

Vocal activity and acoustic structure of the rutting calls of Siberian wapiti (*Cervus elaphus sibiricus*) and their imitation with a hunting luring instrument

Ilya A. Volodin*, Elena V. Volodina, Roland Frey & Inna L. Maymanakova

ABSTRACT. This study on Siberian wapiti (*Cervus elaphus sibiricus*) provides data on rutting vocal activity (bugles per hour), collected using four synchronized automated recording systems in natural habitats in the Western Sayan Mountains (Russia). Also, this study provides first comparison of naturally produced male bugles with their imitation using a traditional hunting technique of blowing into a hollow pipe with a mouthpiece. Stag vocal activity weakly negatively correlated to air temperature and ceased completely during three very cold days with snowfall. Stag bugles ($n = 153$) were high-pitched, with an average maximum fundamental frequency (f_0) of 1.23 ± 0.21 kHz, a minimum f_0 of 0.29 ± 0.05 kHz and a duration of 3.07 ± 0.52 s. Hind alarm barks ($n = 12$) were significantly lower in maximum $f_0 = 0.93 \pm 0.08$ kHz, significantly higher in minimum $f_0 = 0.34 \pm 0.06$ kHz and much shorter (0.20 ± 0.03 s) compared to male bugles. Male bugles were similar in the acoustic structure with their imitations, produced by a human using a luring wind instrument ($n = 27$), what provides a support to the hypothesis of forced airflow through a narrow, highly tensed larynx and vocal tract as a production mechanism of the extremely high-pitched bugles of wapiti.

KEY WORDS: mammals, Cervidae, vocal behaviour, rutting bugles, alarm calls.

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Вокальная активность и акустическая структура гонных криков сибирского марала (*Cervus elaphus sibiricus*) и их имитация с помощью охотничьего манного инструмента

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РЕЗЮМЕ. Это исследование сибирского марала (*Cervus elaphus sibiricus*), в котором приведены данные по гонной вокальной активности (криков в час), собранных с использованием четырех синхронизированных автоматических записывающих систем в естественных местообитаниях марала в Западных Саянах (Россия). Кроме того, в этом исследовании впервые приводится сравнение естественных звуков маралов с их имитацией с помощью традиционной охотничьей методики продувания воздуха в полую трубку с мундштуком. Вокальная активность самцов марала слабо отрицательно коррелировала с температурой воздуха и полностью прекратилась в течение трех очень холодных дней со снегопадом. Звуки самцов ($n = 153$) были высокочастотными, со средней максимальной основной частотой (f_0) 1.23 ± 0.21 кГц, минимальной f_0 0.29 ± 0.05 кГц и длительностью 3.07 ± 0.52 с. Тревожные лаи самки ($n = 12$) были достоверно ниже по максимальной $f_0 = 0.93 \pm 0.08$ кГц, достоверно выше по минимальной $f_0 = 0.34 \pm 0.06$ кГц и намного короче (0.20 ± 0.03 с) по сравнению с гонными звуками самцов. Имитированные ($n = 27$) и естественные гонные звуки самцов были очень сходными по акустической структуре, что косвенно подтверждает гипотезу усиленного продувания воздуха через узкое отверстие в гортани как механизма звукопродукции у маралов и вапити.

КЛЮЧЕВЫЕ СЛОВА: млекопитающие, Cervidae, вокальное поведение, гонные крики, крики тревоги.

