

Roaring dynamics in rutting male red deer *Cervus elaphus* from five Russian populations

Ivan Yu. Rusin, Ilya A. Volodin*, Elena F. Sitnikova, Mikhail N. Litvinov, Rimma S. Andronova & Elena V. Volodina

ABSTRACT. In Russia, current populations of *Cervus elaphus* sensu lato represent a mix of fragmented remnants of ancestral red deer naturally radiated from their center of origin in Middle Asia and populations, either re-stored by people at places where the native red deer are extinct or kept for agricultural production. Male rutting roaring activity represents an important part of red deer reproduction but there are no methods for unified evaluation of roaring dynamics. This study proposes the criteria for subdividing the entire rut period to phases (start, active, fading), applicable irrespectively to differences in population geographical area, animal density, subspecies or absolute values of call number per hour. With this approach, we estimate stag rutting roaring activity on hourly basis in five populations of red deer belonging to three subspecies by using two spaced automated recording devices per population, recording roars for 5 min/hour, 24 h/day, for 52–60 days of rutting period. Two spaced recorders per population provided similar data on rut dynamics, although absolute values of call number per hour were different. In four of the five study populations, rut period covered approximately the same calendar dates, from the last days of August until the last ten days of October. The mean roaring activity over a rut period differed strongly between populations (from 4–15 calls/h to 319–377 calls/h). Effects of time of day on roaring activity differed between rut phases. The possible reasons of this variability are discussed.

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Динамика рева во время гона у самцов благородного оленя *Cervus elaphus* пяти популяций России

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РЕЗЮМЕ. Ныне живущие в России популяции *Cervus elaphus* sensu lato представляют собой фрагментированные популяции, возникшие в результате естественной радиации благородных оленей из центра происхождения в Средней Азии, а также искусственные популяции, которые либо были восстановлены человеком вместо истребленных естественных популяций либо содержатся для получения сельскохозяйственной продукции. Рев самцов оленей во время гона является важной частью их репродуктивного поведения, однако для оценки динамики гонного рева в популяциях нужны унифици-

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пированные методические подходы. В этом исследовании предложены критерии для подразделения всего периода гона на фазы (начальная, активная, затухание), применимые к разным популяциям оленей, вне зависимости от ареала, численности, подвидовой принадлежности и вокальной активности, выраженной в абсолютном числе криков в час. С помощью этого подхода мы оцениваем динамику активности гонного рева самцов на почасовой основе в пяти популяциях трех подвидов благородного оленя с помощью автоматических звукозаписывающих устройств, по два отдельно расположенных устройства на популяцию, записывающих ревы в течение 5 минут каждый час в течение суток на протяжении всего периода гона, длившегося от 52 до 60 дней в разных популяциях. Два отдельно расположенных устройства на популяцию предоставили сходные данные о динамике гона, хотя абсолютные величины числа криков в час различались. В четырех из пяти исследованных популяций гон происходил примерно в одни и те же календарные даты, с последних дней августа до третьей декады октября. Средняя активность рева за период гона сильно различалась между популяциями (от 4–15 криков в час до 319–377 криков в час). Влияние времени дня на активность рева различалось в зависимости от фазы гона. Вероятные причины такой изменчивости обсуждаются.

КЛЮЧЕВЫЕ СЛОВА: автоматизированная запись, *Cervus elaphus*, пассивный акустический мониторинг, период гона, гонные крики самцов, вокальная активность.

Introduction

Animal taxa with global distribution (e.g., sea gulls, auklets, ground squirrels, red deer) represent excellent models for highlighting the evolutionary changes underwent by populations during radiation from their ancestral centers of origin (Mahmut *et al.*, 2002; Ludt *et al.*, 2004; Liebers *et al.*, 2004; Volodin *et al.*, 2013a; Pshenichnikova *et al.*, 2015; Matrosova *et al.*, 2019). The evolutionary changes can be reflected in a complex of traits: morphological (Pshenichnikova *et al.*, 2017), genetic (de Knijff *et al.*, 2001; Mahmut *et al.*, 2002; Liebers *et al.*, 2004; Ludt *et al.*, 2004; Matrosova *et al.*, 2016), behavioural (Pshenichnikova *et al.*, 2017) and acoustical (Volodin *et al.*, 2013a; Matrosova *et al.*, 2016; Pshenichnikova *et al.*, 2017). In polygynous ungulates with impressive male courtship vocal displays, the evolutionary changes may also be reflected in the dynamic parameters of the rut: rut period timing, duration and vocal activity (Briefer *et al.*, 2010; Bocci *et al.*, 2013; Volodin *et al.*, 2013b, 2015b; Yen *et al.*, 2013; Enari *et al.*, 2017; Rusin *et al.*, 2019; Frey *et al.*, 2020).

Male roaring activity during the rut represents an important part of reproduction in red deer and wapiti. During the rut, stags vocalize when compete with other stags for female harems. Acoustic traits of rutting calls advertise male quality (Reby & McComb, 2003). Intensity and endurance of rutting vocal activity reflect male reproductive potential (Clutton-Brock & Albon, 1979; Pepin *et al.*, 2001; McPherson & Chenoweth, 2012). Whereas estimating stag roaring activity is important for deer population management both in the wild and in captivity (Bocci *et al.*, 2013; Yen *et al.*, 2013; Volodin *et al.*, 2015b; Enari *et al.*, 2017; Rusin *et al.*, 2019), there are no unified methods for timing the rut period and for quantitative estimation of male roaring activity.

In both red deer and wapiti, the acoustics of stag rutting calls differ between subspecies (Struhsaker, 1968; Nikol'skii *et al.*, 1979; Bowyer & Kitchen, 1987; Feighny *et al.*, 2006; Kidjo *et al.*, 2008; Frey *et al.*, 2012; Bocci *et al.*, 2013; Passilongo *et al.*, 2013; Della Libera *et al.*,

2015; Volodin *et al.*, 2015b, 2016a, 2019) but are similar between populations within subspecies irrespective of the management: captive, semi-captive or free-ranging (Volodin *et al.*, 2015a; Golosova *et al.*, 2017). At the same time, the absolute values of stag roaring activity may differ within population in the course of the rutting season (Volodin *et al.*, 2013b, 2015b, 2016b) and between recording sites during the rutting season (Rusin *et al.*, 2019). However, a methodical problem arises: how to document stag roaring activity in the course of the rut uniformly at a regular basis (Douhard *et al.*, 2013). The focus of this study is on developing this methodical approach by using the automated recording devices.

Although all populations of the genus *Cervus* in Russia, according to their current formal taxonomical status, belong to four subspecies of *Cervus elaphus*, their taxonomy indeed is challenging and problematic. Populations which are native for the Asian part of Russia are represented by the Siberian wapiti *Cervus elaphus sibiricus* Severtzov, 1872 (Fedosenko, 1980; Kuznetsova *et al.*, 2012; Volodin *et al.*, 2013b) and by the Far East wapiti *Cervus elaphus xanthopygus* Milne-Edwards, 1867 (Kuznetsova *et al.*, 2012; Volodin *et al.*, 2015b; Rusin *et al.*, 2019). Populations occurring on the European part of Russia are represented by the native Caspian red deer *Cervus elaphus maral* Gray 1850 (Ludt *et al.*, 2004; Trepet *et al.*, 2017) and by the *Cervus elaphus hippelaphus* Erxleben, 1777 introduced from Germany (Likhatskij *et al.*, 2012; Kuznetsova *et al.*, 2013). So far, detailed data on stag roaring activity throughout the rut are only available for a single population of Far East wapiti (Rusin *et al.*, 2019). For other world red deer populations, for which published data on rut dynamics are available, they are incomplete, being either collected not on everyday basis or not for the entire rut period (Pepin *et al.*, 2001; Reby *et al.*, 2006; Bocci *et al.*, 2013; Volodin *et al.*, 2013b, 2015b).

