sibiryakova et al., 2018).

Female and young red and fallow deer have less individualized contact calls than female and young Siberian wapiti. For example, for female fallow deer, DFA assigned 115 calls from 15 adult females to correct individuals with 81.1% accuracy. For 140 contact calls of 12 offspring, the accuracy was only 32.1% (Torriani et al., 2006). Similarly, for red deer hinds of the Spanish subspecies *Cervus elaphus hispanicus*, DFA correctly assigned to individual 77.0% of oral contact calls and 61.8% of nasal contact calls (Sibiryakova et al., 2015). For contact calls of calves, DFA correctly assigned to individual 61.1% of oral contact calls and 64.2% of nasal contact calls (Sibiryakova et al., 2015).

Taken together, we can propose, therefore, that stronger vocal individuality is generally more important for mother and young cervids, for restoring spatial proximity, than for rutting stags. For stags producing rutting calls, acoustic traits of quality may prevail over the traits of identity (Briefer et al., 2010).

Nonlinear phenomena in stag rutting calls

In red deer, rutting roars with a large amount of chaos (‘harsh roars’) are related to a higher competition between rival stags (Reby & McComb, 2003b). Compared to a previous study on the same farm during the rutting period of 2015 (Golosova et al., 2017), the percent of bugles with deterministic chaos recorded in this study, was substantially higher (31.2% vs. 4.8%). This variation in the percentages of 'harsh bugles' between rutting seasons was probably related to different calendar dates of the observations, done at periods of different stag rutting vocal activity.

Furthermore, percent of calls with the second (lower) fundamental frequency (f0) in 2018 was somewhat higher than in 2015 (94.0% vs. 86.9%) (Golosova et al., 2017). The values of f0 in the bugles of Siberian wapiti were similar to those obtained in previous studies on wapiti (from 107 to 210 Hz, Golosova et al., 2017; Reby et al., 2016) and practically coincided with f0 of rutting roars of red deer (reviewed in Volodin et al., 2019). Although we did not analyse formants, we can note that some bugles of the Siberian wapiti stags in this study displayed patterns similar to bugles of North American wapiti, in which g0 jumps from one formant to the next in the ascending phase (Reby et al., 2016).

Vocal identity in stag rutting calls: Applicability to censuses practice

Our study showed that male Siberian wapiti can produce a few similar rutting bugles and then produce the bugles of different acoustic structure. This results in a relatively low individuality of their bugles. Consistently, for European red deer, a multi-year study showed that censuses of stags based on their apparently 'individualistic' roars provide incorrect data of animal abundance (Douhard et al., 2013). Furthermore, subjective estimations of stag 'age', 'maturity' and 'quality' based on human-ear perception of fundamental frequency of Siberian wapiti bugles (Zyryanov & Tyurin, 2012), may be incorrect, because this acoustic parameter does not appear to be associated with stag harem-holding status.

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Author contributions

O. V. Sibiryakova: Conceptualization; methodology; software; formal analysis; visualization; writing – review and editing. I. A. Volodin: Conceptualization; methodology; investigation; software; validation; resources; data curation; writing – original draft; writing – review and editing; project administration. E. V. Volodina: Conceptualization; methodology; investigation; resources; writing – original draft; writing – review and editing.

Conflict of interest

The authors declare no competing interests.

Data availability statement

Audio file with rutting bugles is included in this article as Audio S1. Additional raw data will be available from the corresponding author on reasonable request.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Audio S1. Audio wav-file of rutting bugles of male Siberian wapiti. There are 15 bugles from 10 individuals: bugles 1–5 are from peripheral stags ## 3, 5, 27, 35 and 48; bugles 6–10 are from harem-candidate stags ## 42, 52, 53, 56 and 759; and bugles 11–15 are from harem-holder stags ## 42, 52, 53, 56 and 759.