Introduction

The species *Cervus elaphus* L., 1758 is widely distributed all over the Holarctic region. Within this geographical area, *C. elaphus* diverged into a number of subspecies or closely related species differing substantially by their body size (Heptner *et al.*, 1961; Fedosenko, 1980; Geist, 1998; Danilkin, 1999), morphology (Shtarev, 1970; Geist, 1998; Frey *et al.*, 2012; Frey & Riede, 2013), and also by the acoustic structure of stag rutting calls (Nicol'skii *et al.*, 1979, 1987; Nicol'skii, 1984; Geist, 1998; Frey & Riede, 2013; Volodin *et al.*, 2013). Phylogenetic studies suggest a close relationship between Siberian and American wapiti (*Cervus elaphus sibiricus* Severtzov, 1872 and *C. e. canadensis* Erxleben, 1777 or *C. canadensis*), which divergence was caused by geographical isolation by Bering Sea occurred only 9000 years ago (Mahmut *et al.*, 2002; Ludt *et al.*, 2004; Kuznetsova *et al.*, 2012). As a consequence, vocalizations of Siberian wapiti are much more similar to those of American wapiti than to European red deer (Tembrock, 1965; Nikolski & Wallschlagler, 1983; Volodin *et al.*, 2013). European red deer stags produce low-pitched roars with fundamental frequency (f_0) ranges from 40 to 380 Hz: Corsican *C. e. corsicanus* Erxleben, 1777 (mean $f_0 = 40$ Hz: Kidjo *et al.*, 2008); Scottish *C. e. scoticus* Lonnbert, 1906 (mean $f_0 = 107$ –174 Hz: Long *et al.*, 1998; Reby & McComb, 2003); Iberian *C. e. hispanicus* Hilzheimer, 1909 (mean $f_0 = 180$ –186 Hz: Frey *et al.*, 2012; Passilongo *et al.*, 2013); *C. e. hippelaphus* Erxleben, 1777 (maximum $f_0 = 273$ Hz: Bocci *et al.*, 2013). In contrast, the available data for American and Siberian wapiti suggest produce high-pitched bugles with an f_0 above 1000 Hz: Siberian wapiti from Altai *C. e. sibiricus* (Nicol'skii, 2011); Canadian wapiti *C. e. canadensis* (Struhsaker, 1968); Roosevelt wapiti *C. e. roosevelti* Merriam, 1897 (Bowyer & Kitchen, 1987), Tule wapiti *C. e. nannodes* Merriam, 1905 (Volodin *et al.*, 2013) and Rocky Mountain wapiti *C. e. nelsoni* Bailey, 1935 (Feighny *et al.*, 2006; Frey & Riede, 2013). Bactrian stags *C. e. bactrianus* Lydekker, 1900, living today in the area of origin of *C. elaphus* in Central Asia (Heptner *et al.*, 1961; Mahmut *et al.*, 2002; Ludt *et al.*, 2004), produce both a low and a high f_0 , either singly or simultaneously (Nicol'skii, 1975; Volodin *et al.*, 2013). At expansion in opposite directions from the centre of origin, the European red deer lost the high f_0 , whereas the Siberian and American wapiti lost the low f_0 (Frey & Riede, 2013; Volodin *et al.*, 2013).

The reasons and triggering factors of this vocal divergence are unclear to date, although its anatomical basis was investigated in detail (Titze & Riede, 2010; Frey & Riede, 2013). The puzzle of vocal diversity of wapiti is especially incomplete, and acoustic variation has been considered in some detail only for Canadian wapiti (Feighny *et al.*, 2006). In this context, the study of Siberian wapiti is promising, as their rutting vocalization can be expected to be intermediate in acoustic

structure between Bactrian and American subspecies and, at the same time, to differ strongly from those of European subspecies. Published evidence on the acoustic structure of Siberian wapiti is scarce and limited to few spectrograms of rutting bugles (Nicol'skii *et al.*, 1979; Nikolski & Wallschlagler, 1983; Nicol'skii, 1984, 2011; Volodin *et al.*, 2013). Factors affecting the dynamics of vocal activity in Siberian wapiti during the rut were not quantitatively estimated so far.

Another focus of this work was the imitation of stag rutting bugles by human hunters using traditional, self-made devices with a pipe-like luring instrument with mouthpiece. An experienced hunter can reliably imitate the rutting bugles of Siberian wapiti to effectively attract stags and hinds to approach the hunter at close distance. Therefore, the luring instrument provides a model of stag vocal production. The mechanisms of sound production of very high-frequency bugles by wapiti with their long vocal folds are poorly understood so far, in spite of the strong interest of researchers in this problem (Riede & Titze, 2008; Titze & Riede, 2010; Frey & Riede, 2013; Volodin *et al.*, 2013). So, a comparison of the acoustics of stag bugles and their imitations by hunters might be interesting, as they potentially can highlight relevant details of the mechanisms of sound production in wapiti.

Siberian wapiti are very elusive and live in habitats difficult to access, however they produce loud, long-distance calls in the rutting period. Therefore, automated recording systems are useful for studying their vocal behaviour in the wild (Blumstein *et al.*, 2011; Mennill *et al.*, 2012). The automated recording systems can be programmed to a fixed time schedule and air temperature can be registered simultaneously. Our purpose was to compare the acoustics of stag rutting bugles, hind alarm calls and bugles imitated by humans and to document relationships between rutting vocal activity of stags and air temperature.