Stag roaring activity can be tracked on an hourly basis for the entire rut period with a passive acoustic monitoring by using the automated recording devices, which record the target vocalizations (Volodin *et al.*,

2013b, 2015b, 2016b). In addition, the automated recording devices capture the sounds of non-target animals and the environmental noises, thus providing material for ecoacoustical monitoring of environment (Sugai *et al.*, 2019). For evaluating male rutting vocal activity, the commonly used parameter is call rate, estimated as the mean number of calls/hour (Bocci *et al.*, 2013; Rusin *et al.*, 2019). Male red deer and wapiti roaring activity depends on the joint effects of time of day, temperature, speed of wind, humidity, precipitations, animal density, sex ratio and management (Clutton-Brock & Albon, 1979; Bowyer & Kitchen, 1987; Pepin *et al.*, 2001; Bocci *et al.*, 2013; Douhard *et al.*, 2013; Volodin *et al.*, 2013b, 2015b). Due to these and others factors, stag roaring activity varies within a 24-hour cycle and in the course of the season (Clutton-Brock & Albon, 1979; Bowyer & Kitchen, 1987; Pepin *et al.*, 2001; Reby *et al.*, 2006; Bocci *et al.*, 2013; Volodin *et al.*, 2013b, 2015b, 2016b) as well as between seasons (Clutton-Brock & Albon, 1979; Bocci *et al.*, 2013). In addition, multiple peaks of estrus of hinds may prolong the rut (Guinness *et al.*, 1971; Smith, 1994; Garcia *et al.*, 2002). Thus, absolute values of call number per hour can be strongly different along the rut depending on subspecies, population, population distribution area, animal density and recording site (Clutton-Brock & Albon, 1979; Bocci *et al.*, 2013; Volodin *et al.*, 2016b; Rusin *et al.*, 2019).

This study introduces and applies a potential approach for estimating vocal rutting activity throughout the rut period in different populations of red deer: from different parts of species distribution area, belonging to different subspecies and living at different social densities. In this study, we apply such approach for describing stag roaring activity in five red deer populations of Russia and reveal the effects of rut phase and time of day on the roaring activity. By comparison of data from two detached automated recorders per population, we also test, for each population, effects of recording site on the results.

Materials and methods

Study populations and dates

Stag rutting calls were collected in ten study sites in five populations of *Cervus elaphus* with automated recording devices in the autumnal rutting seasons of 2015–2017 (Tab. 1). Two of the studied populations (Belgorod and Bryansk) belong to subspecies *C. e. hippelaphus* Erxleben, 1777; one population (Kostroma) belongs to subspecies *C. e. sibiricus* Severtzov, 1872 and other two populations (Ussuri and Khabarovsk) belong to subspecies *C. e. xanthopygus* Milne-Edwards, 1867 (Tab. 1). Although material was not collected in the same rutting season, life conditions of the five study populations differed so strongly (Tab. 1), that this obviously outweighed the influence of the year of recording.

Both Belgorod and Bryansk populations initially originated from 10 German individual red deer released by Prince Oldenburg in his hunting facility in Russia

at the end of 19th century, to restore the population of *C. e. hippelaphus*, which disappeared in Russia to that time because of extensive hunting (Likhatskij *et al.*, 2012). From the Prince Oldenburg hunting facility, in which territory the Voronezh State Nature Reserve was created in 1927, the increased red deer population was distributed in 1960–1990 over the southern regions of Russia (Likhatskij *et al.*, 2012). The Belgorod study population originated at 1971–1990 from 127 red deer individuals released at the territory “Russky les” (Likhatskij *et al.*, 2012). The Bryansk study population originated at 1960–1980 from 164 individuals (Sitnikova & Mishta, 2008). The subspecies status *C. e. hippelaphus* of the Belgorod and Bryansk populations has been established based on the mitochondrial DNA cytochrome b analysis (Kuznetsova *et al.*, 2013).

The study population Kostroma originated in 2010 from a few dozen Siberian wapiti, translocated to the Kostroma farm (located on the European part of Russia) from their native grounds in the Altai region of Russia (Volodin *et al.*, 2016b; Golosova *et al.*, 2017). Status of this population as pure *C. e. sibiricus* was known because of its native origin. Native populations of Siberian wapiti are widespread at the western Asian part of Russia (Siberia), where these animals are numerous and either wild-living or bred for velvet antlers since the middle of 20th century (Lunitsin & Borisov, 2012).

The study population Ussuri represented the wild-living Far East wapiti population of the Nature Reserve “Ussuriisky” and the Khabarovsk study population represented the wild-living Far East wapiti of the Nature Reserve “Bolshekhkheksirsky” (both at Far East of Russia). Status of these populations as pure *C. e. xanthopygus* was known because both are the native populations of the local subspecies (Volodin *et al.*, 2015b). Wild-living *C. e. xanthopygus* are common at Far East of Russia (Volodin *et al.*, 2015b). Farming or semi-captive management are never applied to this subspecies.

Acoustic recording

For the automated acoustic recording of stag rutting calls, we used SongMeter SM2+ devices (Wildlife Acoustics Inc., Maynard, MA, USA), one in each recording site, two sites per population, five populations in total (Tab. 1). The devices were set to 22.05 kHz, 16 bit and stereo recording and were mounted on trees or pillars 2–4 m above the ground. Each device had two omnidirectional microphones, established horizontally at the angle of 180 degrees to each other. The recording sites within population were selected as the places of most active rut in previous seasons based either on previous observations of the authors or on reports of the staff of the localities. All devices remained on their places permanently for the entire rut period. People did not visit them during the rut, to avoid potential animal disturbance.

Each device recorded calls every day, the total length of acoustic monitoring was from 53 to 62 d depending on population (Tab. 1). The recording schedule was set

Table 1. Sites of acoustic recording in the five study populations of *Cervus elaphus* (10 recording devices, one in each recording site, two devices #1 and #2 per population).

Location of two recording sites (devices #1 and #2), per population	Population description	Recording dates	Population area / Recording site description
Belgorod#1 (50.61581 N, 36.8849 E) Belgorod#2 (50.6283 N, 36.87233 E) between-device distance 1.7 km	<i>C. e. hippelaphus</i> , about 1500 wild-living individuals, introduced from Germany (Likhatskij <i>et al.</i> , 2012), supplementary fed, hunted	30 Aug – 26 Oct 2016, 58 d in total	The 20000-hectare unrestricted area covered with forest, agriculture fields and ravines. #1: Ravine covered with forest near with large clearings, middle of the northern slope. #2: Shallow ravine near the agricultural field.
Bryansk#1 (52.50246 N, 34.07683 E) Bryansk#2 (52.50852 N, 33.99277 E) between-device distance 5 km	<i>C. e. hippelaphus</i> , about 70–90 wild-living individuals, introduced from Germany (Likhatskij <i>et al.</i> , 2012), not supplementary fed, not hunted (Sitnikova & Mishta, 2006)	30 Aug – 27 Oct 2016, 59 d in total.	The 12186-hectare unrestricted area of the “Bryansk Forest” Nature Reserve. #1: A forested place at the edge of a clearing. #2: A clearing of the forest near the swamp.
Kostroma#1 (58.40649 N, 43.25794 E) Kostroma#2 (58.40942 N, 43.25787 E) between-device distance 0.3 km	<i>C. e. sibiricus</i> , 140 farmed individuals, including 38 stags, 57 hinds and 45 calves, originated from animals translocated from the Altai region of Russia (Volodin <i>et al.</i> , 2016b)	5 Sep – 5 Nov 2015, 62 d in total.	#1 & #2: the 70-hectare enclosed property covered by old gardens and forest with large clearings.
Ussuri#1 (43.65262 N, 132.66246 E) Ussuri#2 (43.63793 N, 132.6516 E) between-device distance 1 km	<i>C. e. xanthopygus</i> , about 150 wild-living individuals, native, not supplementary fed, not hunted (Litvinov 2008)	31 Aug – 22 Oct 2015, 53 d in total	The 40432-hectare unrestricted area of the Ussuriisky Nature Reserve. #1: The elevation between two small rivers, Suvorovka and Koryavaya. #2: The valley of the Suvorovka River, at the edge of a large clearing.
Khabarovsk#1 (48.14664 N, 134.84618 E) Khabarovsk#2 (48.11356 N, 134.85674 E) between-device distance 3 km	<i>C. e. xanthopygus</i> , about 200 wild-living individuals, native, not supplementary fed, not hunted (Letopis prirody, 2017)	23 Aug – 22 Oct 2017, 60 d in total	The 45000-hectare unrestricted area of Bolshekhekhetskirsirsky Nature Reserve. #1: The cliff above the surrounding forest. #2: The large clearing in the forest.

