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Nocturnal chats of farmed animals: non-rutting vocalisations of male Iberian red deer, *Cervus elaphus hispanicus*

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ABSTRACT

Context. Captive environment may inhibit the emission of some call types by non-domesticated farm and zoo animals; so, their complete vocal repertoires remain unknown. Automated acoustic recording might help fill this gap of knowledge. **Aim.** The aim of this study was to describe vocalisations of farmed Iberian red deer, *Cervus elaphus hispanicus*, stags out of the autumnal rutting period (in summer and in winter) applying the manual and automated acoustic recording. **Methods.** In this pilot study, automated audio recording of undisturbed animals followed with spectrographic analysis showed hidden parts of social acoustic communication in farmed male Iberian red deer in non-breeding period. **Key results.** We detected three call types (roars, contact calls and bellows). Stag contact calls and bellows were described in the first time in red deer. Non-rutting roars were acoustically similar with rutting roars reported for wild-living Iberian red deer stags but of lower-frequency than were stag rutting roars recorded on the same farm in previous studies. Stag contact calls were reminiscent of hind contact calls recorded on the same farm in previous studies, but lower in frequency and shorter. Stag bellows were acoustically similar with bellows of male domestic cattle. **Conclusion.** This study reveals previously unknown parts of male red deer vocal repertoire. **Implications.** The lack of certain components of behavioural and vocal repertoire may indicate potential welfare problems in farmed and zoo animals.

Keywords: acoustic communication, animal behaviour, animal welfare, automated recordings, call types, non-rutting period, red deer, stag calls.

Introduction

Captive environment may affect animal welfare (Zulkifli 2013; Mota-Rojas *et al.* 2020) and communication with conspecifics (Manteuffel *et al.* 2004) or humans (Gogoleva *et al.* 2013). On farms, in the lack of interfering factors, such as, for example, presence of farm staff, variation in animal communicative behaviour may increase substantially, similarly to these effects found in nature (Wilson *et al.* 2020). As the result of this effect, in artiodactyls, some call types that are common in animal vocal repertoires may never occur in daytime during farm or zoo working hours and might be produced only at night, such as, for example, nocturnal humming by captive giraffes, *Giraffa camelopardalis* (Baotic *et al.* 2015). This cascading effect on vocal communication with conspecifics out of the working hours has yet to be studied in farmed red deer.

Farmed red deer stags (*Cervus elaphus*) often do not approach people or display a wide spectrum of behaviours when near humans. In adult male Iberian red deer (*Cervus elaphus hispanicus*), only the rutting roars were previously investigated (Frey *et al.* 2012; Passilongo *et al.* 2013; Volodin *et al.* 2013*a*, 2015). Additionally, in adult female and in young Iberian red deer, only mother and offspring contact calls were previously investigated (Sibiryakova *et al.* 2015; Volodin *et al.* 2015, 2018*a*, 2018*b*). Similar knowledge gap regarding call-type analysis exists in literature regarding other European subspecies of red deer. Studies of stag vocalisations are focused on their rutting roars as mating calls (Reby and McComb 2003;

Kidjo *et al.* 2008; Bocci *et al.* 2013; Volodin *et al.* 2019*a*; Golosova *et al.* 2021). At the same time, studies of female and young vocalisations are focused on their contact calls as vocalisations supporting mother and offspring relationship (Vaňkova and Málek 1997; Vaňková *et al.* 1997; Kidjo *et al.* 2008; Della Libera *et al.* 2015).

However, we expect that repertoire of call types in red deer is shared by both sexes from the point of view of their acoustic structures, although their functions may be different between sexes. These expectations come from the findings that, in Asian wapiti *Cervus canadensis sibiricus*, which are closely related to European red deer (Hu *et al.* 2019; Doan *et al.* 2022), farmed stags produce female-like contact calls at low arousal during playful competitive interactions with male conspecifics during the rut or out of the rutting period (Volodin *et al.* 2016). Furthermore, for American wapiti, *Cervus canadensis canadensis* (Meiri *et al.* 2018), early studies mention stag cohesion and sparring calls, which (although not studied spectrographically) can also represent male contact calls (Struhsaker 1967; Bowyer and Kitchen 1987). In their order, hinds of the Asian wapiti and also of American wapiti produce bugles indistinguishable from stag rutting bugles when they are at high emotional arousal due to the danger for their offspring (Murie 1932; Feighny *et al.* 2006; Volodin *et al.* 2016). In addition, both sexes of American and Asian wapiti produce alarm barks toward predators (Struhsaker 1967; Bowyer and Kitchen 1987; Volodin *et al.* 2013*b*; Volodina *et al.* 2018).