Methods

Data were collected in period from 16 to 25 September, 2012 at the northern foothills of West Sayan Mountains, in the upper parts of Kayzas Valley, near the border of the "Malyi Abakan" territory of the State Natural Reserve "Khakassian", Republic of Khakassia, Russia (52°07'19"N, 89°32'15"E). This is a narrow valley, with a spring, in the upper part of mountain taiga, extending in meridian direction with a noticeable descent to the north from 1680 m. Forests of *Abies* sp. and *Pinus* sp. with large clearings cover the stony slopes of the valley.

We used four automated recording systems Song Meter SM2+ (Wildlife Acoustics Inc., Concord, MA, USA) for acoustic recordings (22.05 kHz, 16 bit, stereo). Each recording system was equipped with two omni-directional microphones, fixed horizontally under an angle of 180 degrees relative to each other. The recording systems were placed on the valley slopes in a

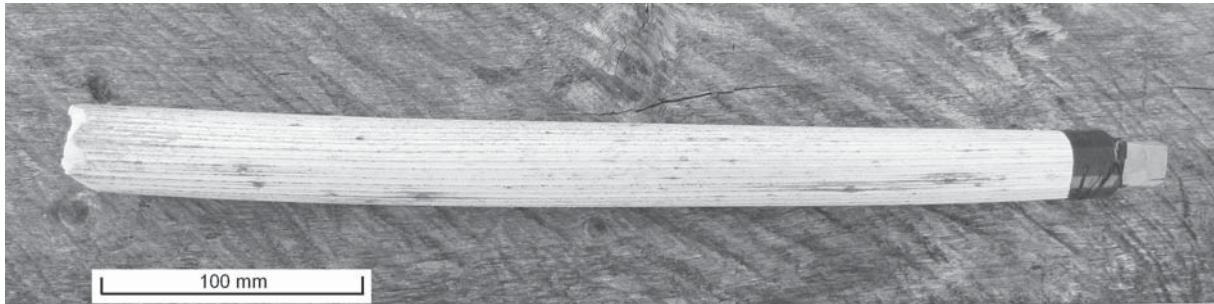


Fig. 1. Traditional instrument of hunters for luring male and female Siberian wapiti. The body of this instrument is made of a hollow stem of a dry plant *Heracleum* sp. The mouthpiece was obtained by careful trimming of a piece of double-folded birch bark. In the current study, we used this instrument for imitating the rutting bugles of male Siberian wapiti.

broken line. The distances between neighboring recording systems ranged from 500 to 3400 m between the most distant recording systems. Two of the recording systems were stationary, whereas two others were transferred to various sites during the data collection period.

Sound recording period was set to 15 hours per day, from 17:00 to 07:50 in a 10 min recording/10 min interval schedule, synchronously in all four recording systems. During sound recording, the recording systems registered the air temperature every 5 min. Duration of sound recordings with four automated recording systems was 320 hours in total. During all period of data collection, researchers were in the vicinity of the recording systems (about 700 m to the nearest). During daylight hours, when the recording systems did not record, researchers walked across the area for revealing places of high rutting activity of Siberian wapiti (feces, tracks, places where stags dig the ground with their antlers, places where stags had rubbed their antlers along young trees).

We confronted sounds recorded synchronously by different recording systems and prepared a sample of 153 rutting bugles in total, where each recorded call was included only once. The number of recorded calls for each hour of recording allowed to calculate the dynamics of male vocal activity on an hourly basis (averages for a given hour, calculated for all 14 days) and on a daily basis (daily averages, calculated for all 15 hours of recording per day). For each hour, we also calculated the average temperature, and by the same way as for the calls, we calculated the dynamics of the average temperature per hour and per day.

To describe the acoustic structure of male rutting bugles we measured the maximum f_0 and the duration of each call. The minimum f_0 was measured only in calls of good quality, i.e. not strongly degraded by propagation distance and environmental obstacles. For the acoustic measurements, we used Avisoft SASLab Pro software (Avisoft Bioacoustics, Germany, Berlin). Spectrograms were created with a sampling rate of 22.05 kHz, Hamming window, Fast Fourier Transform 1024, frame 50%, and overlap 75%.