to record 5 min per hour, 120 min in total per 24-h cycle per device. In total, we obtained from 106 h to 124 h of acoustic recording per device, in total about 1200 h of recording in all the five populations.

Within population, the distance between two devices varied from 0.3 km to 5 km (Tab. 1). The devices were set at maximum possible sensitivity and potentially collected all stag rutting calls from the distance of about 1 km. The rutting calls of *Cervus elaphus* propagate to a distance up to 1.5 km, as it was shown by comparison of the same calls recorded automatically in a close vicinity of a stag caller and recorded manually at the distance of 1.5 km established by GPS-coordinates (Volodin *et al.*, 2016b). To exclude even minor possibility of recording the same calls with two devices simultaneously, we desynchronized their working schedules within each hour. The first device started recording at the beginning of each hour, whereas the second one at the middle of each hour.

Acoustic analyses

Data for each device were treated separately. All sound files were viewed with Avisoft SASLab Pro software (Avisoft Bioacoustics, Germany, Berlin) main window (sampling rate 22.05 kHz, Hamming window, FFT 512, frame 100%). The number of calls in each audio file irrespective of their quality was counted (Fig. 1). Some calls were faint and indistinguishable by ear from the background noise, but they were still detectable by spectrograms (Volodin *et al.*, 2016b; Rusin *et al.*, 2019). In total for the 10 devices from the five populations, we registered 111824 rutting calls (78023 at Belgorod, 12223 at Bryansk, 17955 at Kostroma, 926 at Ussuri, and 2697 at Khabarovsk). The automated recordings did not allow identifying individuals.

For each of the 10 recording devices, the daily mean call number/h for each 24-h cycle was calculated as the total number of calls/d, divided by 24, along

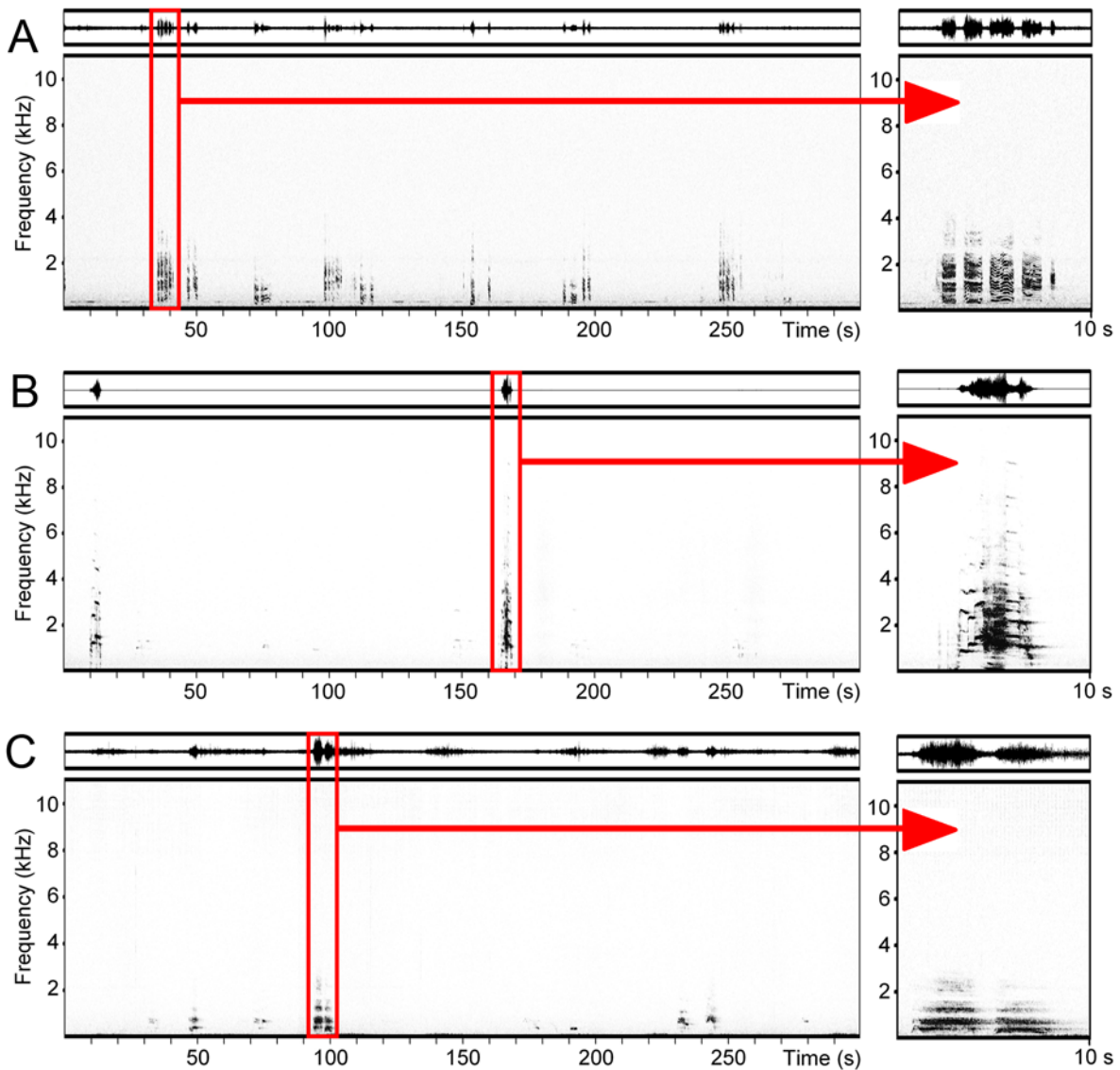


Fig. 1. Visualizing rutting calls of stags of different subspecies recorded with automated recording devices Song Meter SM2+. Axis X represents time in seconds; axis Y represents frequency in kHz. Left: Spectrogram of a 5-min-long sound file. Right: Expanded spectrogram of the selected 10 s fragment. (A) *C. e. hippelaphus* of the Belgorod population, five rutting calls in the 10 s fragment, (B) *C. e. sibiricus* of the Kostroma population, one rutting call in the 10 s fragment, (C) *C. e. xanthopygus* of the Ussuri population, two rutting calls in the 10 s fragment.

the recording period, from 53 to 62 d depending on population (Tab. 1). For evaluating the hourly activity patterns of stag vocalizations, we calculated the mean number of calls/h for each time of day (averaged across the number of days of recording in each population). Similar calculations were done for each of the three phases of the rut (see below).