Thus, in wapiti, stag and hind vocal repertoires are similar regarding the sets of call types and the acoustic structure of the calls. Both hind and stag sets of call types include the following: the alarm barks towards potential danger; the contact calls at low arousal; and the rutting-like calls at high arousal. At the same time, there are strong differences in functions of bugles and contact calls produced by stags and hinds, in spite of similarities in the acoustic structure of these calls between sexes. The high level of emotional arousal evoking the rutting-like calls occurs in stags in the rutting period (Struhsaker 1967; Feighny *et al.* 2006; Golosova *et al.* 2017, 2021), whereas in hinds, it occurs during the calf-raising season (Murie 1932; Feighny *et al.* 2006; Volodin *et al.* 2016). Among other Artiodactyla, the high level of emotional arousal provokes the rutting-like calls in female camels (*Camelus bactrianus* and *Camelus dromedarius*; Volodin *et al.* 2022).

It remains unknown whether red deer hinds, similar to wapiti hinds, are also capable of producing the calls similar to stag rutting roars. Additionally, it also remains unknown whether red deer stags are capable of producing the contact calls similar to hind contact calls during communication with conspecifics. For the European red deer stags, in the research conducted so far, only the rutting roars were described and only within the rutting period. Among the European native populations of red deer, the alarm barks were described only in the Scottish populations (Long *et al.* 1998).

Thus, compared with farmed wapiti, vocal repertoire described for farmed European red deer seems to be incomplete. In nature, obtaining such kinds of data is difficult, because, distinctive from the rutting calls, the contact calls of red deer are faint and can be heard and recorded only in close proximity to the animals. On farms, red deer stags perform a natural vocal behaviour during the rutting period, whereas red deer hinds perform a natural vocal behaviour during the rutting and calving periods (Sibiryakova *et al.* 2015; Volodin *et al.* 2015). In wild Iberian red deer, the rutting period is usually in September–October (Frey *et al.* 2012; Passilongo *et al.* 2013); the farmed Iberian red deer stags vocalise most actively in September (Volodin *et al.* 2015). We expected therefore that if male red deer vocalise out of the rutting period, then their calls could be documented on the farm.

For the Iberian red deer, acoustic variables were investigated in all sex and age classes, namely, stags (Frey *et al.* 2012; Passilongo *et al.* 2013; Volodin *et al.* 2015), hinds (Sibiryakova *et al.* 2015; Volodin *et al.* 2015, 2018*a*, 2018*b*) and calves (Sibiryakova *et al.* 2015; Volodin *et al.* 2015). However, vocalisations of the Iberian red deer stags (rutting roars) were investigated only during the rutting periods. The aim of this study was to describe vocalisations of farmed Iberian red deer stags out of the autumnal rutting period (in summer and in winter) on the basis of a pooled call sample from a group of animals recorded in the automated mode, and to estimate their diurnal or nocturnal prevalence.

Materials and methods

Animals, site, and dates of work

Our subjects were five adult Iberian red deer stags, aged from 3.5 to 7.5 years, kept at the experimental farm of the University of Castilla-La Mancha (Albacete, Spain, 38°57′10″N, 1°47′00″W, 690 m asl). The deer on this farm are handled only for weighing, taking blood samples, and other experimental and management purposes. Therefore, no handling or 'gift' feeding is undertaken to increase their tameness, and thus animals usually keep distance from humans if possible. Routine feeding during data collection period occurred once or twice a day; volume food was given at 09:00 hours to 10:00 hours in the morning on Monday, Wednesday and Friday; whereas concentrated food was given every day at dusk to avoid birds eating it.