We also recorded and analysed alarm calls of one adult female of Siberian wapiti, consisting of a series of 12 barks, produced by the female after having noticed two observers, who had attracted her imitating male rutting bugles. In addition, we analysed 27 imitated bugles produced by a hunter using a hand-made luring instrument. The body of the instrument was constructed by cutting out a hollow piece of stem of a dry plant *Heracleum* sp. The mouthpiece was obtained by trimming a double-folded small piece of birch bark (Fig. 1). The length of the instrument was 420 mm without mouthpiece; its internal diameter was 22 mm. For recording the female alarm barks and the imitated male bugles we used a solid state recorder Marantz PMD-660 (D&M Professional, Kanagawa, Japan) with a Sennheiser K6-ME66 microphone (Sennheiser Electronic, Wedemark, Germany). In the female alarm barks and in the imitated male bugles we measured the same acoustic variables and analysed them with the same settings as the natural male rutting bugles.

All statistic analyses were made with STATISTICA, v. 6.0 (StatSoft Inc., Tulsa, OK, USA). All means are given as mean \pm SD. For estimating the influence of air temperature on the dynamics of vocal activity we used the Spearman correlation. As some distributions of values departed from normality (Kolmogorov-Smirnov test), we used the non-parametrical Mann-Whitney U -test for comparing the acoustic parameter values among stag rutting bugles and bugles imitated by humans.

Results

Our observations showed that the upper parts of the Kayzas Valley were indeed a rutting place of Siberian wapiti. This was obvious from acoustic recordings by the automated recording systems, the presence of large amounts of old and fresh feces, damaged young trees and from tracks in the freshly fallen snow. In addition, during the data collection we met one adult male and one adult female, who both called in response to imitated male rutting bugles produced by a human. Judging from sequential recordings by the recording systems and from tracks in the snow, the stags regularly moved during the period of data collection.

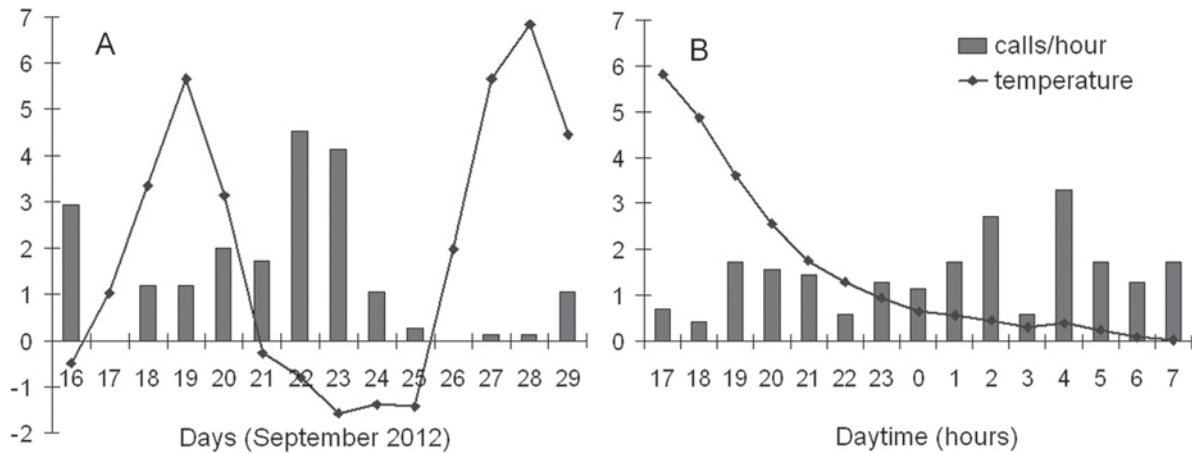


Fig. 2. Dynamics of male Siberian wapiti rutting vocal activity and air temperature. Vertical bars represent average numbers of bugles/hour and points connected with line represent average values of air temperature/hour: (A) in each day through the study period from 16 to 29 September 2012; (B) in each hour of day and night from 17:00 to 07:50.