Rut period timing

For comparison of the roaring activity among each two recording sites within population and across the five study populations, we used the formal criteria for timing the rut onset and completion in each recording site (= each recording device). First, we determined the

day with the maximum roaring activity (calls/h). Then, for each recording site, we selected the days of rut onset and completion as the days when call number/h reached 1% of the maximum (Fig. 2).

We also used the formal criteria for subdividing the entire rut period into three phases (start, active and fading). For each device, we calculated the mean call number/h across rut period from onset to completion (Fig. 2). We took the period between the day of rut onset and the day with mean call number/h as the start phase. We took the period between the two days with mean call number/h as the active phase. We took the period from the day with mean call number/h to the day of rut completion as the fading phase (Fig. 2). This approach

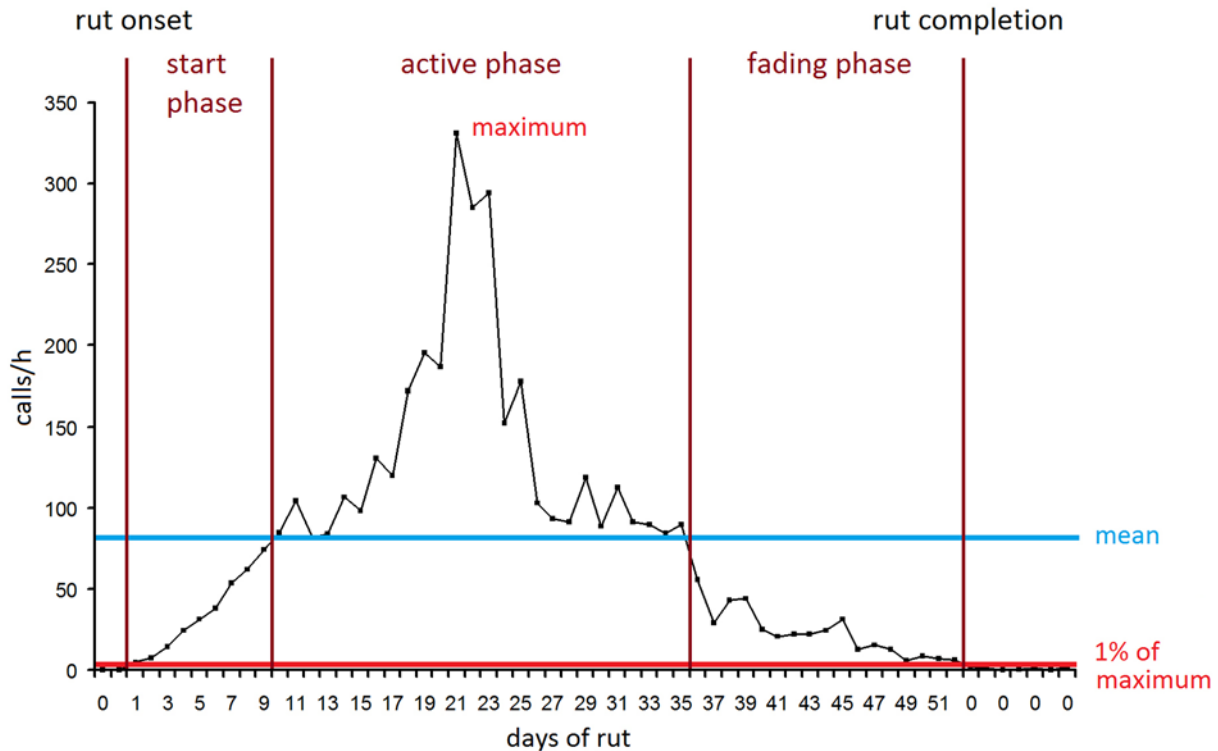


Fig. 2. Timing the onset and completion dates of rut period and subdividing the entire rut period into the three phases (start, active, fading). Maximum = the maximum roaring activity; mean = the mean calls/h across rut period from its onset to completion.

followed Bocci *et al.* (2013), also using the mean vocal activity as cut-off line for determining the peaking rut phase in red deer.

Statistical analyses

All statistical analyses were made with STATISTICA v. 8.0 (StatSoft Inc., Tulsa, OK, USA). Means are given as mean \pm SE, all tests were two-tailed, and differences were considered significant whenever $p < 0.05$. We used Pearson's correlation to compare the dynamics of roaring activity between recording sites within populations. We used one-way ANOVA to compare mean roaring activity between recording sites within populations for both the entire rut period and for the three phases of the rut. We used two-way ANOVA to estimate the effects of phase of the rut, time of day (hourly) and interaction effect of rut phase and time of day on the number of calls/h, taking time of day and phase of the rut as fixed factors. We used one-way ANOVA to estimate the effect of time of day (hourly) on the number of calls/h at the three phases of the rut.

We provided effect size (ES) statistics to measure the strength of an effect in addition to statistical significance. We calculated the effect size for ANOVA using η^2 ($\eta^2 = 0.01$ for a small effect, 0.06 for a medium effect and 0.14 for a large effect) (Cohen, 1992; Fritz *et al.*, 2012).

Results

In four of the five study populations, rut period covered approximately the same calendar dates, from the last days of August until the last ten days of October (Tab. 2, Fig. 3). Rut period was the longest at Belgorod, Kostroma and Khabarovsk (51–56 d), intermediate at Ussuri (43–45 d) and the shortest at Bryansk (35–39 d). Exclusion was Bryansk, where the rut period was the shortest and completed on 8 October. The shortening of the rut period was due to either the shorter fading phase at Bryansk or to the shorter active phase at Ussuri (Tab. 2, Fig. 3). Across populations, the active phase of the rut lasted for about three weeks, from 8–19 September to the first days of October (Bryansk, Ussuri and Khabarovsk) or to the first ten days of October (Belgorod and Kostroma). The active phase of the rut and the roaring activity maximum were skewed towards the start of the rut at Kostroma, Ussuri and Khabarovsk, but at Belgorod and Bryansk they were skewed towards the completion of the rut (Tab. 2, Fig. 3). The roaring activity was the highest at Belgorod (mean 319–377 calls/h), intermediate at Bryansk and Kostroma (mean 51–117 calls/h) and the lowest at Khabarovsk and Ussuri (4–15 calls/h).

Whereas the devices within population displayed similar maximum and mean numbers of calls/h at Belgorod, Kostroma and Khabarovsk, at Bryansk and Ussuri the maximum and mean numbers of calls/h

Table 2. Parameter values of roaring activity at five study populations in the course of rut period and one-way ANOVA results for comparison the roaring activity (calls/h) between recording sites within population. Analyses include one rut period per population, 10 recording sites, one recording device in each recording site, two devices #1 and #2 per population. Significant differences are labeled in bold. Belgorod, Bryansk, Kostroma, Ussuri, Khabarovsk—the five study populations.