In 2011, calls were recorded between 10 June 2011 and 25 June 2011 from Stag 1 of 6 years old kept in the paddock of 0.3 ha with five other adult males aged 6–8 years. In 2018, calls were recorded (without individual identification) between 22 January 2018 and 26 January 2018 from four stags (Stags 2–5, of 7.5, 5.5, 4.5 and 3.5 years of age) kept together in the paddock of 0.3 ha. In both 2011 and 2018, the stags were kept separately from the hinds in the paddock with metal walls; there were no common walls between paddocks of hinds and stags. In both 2011 and 2018, only one group of adult stags was kept on the study farm.

Subject stags belonged to a population established in 1994 from 15 male and 50 female red deer from two native Iberian populations; these animals were from a nearby Las Dehesas public game reserve in Alpera (Albacete) and from Cabañeros National Park (Toledo). Subject stags were fed *ad libitum* with a diet of barley straw and meal from barley, alfalfa, oats and sugar beets (Landete-Castillejos *et al.* 2003; Volodin *et al.* 2018*a*).

Acoustic recording

In 2011, for the manual recordings of stag vocalisations from Stag 1 with a hand-held microphone, we used a Marantz PMD-660 solid-state recorder (D&M Professional, Kanagawa, Japan) with an AKG-C1000S (AKG-Acoustics Gmbh, Vienna, Austria) cardioid electret condenser microphone. Distance to microphone varied from 2.0 to 20 m; the orientation of an animal to the microphone was mostly frontal; the level of recording was adjusted during the recordings accordingly to the intensity of the produced calls. We recorded calls (sampling rate at 48 kHz, 16 bit, mono) daily, for 8 days in total (eight recordings in total, ranging in duration from 4 to 17 min; 86 min of recording in total). All manual recordings were made during daylight hours.

In 2018, for the automated recordings (22.05 kHz, 16 bit, stereo) of vocalisations from Stags 2–5, we used a SongMeter SM2+ device (Wildlife Acoustics Inc., Maynard, MA, USA) mounted on a feeder (one feeder in the paddock), about 2 m above the ground. The device had two omnidirectional microphones, established horizontally at an angle of 180° to each other. The device was set to the maximum sensitivity of recording; so, it potentially recorded all calls, faint and loud, emitted by the stags in the paddock. The device remained on its place permanently during the recording period. Researchers did not visit it, to avoid potential animal disturbance; so, only routine feeding by farm staff occurred during the recording period.

The device recorded calls every day nearly continuously; the total length of acoustic monitoring was 90 h in total, from 16:30 hours 22 January 2018 to 10:30 hours 26 January 2018. The recording schedule was set to record 29 min and 1 min pause, which cut the permanent recording to wav-files of appropriate length for analysis. In total, the device recorded 180 audio files, each file 29 min, amounting to 87 h of recording in total. In January 2018, the duration of 'day' in the recording site was 10 h (from sunrise at 08:20 hours to sunset at 18:20 hours), whereas the duration of 'night' was 14 h, which comprised 34 h of recordings in daytime and 56 h of recording in night-time. We calculated the number of calls of each type for each hour of recording (calls/h), separately for daytime and night-time, and then calculated the mean ± s.d.

Call samples and acoustic analysis

Individual emitters of the recorded calls could not be identified from the automated recorders, so the calls were then treated as a pooled sample, without individual identification, following Baotic *et al.* (2015). For the analyses of acoustic data, we used Avisoft SASLab Pro (Avisoft Bioacoustics, Berlin, Germany). Sampling frequency was downsampled to 11.025 kHz for increasing the frequency resolution. Spectrograms for analysis were created using Hamming window, FFT-length 1024 points, frame 50%, and overlap 96.87%. From spectrograms, we registered all stag calls visually, irrespectively of their quality, and labelled their position in time domain on spectrogram. One researcher (S.S.G.), bioacoustically experienced but blind to recording design, classified calls by their spectrograms to one of three types (roars, contact calls, bellows) according to their vocal traits and then another researcher (I.A.V.) verified the classification. The discriminating trait for separating the contact calls was their short duration, whereas the bellows and roars could be clearly discriminated on the basis of their maximum fundamental frequency, about twice lower in the bellows (see Results).