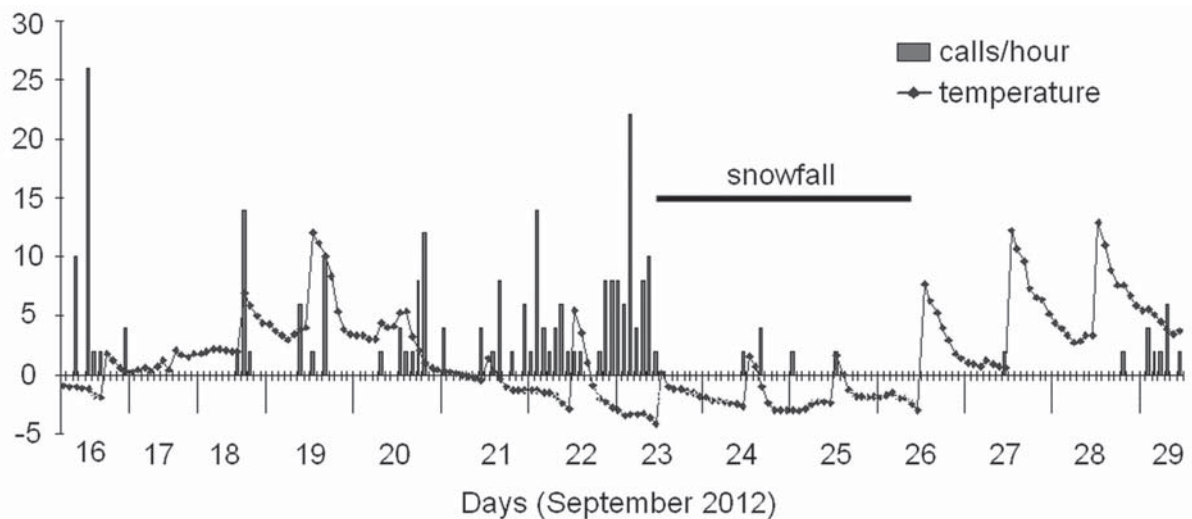


Fig. 3. Dynamics of male Siberian wapiti rutting vocal activity and air temperature, calculated for individual hours over the entire data collection period. Vertical bars represent average numbers of bugles/hour and points connected with line represent average values of air temperature/hour. The black horizontal bar indicates three days of cold and windy weather with strong snowfall.

During our study we did not observe male or female aggregations, so probably animals were dispersed over a large area. Nevertheless, the recorded data documented a few male responses to each other.

The number of male bugles was unevenly distributed among the days of recording (Fig. 2). The maximum number of calls (4.53 per hour) was registered on September 22, i.e. the day preceding the fall of air temperature that was accompanied by strong snowfall and wind. The number of bugles per hour negatively correlated with air temperature, although the correlation between air temperature and the number of bugles per hour was not significant ($r_s = -0.42$, $p = 0.13$, $n = 14$).

The number of bugles between the hours of a day was distributed relatively evenly, however during the first half of the night (between 20:00 and 01:00) the

stags produced about one third less bugles compared to the second half of the night (between 02:00 and 07:00), i.e. 1.29 and 1.88 bugles per hour respectively (Fig. 2). Within days, the number of bugles per hour also negatively correlated with air temperature, but correlation did not reach significance ($r_s = -0.39$, $p = 0.15$, $n = 15$).

However, comparing the number of calls and air temperatures per hour over the entire data collection period, we found a significant negative correlation between the number of calls with the air temperature ($r_s = -0.15$, $p < 0.05$, $n = 180$). Vocal activity nearly ceased after September 23 (Fig. 3). This coincided with the decrease of air temperature, wind, snowfall and development of 15 cm snow cover. Therefore, although the stag vocal activity increased at temperatures slightly