Rut parameter	Belgorod		Bryansk		Kostroma		Ussuri		Khabarovsk	
	#1	#2	#1	#2	#1	#2	#1	#2	#1	#2
Rut onset (date)	31 Aug	31 Aug	04 Sep	31 Aug	06 Sep	06 Sep	02 Sep	05 Sep	30 Aug	01 Sep
Start of rut active phase (date)	11 Sep	10 Sep	17 Sep	09 Sep	15 Sep	16 Sep	19 Sep	19 Sep	08 Sept	09 Sep
Roaring maximum (date)	01 Oct	02 Oct	28 Sep	21 Sep	26 Sep	28 Sep	22 Sep	22 Sep	22 Sep	19 Sep
Start of rut fading phase (date)	08 Oct	09 Oct	05 Oct	29 Sep	11 Oct	10 Oct	01 Oct	01 Oct	02 Oct	01 Oct
Rut completion (date)	25 Oct	25 Oct	08 Oct	08 Oct	27 Oct	27 Oct	16 Oct	17 Oct	21 Oct	21 Oct
Rut total duration (days)	56	56	35	39	52	52	45	43	53	51
Rut start phase duration (days)	11	10	13	9	9	10	17	14	9	8
Rut active phase duration (days)	27	29	18	20	26	24	12	12	24	22
Rut fading phase duration (days)	18	17	4	10	17	18	16	17	20	21
Duration to rut maximum (days)	31	32	24	21	20	22	20	17	23	18
Rut start phase percentage (%)	20	18	37	23	17	19	38	33	17	16
Rut active phase percentage (%)	48	52	51	51	50	46	27	28	45	43
Rut fading phase percentage (%)	32	30	11	26	33	35	36	40	38	41
Percentage to rut maximum (%)	55	57	69	54	38	42	44	40	43	35
Maximum roaring activity (calls/h)	1324.5	1560.5	512	271	331	351	46	19	54	33.5
Median roaring activity (calls/h)	204.5	190	61	22.5	78.3	78.5	4.5	1.5	10.5	8
All-rut mean \pm SE roaring activity (calls/h)	377.3 \pm 49.4	319.4 \pm 48.6	117.4 \pm 23.0	50.9 \pm 10.7	82.1 \pm 10.5	90.3 \pm 11.2	6.8 \pm 1.2	3.7 \pm 0.8	14.5 \pm 1.6	11.4 \pm 1.4
ANOVA results	$F_{1,110}=0.70$; $p=0.41$; $\eta^2=0.006$, small ES	$F_{1,110}=7.37$; $p=0.008$; $\eta^2=0.093$, medium ES	$F_{1,72}=0.41$; $p=0.53$; $\eta^2=0.020$, small ES	$F_{1,72}=7.37$; $p=0.008$; $\eta^2=0.093$, medium ES	$F_{1,102}=0.28$; $p=0.60$; $\eta^2=0.003$, small ES	$F_{1,102}=0.28$; $p=0.60$; $\eta^2=0.003$, small ES	$F_{1,86}=4.60$; $p=0.03$; $\eta^2=0.051$, small ES	$F_{1,102}=2.09$; $p=0.15$; $\eta^2=0.020$, small ES	$F_{1,102}=2.09$; $p=0.15$; $\eta^2=0.020$, small ES	$F_{1,102}=2.09$; $p=0.15$; $\eta^2=0.020$, small ES
Start phase mean \pm SE roaring activity (calls/h)	158.5 \pm 21.4	112.5 \pm 26.4	10.7 \pm 6.1	15.9 \pm 4.3	34.6 \pm 8.2	45.9 \pm 8.8	5.8 \pm 1.0	3.0 \pm 0.7	6.9 \pm 1.9	4.8 \pm 1.1
ANOVA results	$F_{1,19}=1.86$; $p=0.19$; $\eta^2=0.089$, medium ES	$F_{1,20}=0.41$; $p=0.53$; $\eta^2=0.020$, small ES	$F_{1,20}=0.41$; $p=0.53$; $\eta^2=0.020$, small ES	$F_{1,20}=14.97$; $p<0.001$; $\eta^2=0.294$, large ES	$F_{1,17}=0.87$; $p=0.36$; $\eta^2=0.049$, small ES	$F_{1,17}=0.87$; $p=0.36$; $\eta^2=0.049$, small ES	$F_{1,29}=4.57$; $p=0.04$; $\eta^2=0.136$, medium ES	$F_{1,15}=0.93$; $p=0.35$; $\eta^2=0.058$, small ES	$F_{1,15}=0.93$; $p=0.35$; $\eta^2=0.058$, small ES	$F_{1,15}=0.93$; $p=0.35$; $\eta^2=0.058$, small ES
Active phase mean \pm SE roaring activity (calls/h)	672.4 \pm 62.7	535.3 \pm 73.1	216.0 \pm 29.2	89.3 \pm 16.7	137.3 \pm 13.8	154.4 \pm 15.6	14.4 \pm 3.2	8.5 \pm 2.0	24.2 \pm 2.1	20.0 \pm 1.9
ANOVA results	$F_{1,54}=2.00$; $p=0.16$; $\eta^2=0.036$, small ES	$F_{1,54}=14.97$; $p<0.001$; $\eta^2=0.294$, large ES	$F_{1,36}=14.97$; $p<0.001$; $\eta^2=0.294$, large ES	$F_{1,36}=14.97$; $p<0.001$; $\eta^2=0.294$, large ES	$F_{1,48}=0.68$; $p=0.41$; $\eta^2=0.014$, small ES	$F_{1,48}=0.68$; $p=0.41$; $\eta^2=0.014$, small ES	$F_{1,22}=2.47$; $p=0.13$; $\eta^2=0.101$, medium ES	$F_{1,44}=2.16$; $p=0.15$; $\eta^2=0.046$, small ES	$F_{1,44}=2.16$; $p=0.15$; $\eta^2=0.046$, small ES	$F_{1,44}=2.16$; $p=0.15$; $\eta^2=0.046$, small ES
Fading phase mean \pm SE roaring activity (calls/h)	68.1 \pm 17.5	72.8 \pm 13.1	20.5 \pm 9.6	5.7 \pm 2.9	22.8 \pm 3.5	29.4 \pm 4.7	2.1 \pm 0.8	0.9 \pm 0.4	6.2 \pm 1.2	4.8 \pm 0.9
ANOVA results	$F_{1,33}=0.04$; $p=0.84$; $\eta^2=0.001$, small ES	$F_{1,12}=4.02$; $p=0.07$; $\eta^2=0.251$, large ES	$F_{1,12}=4.02$; $p=0.07$; $\eta^2=0.251$, large ES	$F_{1,12}=4.02$; $p=0.07$; $\eta^2=0.251$, large ES	$F_{1,33}=1.22$; $p=0.28$; $\eta^2=0.036$, small ES	$F_{1,33}=1.22$; $p=0.28$; $\eta^2=0.036$, small ES	$F_{1,31}=1.87$; $p=0.18$; $\eta^2=0.057$, small ES	$F_{1,39}=0.93$; $p=0.34$; $\eta^2=0.024$, small ES	$F_{1,39}=0.93$; $p=0.34$; $\eta^2=0.024$, small ES	$F_{1,39}=0.93$; $p=0.34$; $\eta^2=0.024$, small ES