For analysis of the occurrence of different calls types at daytime versus night-time, we took only the recordings of 2018. In total, in the 180 audio files, we found 679 calls, including 55 roars, 597 contact calls and 27 bellows made by stags. Then, we calculated the number of calls per hour for daytime and night-time separately for each call type.

For spectrographic analysis, we took the recordings of both 2011 and 2018. We selected calls of good quality, i.e. not broken with wind, not overlapped with noise and/or calls of birds, of sufficient intensity. In total, we included in the spectrographic analysis 95 calls (all were the roars) from Stag 1 (2011) and 531 calls (49 roars, 460 contact calls and 22 bellows) from Stags 2–5 (2018).

Before spectrographic analysis, the files were high-pass filtered at 0.05 kHz to remove the background noise. The filtering did not affect the acoustic measurements, because a preliminary visual inspection of spectrograms showed that all call parts were higher than 0.05 kHz. In all calls, we measured the following eight acoustic variables: one temporal, three variables of fundamental frequency and four power variables (Fig. 1). All measurements were exported automatically to Microsoft Excel (Microsoft Corporation, Redmond, WA, USA). We measured the duration on the screen with the standard marker cursor in the spectrogram window. We measured the beginning, maximum and end fundamental frequencies (f0beg, f0max, f0end) with reticule cursor in the spectrogram window (Fig. 1). We measured the peak frequency (fpeak) and the three power

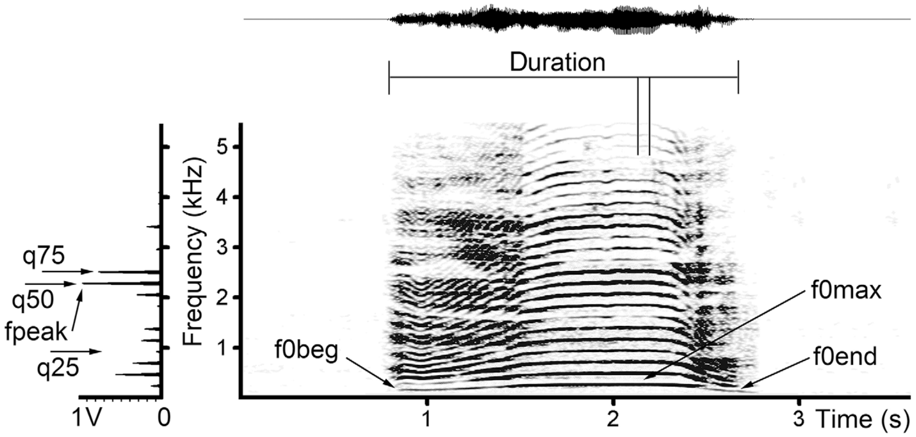

Fig. 1. Measured variables for Iberian red deer stag calls exemplified by a roar from Stag 1 in summer 2011. Spectrogram (right), wave-form (above) and mean power spectrum (left) of the 50 ms call segment around the f0-maximum area of the call (labelled with two vertical lines). Designations: duration, call duration; f0beg, the fundamental frequency at the onset of a call; f0end, the fundamental frequency at the end of a call; f0max, the maximum fundamental frequency; fpeak, the frequency of maximum amplitude; q25, q50, q75, the lower, the medium and the upper quartiles. The spectrogram was created using a sampling frequency of 11.025 kHz, Hamming window, FFT 1024 points, frame 50% and overlap 96.87%. Wav-file of the call is available in Supplementary material Audio 1.

quartiles (q25, q50, q75) covering respectively 25%, 50% and 75% of call energy, from the power spectrum created in the 50 ms segment of the f0-maximum area of the call (Fig. 1). The power spectrum created in the 50 ms segment was used to standardise the measurements for calls of different durations and to decrease the effect of background noise to power variables, because the signal-to-noise ratio was higher at the area of the fundamental frequency maximum (Sibiryakova *et al.* 2015; Volodin *et al.* 2018*a*).