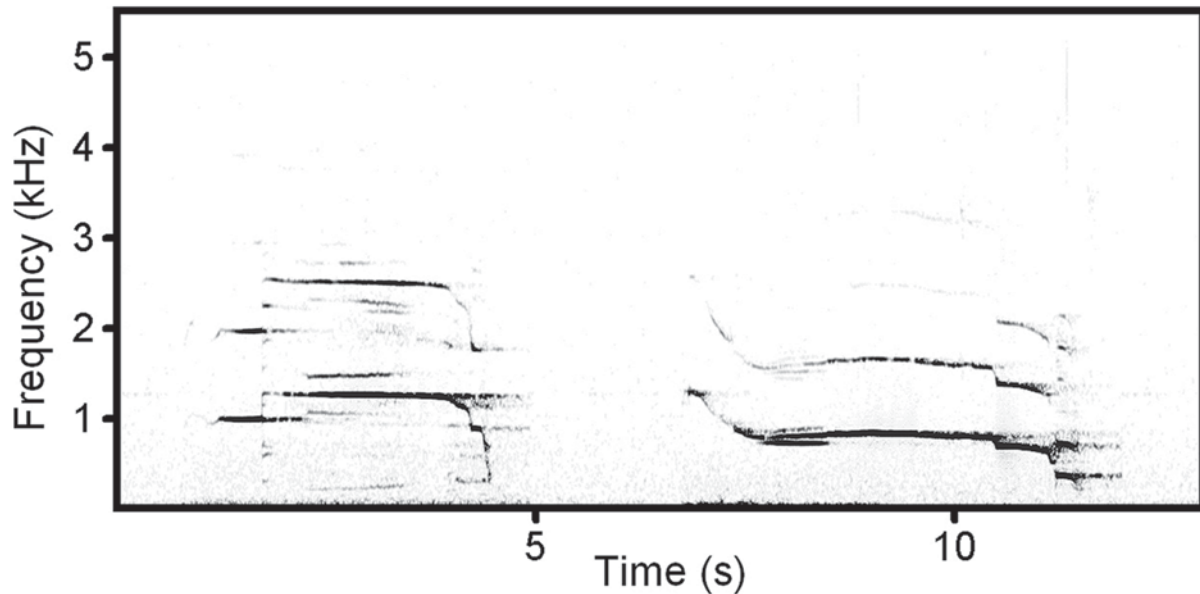


Fig. 4. Spectrogram of two rutting bugles of male Siberian wapiti, recorded by the automated recording systems.

Table 1. Values (mean \pm SD; min–max) for acoustic variables of Siberian wapiti stag rutting bugles, bugles imitated by a human, and Mann-Whitney U -test results of their comparison. Acoustic variables: maximum f_0 — the maximum fundamental frequency; minimum f_0 — the minimum fundamental frequency; duration — duration of bugles (in seconds).

Acoustic variable	Stag bugles	Imitated bugles	Mann-Whitney U -test
Maximum f_0 (kHz)	1.23 \pm 0.21 0.79–1.89 $n = 153$	1.34 \pm 0.21 1.03–1.89 $n = 27$	$U = 1470, Z = 2.38,$ $p < 0.05$
Minimum f_0 (kHz)	0.29 \pm 0.05 0.23–0.40 $n = 13$	0.87 \pm 0.05 0.77–0.96 $n = 27$	$U = 0, Z = 5.07,$ $p < 0.001$
Duration (s)	3.07 \pm 0.52 2.09–4.63 $n = 54$	3.19 \pm 0.59 2.12–4.53 $n = 27$	$U = 647, Z = 0.82,$ $p = 0.41$

below zero, it nearly stopped during strong snowfall with wind.

Most of the recorded male rutting bugles were substantially degraded because of large distances between the calling animals and the recording systems and because of the landscape complex relief. Most rutting calls were single bugles, and only some of them contained a few short calls subsequent to one longer bugle (Fig. 4). We measured acoustic variables only from the long bugles (Tab. 1). The maximum f_0 could be measured in all recorded bugles and was 1.23 \pm 0.21 kHz on average. The minimum f_0 (0.29 \pm 0.05 kHz) and the duration (3.07 \pm 0.52 s) were measured only in bugles of good quality, i.e. not strongly degraded by propagation distance and environmental obstacles (Tab. 1).

The alarm barks of the adult female Siberian wapiti (Fig. 5) had a lower maximum f_0 (0.93 \pm 0.08 kHz, $n = 12$) and a higher minimum f_0 (0.34 \pm 0.06 kHz, $n = 10$) compared to the male rutting bugles. The duration of the female barks was 15 times shorter than the male rutting bugles and lasted only 0.20 \pm 0.03 s.