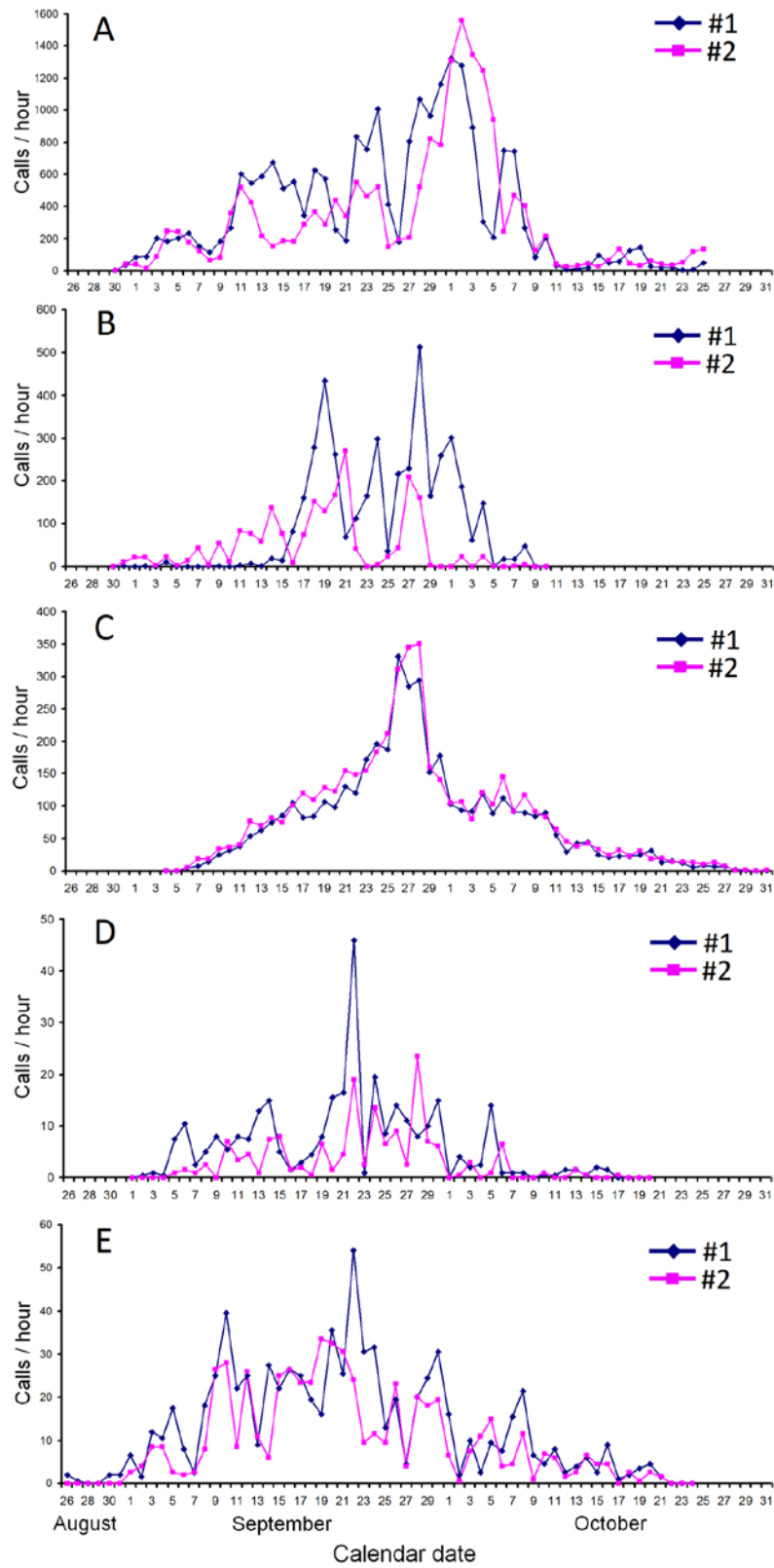


Fig. 3. The general dynamic of roaring activity in five study populations of *Cervus elaphus*: (A) Belgorod; (B) Bryansk; (C) Kostroma; (D) Ussuri; (E) Khabarovsk. #1 and #2: data from the two recording devices, one in each of the two recording sites per population. Calls/hour: the mean number of calls per hour per 24-h cycle. Please pay attention that dimensions of the ordinate axis are different for different populations.

differed between two devices within population (Tab. 2). Estimation of effect size also indicated the strongest differences in Bryansk and the average differences in Ussuri, whereas in Belgorod, Kostroma and Khabarovsk, the differences were at minimal level (Tab. 2).

In all populations, the dynamic of roaring activity during the rut between two devices within population showed a significant positive correlation: Belgorod (from 31 Aug to 25 Oct, $r = 0.718$, $p < 0.001$, $n = 56$ d), Bryansk (from 4 Sep to 8 Oct; $r = 0.335$, $p < 0.05$, $n = 35$ d), Kostroma (from 6 Sep to 27 Oct; $r = 0.978$, $p < 0.001$, $n = 52$ d), Ussuri (from 5 Sep to 16 Oct; $r = 0.615$, $p < 0.001$, $n = 42$ d), Khabarovsk (from 1 Sep to 21 Oct; $r = 0.730$, $p < 0.001$, $n = 51$ d). The highest correlation was found at Kostroma, whereas the weakest (although significant) at Bryansk. Probably, the value of correlation depended on the distance between the acoustic devices, being the least in Kostroma (0.3 km) and the largest in Bryansk (5 km) (Tab. 1).

The mean hourly number of calls/h per time of day differed between populations (Fig. 4). For all populations with the exclusion of Kostroma, we found a substantial decrease of roaring activity in light time of day, from about hours 09:00 to 17:00–18:00. The roaring maximum was achieved between hours 01:00 and 03:00 at Bryansk, Ussuri and Khabarovsk, and between hours 05:00 and 06:00 at Belgorod and Kostroma. Additional two peaks of roaring activity were the early-morning peak before sunrise (between hours 05:00 and 07:00 for different populations) and the late-evening peak after sunset (between hours 17:00 and 18:00 for Kostroma and between hours 19:00 and 21:00 for Belgorod, Bryansk, Ussuri and Khabarovsk) (Fig. 4). The roaring activity, for the exclusion of Kostroma, faded steadily for a few hours after sunrise, but only very rarely started before sunset. Within population, different recording sites displayed very similar dynamics of the number of roars during 24-h cycle, whereas the differences were well expressed between populations.

We estimated the effects of rut phase, time of day (hourly) and interaction effect of rut phase and time of day on the number of calls/h (Tab. 3). For all the five populations, the number of calls/h depended strongly on the rut phase and time of day. As the effect of rut phase on the number of calls/h was prominent, we additionally analysed the relationship between the number of calls/h and time of day separately for each rut phase for each recording site of each population (Tab. 4). We found that the dependence between the number of calls/h and time of day was substantially more prominent at the active phase than either at the start or fading phases (Tab. 4). For the active phase, we found perfectly coinciding results between two recording sites within populations, whereas for the start and fading phases, the results between two recording sites within population could differ (Tab. 4).

Discussion

This study of five populations of *Cervus elaphus* of Russia introduces the formal criteria for determining rut

onset, completion and applies the three rutting phases: start, active and fading. Days of rut onset and completion were established when call number/h reached 1% of the maximum roaring activity. Subdividing the rutting period into three phases was based on the mean call number/h from rut onset to completion. This approach enabled to compare the roaring activity in the five study populations living at strongly different climate zones, differing in calendar dates of the rut and in rut duration. Our results on rut dynamics in five populations of Russia provide referential information for further passive acoustic monitoring and population management (Volodin *et al.*, 2015b, 2016b).

Potentially, these formal criteria can be expanded to other Cervidae species displaying male rutting vocal activity, as fallow deer *Dama dama* (Briefer *et al.*, 2010), sika deer *Cervus nippon* (Yen *et al.*, 2013; Enari *et al.*, 2017) and to Bovidae species, producing impressive vocal displays throughout rutting period, as e.g. impala *Aepyceros melampus* (Frey *et al.*, 2020). Our data can be valuable for managers of natural reserves and hunting facilities for preparing the schedules of the ecoacoustical excursions and hunting games using the hunting luring instruments during the rut (Volodin *et al.*, 2013b). In semi-captive populations of Siberian wapiti kept for velvet antlers, as Kostroma population in our study, the knowledge of timing of the rut in previous years enables to plan e.g. releasing of the older and younger stags to the herd before the rut as well as pre-winter separation of females and the young after the rut (Sibiryakova *et al.*, 2018). In the Ussuri populations, the reference data on stag rutting activity at different recording sites can be used for planning the every-year human counts of roaring stags by ear. In addition, data provide reference information for estimating the effect of climate changes on the shifts in rut period timing in the study sites in the following years, in comparison with data from the meteorological stations, nearest to the recording sites.