Statistics

Statistical analyses were performed with STATISTICA, v. 8.0 (StatSoft, Tulsa, OK, USA). We calculated descriptive statistics to obtain general information about the recorded vocalisations by examining the mean, minimum, maximum values and standard deviations for all acoustic parameters. We used the discriminant function analysis (DFA) standard procedure based on the eight measured acoustic variables to estimate the potential for distinguishing the three call types (roars, contact calls and bellows) of Iberian red deer stags, recorded in winter 2018. As most (22 of 32 distributions) were normally distributed (Kolmogorov–Smirnov test), this did not prevent applying the parametric DFA, which is robust to departures from normality (Dillon and Goldstein 1984). We used Wilks' Lambda values to estimate how strongly acoustic variables of calls contribute to the discrimination of call types (Sibiryakova *et al.* 2015; Volodin *et al.* 2018*c*). To validate our DFA results, we calculated the random values of correct assignment of calls to call type by applying randomisation procedure with macros, created in R (R Foundation for Statistical Computing, at http://www.R-project.org). The random values were averaged from DFAs performed on 1000 randomised permutations on the data sets (Solow 1990).

Ethics

Animal care and all experimental procedures were in accordance with the International Society for Applied Ethology guidelines. We adhered to the 'Guidelines for the treatment of animals in behavioural research and teaching' (Anim. Behav., 2020, 159, I–XI) and to the laws on animal welfare for scientific research of Spain, where the study was conducted. Data collection protocol # 2011-36 was approved by the Committee of Bio-ethics of Lomonosov Moscow State University. Because the experimental procedure involved no extra handling of the deer, no ethical permit was needed from UCLM University.

Results

Stag calls produced out of the rutting period were classified into three types, namely, roars, contact calls and bellows (Fig. 2). All roars were single calls, and they were not organised in bouts. The contact calls sometimes occurred in series of a few calls, whereas the bellows were always single calls. The roar was the longest among the three call types, with the highest maximum fundamental (f0max) and peak (fpeak) frequencies (Table 1). The contact call was the

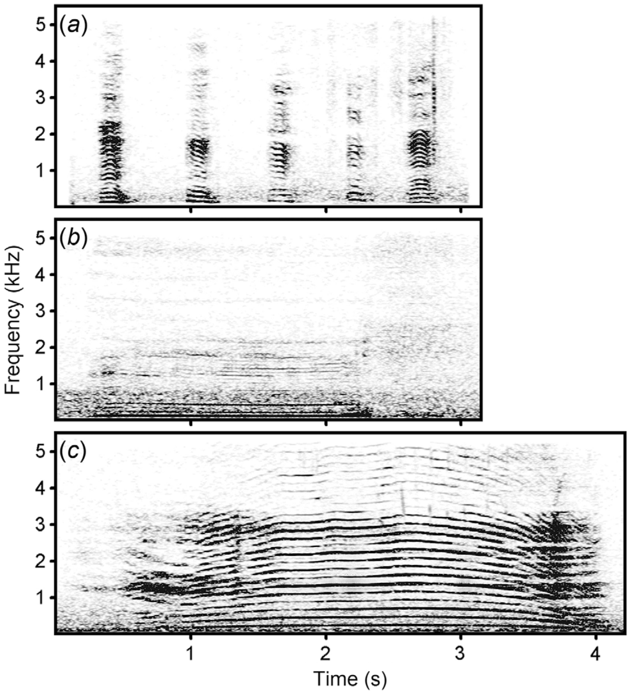

Fig. 2. Spectrograms illustrating the three call types from the automated recordings of Iberian red deer stags (Stags 2–5) in winter 2018. (*a*) Five contact calls; (*b*) bellow, followed with expiration visible as a noisy cloud; (*c*) roar. The spectrograms were created using a sampling frequency of 11.025 kHz, Hamming window, FFT 1024 points, frame 50% and overlap 96.87%. Wav-file of the calls is available in Supplementary Audio 1.

shortest in duration and had f0max intermediate between the roars and bellows, with peak frequency lower than in the roar but not differing from that in the bellow. The bellow was the lowest in f0max and intermediate in duration between the roar and contact call (Table 1).