The imitated bugles were of high-frequency and long duration (Fig. 6). The average maximum f_0 of the imitated bugles was 1.34 \pm 0.21 kHz, the average minimum f_0 was 0.87 \pm 0.05 kHz, and the average duration was 3.19 \pm 0.59 s (Tab. 1). A comparison of natural male rutting bugles with the imitated ones revealed a close similarity in the acoustic structure (Tab. 1). The natural bugles did not differ from the imitated ones by duration; the maximum f_0 was slightly but significantly

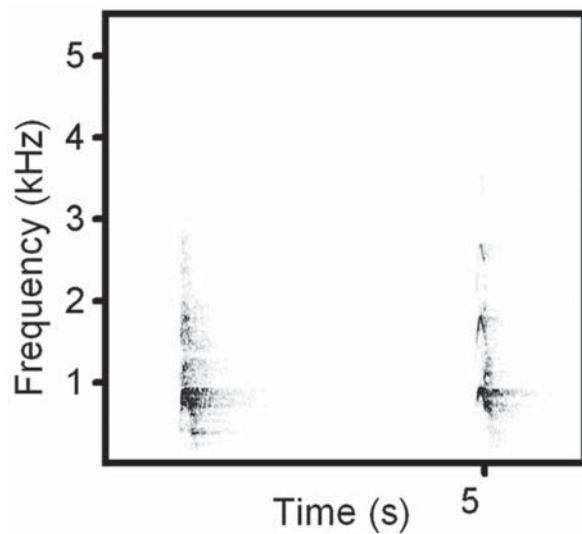


Fig. 5. Spectrogram of two alarm barks of an adult female Siberian wapiti, which had become aware of human observers.

wapiti, which also produce mainly single high-pitched long bugles (Nicol'skii *et al.*, 1979; Feighny *et al.*, 2006). The duration of bugles of the Siberian wapiti from Altai is usually more than 2–3 s, and the maximum f_0 reaches 1.50 kHz (Nicol'skii *et al.*, 1979; Nicol'skii, 2011). The maximum f_0 of Canadian wapiti exceeds 2 kHz, and the duration is 2.4–2.9 s (Struhsaker, 1968; Feighny *et al.*, 2006), whereas the maximum f_0 of male Roosevelt wapiti rutting bugles exceeds 1.5 kHz (Bowyer & Kitchen, 1987).

Compared to Siberian wapiti females, the Canadian wapiti female alarm barks also have a high maximum f_0 and a comparable short duration of around 0.25 s (Struhsaker, 1968). Scottish red deer females produce alarm barks of a similar short duration (0.22 s), but their maximum f_0 , however, is much lower (0.15 kHz) (Long *et al.*, 1998). In contrast to our study, alarm barks of female Roosevelt wapiti were registered in the non-rutting period only (Bowyer & Kitchen, 1987).

The acoustics of rutting bugles of male Siberian wapiti closely resembled the imitated bugles. We observed the similarity in the overall pattern of frequency