Two recording sites within population provide similar data on the dynamics of roaring activity over the entire rut period. Differences in the actual values of stag roaring activity between sites within populations may reflect the differences in use of these sites by stags during the rut. The inter-device distance affects the coincidence of data on dynamics of roaring activity, as the stronger correlation was obtained for the population in which the devices are closest. The reason can be in transitions of stags over the territory during the rut (Clutton-Brock & Albon, 1979; Fedosenko, 1980), so that the closest devices can capture calls in the same male. Between populations, the differences in the dynamics and in the actual values of stag roaring activity were much more prominent.

Between populations, the roaring activity over a rut period differed strongly (up to 50 times), ranging from 4–7 calls/h at Ussuri to 319–377 calls/h at Belgorod. This could be due to many factors, primarily the local population density. In this study, the largest population density was in Kostroma (Tab. 1). For the exclusion of this captive population, among the natural populations

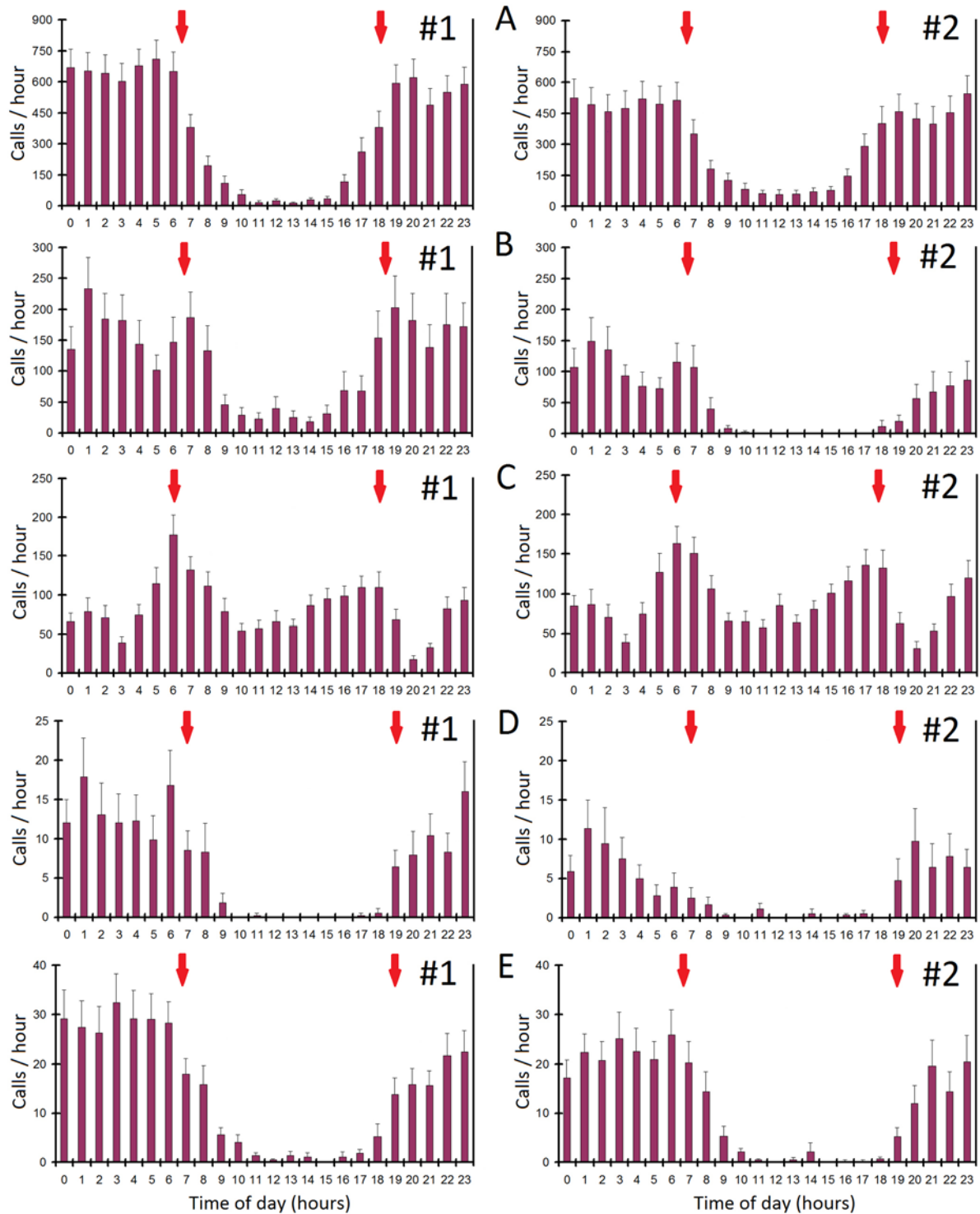


Fig. 4. Time of day (hourly) graphs of stag roaring activity in the five populations of *Cervus elaphus*: (A) Belgorod; (B) Bryansk; (C) Kostroma; (D) Ussuri; (E) Khabarovsk. #1 and #2 — two recording devices per population, one in each recording site. Calls/h: the mean number of calls per time of day (averaged across the number of days per rut period, from 53 to 62 d depending on population); whiskers indicate SE. For each recording site, the time of sunrise and sunset for the day with the maximum roaring activity are indicated by arrows. Please pay attention that dimensions of the axes are different for different populations.

Table 3. Effects of rut phase, time of day (hourly) and interaction effect of rut phase and time of day on the number of calls/h at five populations and 10 recording sites (two recording sites per population). Significant differences are labeled in bold.

Population	Recording sites	Rut phase	Time of day (hourly)	Rut phase & Time of day (hourly)
Belgorod	#1	$F_{2,1272} = 395.80; p<0.001$	$F_{23,1272} = 17.87; p<0.001$	$F_{46,1272} = 7.99; p<0.001$
	#2	$F_{2,1272} = 174.21; p<0.001$	$F_{23,1272} = 5.29; p<0.001$	$F_{46,1272} = 2.33; p<0.001$
Bryansk	#1	$F_{2,768} = 144.07; p<0.001$	$F_{23,768} = 1.84; p<0.01$	$F_{46,768} = 2.02; p<0.001$
	#2	$F_{2,864} = 48.45; p<0.001$	$F_{23,864} = 3.00; p<0.001$	$F_{46,864} = 2.08; p<0.001$
Kostroma	#1	$F_{2,1176} = 233.17; p<0.001$	$F_{23,1176} = 3.89; p<0.001$	$F_{46,1176} = 1.85; p<0.001$
	#2	$F_{2,1176} = 245.48; p<0.001$	$F_{23,1176} = 4.68; p<0.001$	$F_{46,1176} = 2.22; p<0.001$
Ussuri	#1	$F_{2,1008} = 45.66; p<0.001$	$F_{23,1008} = 7.25; p<0.001$	$F_{46,1008} = 2.00; p<0.001$
	#2	$F_{2,960} = 29.52; p<0.001$	$F_{23,960} = 4.14; p<0.001$	$F_{46,960} = 1.86; p<0.001$
Khabarovsk	#1	$F_{2,1200} = 86.68; p<0.001$	$F_{23,1200} = 7.97; p<0.001$	$F_{46,1200} = 2.97; p<0.001$
	#2	$F_{2,1152} = 72.16; p<0.001$	$F_{23,1152} = 6.34; p<0.001$	$F_{46,1152} = 2.44; p<0.001$

Table 4. Effects of time of day (hourly) on the number of calls/h at the three rut phases for five populations and 10 recording sites (two recording sites per population). Significant values are labeled in bold.