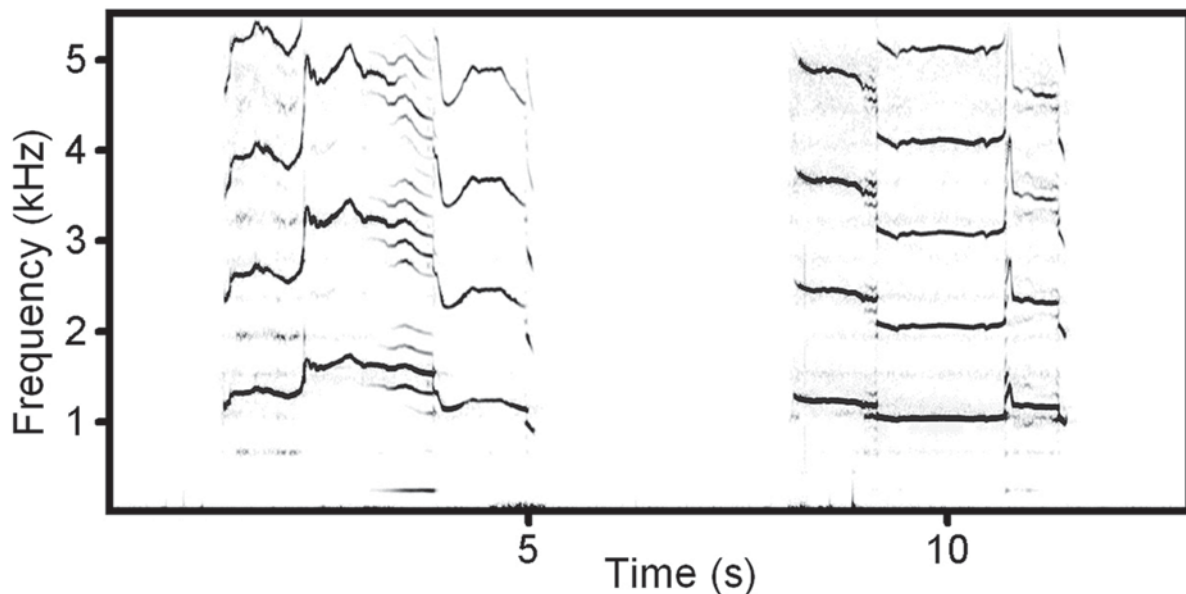


Fig. 6. Spectrogram of imitated male bugles of Siberian wapiti. Imitation was performed by an experienced human hunter with the traditional luring instrument depicted in Fig. 1.

higher in the imitated bugles, and only the minimum f_0 was almost three times lower in the natural bugles than in the imitated ones. The minimum f_0 degraded much stronger with distance compared to the maximum f_0 , so it was missing in about 90% of the spectrograms of bugles that were recorded at far distance.

Discussion

The acoustic structure of the rutting bugles of male Siberian wapiti in this study was similar to those of Siberian wapiti from Altai and from North American

modulation and in the combination of a high f_0 with a prolonged duration (Nicol'skii *et al.*, 1979). In both natural and imitated bugles, the fundamental frequency increased stepwise up to plateau and then decreased stepwise to the end of a call. In some cases the similarity between imitated bugles and natural bugles of male Siberian wapiti extended to fine details of the acoustic structure, such as the appearance of a low-frequency band, visible both in the left natural bugle in Fig. 4 and in the left imitated bugle in Fig. 6. This provides additional support to a hypothesis of forced airflow through a narrow, highly tensed larynx and vocal tract as a

production mechanism of the extremely high-pitched bugles of wapiti (Frey & Riede, 2013). This hypothesis assumes incompatibility of this high impedance mechanism with the simultaneous production of a low fundamental frequency, produced by vibration of more relaxed vocal folds. Blowing into the luring pipe through the attached rigid, slit-like mouthpiece produced a low frequency band in the spectrogram. Therefore, the origin of a similar low-frequency band in the natural bugles of Siberian wapiti, too, might not be affected by vibration of the vocal folds. Apart from our study, the low-frequency band in the spectrogram of the bugles of male Siberian wapiti was already described by Nikol'skii (2011). Producing bugles by means of luring pipes of variable lengths and diameters may be considered as a kind of primitive model of vocal production in wapiti. We do not know, however, whether the low-frequency bands are restricted to the bugles of Siberian wapiti or can also be found in other Asian and North American wapiti.

During our study we did neither observe male nor female aggregations, so the males and females were probably dispersed over a large area. Some authors confirm that, during the rut, male Siberian wapiti keep a distance from each other and rarely engage in direct physical conflict (Shtarev, 1970; Fedosenko, 1980), however one stag aggregation was documented (Nicol'skii, 1991). Rutting aggregations of females and males in a restricted area are found in Bactrian, Caucasian (*C. e. maral* Gray, 1850), Iberian and Canadian subspecies, so that the researcher usually can observe several stags and hinds simultaneously (Struhsaker, 1968; Pereladova, 1981; Frey *et al.*, 2012). Possible explanation for the lack of rutting aggregations in our study site is the short period of data collection, atypical weather, or disturbance of the animals by the presence of humans in the area covered by the automated recording systems.

We could not directly estimate the maximum propagation distance for the rutting bugles of male Siberian wapiti in the mountain taiga forests of our study site. However, comparing the subjective audibility of rutting bugles registered by human listeners with the points of recording of the same bugles by the automated recording systems allowed to estimate the maximum distance of human audibility as 1.5–2 km in this type of landscape. Similar data were obtained when imitated bugles were recorded at different distances from the automated recording systems. As in the case of the naturally produced rutting bugles, the spectrograms of degraded far-distant imitated bugles contained only parts of f_0 maximum plateau.

In summary, this study provides information about acoustic variation of Siberian wapiti vocalization during rut. However, the short samples and the lack of individual recognition suggest for further analyses of vocalization of *C. e. sibiricus* and other Siberian and Far East subspecies of *Cervus elaphus*.

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