Population	Recording sites	Rut start phase	Rut active phase	Rut fading phase
Belgorod	#1	$F_{23,240} = 8.31; p<0.001$	$F_{23,624} = 23.22; p<0.001$	$F_{23,408} = 3.29; p<0.001$
	#2	$F_{23,216} = 4.72; p<0.001$	$F_{23,672} = 7.74; p<0.001$	$F_{23,384} = 1.77; p=0.02$
Bryansk	#1	$F_{23,288} = 0.97; p=0.50$	$F_{23,408} = 5.18; p<0.001$	$F_{23,72} = 0.90; p=0.60$
	#2	$F_{23,192} = 1.94; p=0.008$	$F_{23,456} = 5.65; p<0.001$	$F_{23,216} = 1.20; p=0.25$
Kostroma	#1	$F_{23,192} = 1.42; p=0.10$	$F_{23,600} = 5.68; p<0.001$	$F_{23,384} = 4.55; p<0.001$
	#2	$F_{23,216} = 2.07; p=0.004$	$F_{23,552} = 5.47; p<0.001$	$F_{23,408} = 3.71; p<0.001$
Ussuri	#1	$F_{23,384} = 2.56; p<0.001$	$F_{23,264} = 3.44; p<0.001$	$F_{23,360} = 1.41; p=0.10$
	#2	$F_{23,312} = 1.27; p=0.18$	$F_{23,264} = 2.35; p<0.001$	$F_{23,384} = 1.59; p=0.04$
Khabarovsk	#1	$F_{23,192} = 1.76; p=0.02$	$F_{23,552} = 9.51; p<0.001$	$F_{23,456} = 3.14; p<0.001$
	#2	$F_{23,168} = 2.14; p=0.003$	$F_{23,504} = 6.91; p<0.001$	$F_{23,480} = 3.93; p<0.001$

the population density was the highest in Belgorod and the lowest in Khabarovsk and Ussuri, in coincidence with the value of all-rut mean roaring activity, which was the maximal in Belgorod and the minimal in Ussuri. The density at recording sites could also depend on supply and distribution of supplementary feeding (Sánchez-Prieto *et al.*, 2004; Pérez-González *et al.*, 2010) available in Kostroma and Belgorod and lacking in other study populations.

Subspecies of a monitored population could also affect the roaring activity, because wild-living Siberian and Far East wapiti normally do not have the rutting aggregations (Fedosenko, 1980; Volodin *et al.*, 2013b, 2015b; Golosova *et al.*, 2017). At the same time, the rutting aggregations are characteristic for the European subspecies of red deer (Clutton-Brock & Albon, 1979; Sánchez-Prieto *et al.*, 2004; Douhard *et al.*, 2013). For

example, in wild-living populations of European subspecies of red deer, the rutting roaring activity reaches 400 calls/h at the period of most active rut (Bocci *et al.*, 2013) or reaches 200 calls/h at the peak of a 24-h-cycle rutting roaring activity (Clutton-Brock & Albon, 1979; Bocci *et al.*, 2013). These values were approximately the same as were obtained in this study for Bryansk population, which is representative of European red deer population without providing the supplementary feeding.

Although some study populations were separated by many thousand kilometers, in all free-ranging populations (four out of five) the roaring peaked between hours 03:00 and 06:00, nearly lacked between 10:00 and 18:00, steadily increased from 20:00 to 03:00 to maximum and then rapidly decreased from 06:00 to 09:00 to minimum. A single captive population in this study (Kostroma) differed strongly by the hourly roaring activity during a

24-h cycle from other populations. Primary difference was the absence of the nocturnal peak of roaring activity due to the continuous roaring in the light time of day. This could be due to the effect of farming on a restricted territory, without a possibility for animals to leave a centre of rutting activity along to providing food regularly in the light time of day. Providing food regularly on some deer farms (as Kostroma) and in hunting facilities provokes hinds to move to the food sources and evokes an enhanced arousal of stags, trying to control the female harems (Sánchez-Prieto *et al.*, 2004; Pérez-González *et al.*, 2010; Golosova *et al.*, 2017).

At rutting season of 2013, stag roaring activity in Kostroma population displayed the same pattern of peaks as sunset and sunrise and relatively low roaring activity in the dark time (Volodin *et al.*, 2016b). At the same time, the actual values of roaring activity increased 10 times between seasons of 2013 and 2015 (Volodin *et al.*, 2016b and this study). This prominent increase of roaring activity could be due to the time space passed since translocation (three years to the 2013 rutting season and five years to the 2015 rutting season), so the young stags became older and the total number of adults in the herd also increased.

Supplementary feeding was practiced also at Belgorod, however, the Belgorod population is free ranging distinctive to Kostroma population. This could be the reason why stag roaring dynamic in Belgorod was closer to those observed in the populations of natural reserves (Bryansk, Ussuri, Khabarovsk) than to those in the farmed Kostroma population. At Ussuri population, data of the rutting season of 2014 (at active phase) were very similar with data of this study by the lack of calls in the middle of the day and by well-expressed peak of nocturnal activity, at approximately the same absolute values of rutting calls/h (Volodin *et al.*, 2015b).

However, the higher vocal activity during the light time of day compared to the night time is characteristic not only for farmed red deer (Pepin *et al.*, 2001), but also reported for a wild-living population of *C. e. scoticus* on the Rhum Island (Clutton-Brock & Albon, 1979). At the same time, a semi-captive population of *C. e. sibiricus* displays a usual relationship of roaring activity with time of day, with three peaks, at sunrise, at sunset and in the middle of the night (Volodin *et al.*, 2016b), similar to the wild-living Alpine population *C. e. hippelaphus* (Bocci *et al.*, 2013). General factors and mechanisms that lead to nocturnal or diurnal vocal activity of red deer have yet to be studied.

In addition, the start of rutting roaring of Cervidae species can be considered as a seasonal key marker for creating false color spectrograms of the acoustic landscapes (soundscapes) in frames of a modern ecoacoustical approach using big-data analysis for tracking the changes in the acoustic environment (Ferreira *et al.*, 2018; Lillis *et al.*, 2018; Towsey *et al.*, 2018; Sugai *et al.*, 2019). Calls of mammals are often considered among the key markers for describing the acoustic landscapes (soundscapes) (Ferreira *et al.*, 2018; Farina, 2019), in addition to the key markers of insect,

anuran, bat or bird choruses (Jeliaskov *et al.*, 2016; Gasc *et al.*, 2017; Doohan *et al.*, 2019; Desjonquères *et al.*, 2020), because many mammalian species produce high-amplitude long-distance vocalizations, representing important bioacoustical components of the environment: lion *Panthera leo* (McComb *et al.*, 1994), maned wolf *Chrysocyon brachyurus* (Balieiro & Monticelli, 2019) and red deer (Bocci *et al.*, 2013; Douhard *et al.*, 2013; Volodin *et al.*, 2013b, 2015b; Rusin *et al.*, 2019).

As two recording sites within population provide similar data on the dynamics of roaring activity, we can conclude that one recording device/site per population is sufficient for population passive acoustic monitoring at least in small natural habitats and in enclosures. At the same time, two or even more remotely spaced devices may be necessary for the large territories. We also can conclude that whereas a position of the recording site within population area does not affect noticeably the roaring dynamics, it may nevertheless strongly affect the actual number of recorded calls. Effects of time of day on roaring activity depended on phase of the rut and were similar in all populations.

Future passive acoustic monitoring of *Cervus elaphus* populations at the same recording sites in the following seasons should confirm the sustainable or shifted calendar dates of the rut and variation in absolute numbers of calls/h within and between populations. Further research is necessary to estimate the effect of different natural factors on the roaring activity: temperature, humidity, power of wind, cloudiness, atmosphere pressure, precipitations.

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