The boundaries between the three call types (recorded in winter 2018) were well distinguishable. The contact calls differed from bellows or roars by their short duration (Table 1). The longest duration of the contact calls (0.49 s) was shorter than the shortest duration of bellows (0.52 s) or roars (2.22 s). The bellows had lower values of f0max and duration (Table 1). The highest f0max in the bellows (150 Hz) was lower than the lowest f0max in the roars (160 Hz), and the longest duration in the bellows (2.06 s) was shorter than the shortest duration in the roars (2.22 s).

DFA assigned stag calls recorded in winter 2018 to call types with an accuracy of 99.25%. All roars (100%) and all contact calls (100%) were assigned to the correct call type. However, only 18 of 22 bellows (81.82%) were correctly assigned to call type ‘bellow’, whereas the remaining four bellows were incorrectly assigned to call type ‘contact call’ (Fig. 3). The result of correct classification was significantly higher than chance level (33.6 ± 0.8%, $P < 0.001$, permutation text, 1000 permutations). Wilks’ lambda values showed that variables mainly contributing to discrimination were duration, f0max and q75 (in order of decreasing importance). The first discriminant function was highly correlated ($r = 0.97$) with duration, whereas the second

Table 1. Mean, standard deviation, minimum and maximum values of acoustic variables for the three call types of Iberian red deer stags, recorded in 2011 and in 2018.

Acoustic variable	**Call type**			
	Roar 2011 *n* = 95; *N* = 1	**Roar 2018 *n* = 49; *N* = 4**	**Contact call 2018 *n* = 460; *N* = 4**	**Bellow 2018 *n* = 22; *N* = 4**
Duration (s)	2.74 ± 0.42 1.64–3.63	3.47 ± 0.47 2.22–4.44	0.19 ± 0.05 0.09–0.49	1.07 ± 0.42 0.52–2.06
f0beg (Hz)	119 ± 35 50–200	123 ± 21 80–160	128 ± 28 70–200	87 ± 20 60–120
f0max (Hz)	224 ± 18 180–270	222 ± 28 160–290	148 ± 24 100–210	120 ± 15 90–150
f0end (Hz)	96 ± 16 70–170	133 ± 20 90–160	108 ± 22 60–180	95 ± 14 70–110
fpeak (Hz)	652 ± 341 190–2260	573 ± 554 160–2700	189 ± 279 90–3120	105 ± 14 60–130
q25 (Hz)	569 ± 177 200–1060	429 ± 147 190–770	311 ± 191 110–1290	135 ± 54 90–360
q50 (Hz)	1008 ± 316 400–2250	920 ± 308 370–1620	890 ± 427 150–2140	292 ± 278 120–1470
q75 (Hz)	2055 ± 578 750–3020	1857 ± 374 1010–2720	1903 ± 541 440–3340	902 ± 472 310–2450

Designations: duration, call duration; f0beg, the fundamental frequency at the onset of a call; f0max, the maximum fundamental frequency; f0end, the fundamental frequency at the end of a call; fpeak, the frequency of maximum amplitude, q25, q50, q75, the lower, the medium and the upper quartiles; *n*, number of calls; *N*, number of individual stags.

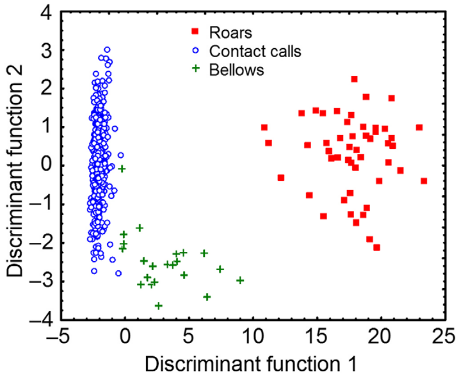

Fig. 3. Scatterplot showing separation produced by the first two discriminant functions for three call types of Iberian red deer stags recorded in winter 2018.

discriminant function was correlated with f0max (*r* = 0.75) and q75 (*r* = 0.72).

Roars recorded in summer 2011 were very similar to roars recorded in winter 2018 by f0max, f0beg and fpeak (Table 1). However, the roars recorded in summer 2011 were shorter, lower in f0end and had higher q25, q50 and q75 than did the roars recorded in winter 2018.

In winter 2018, stag vocal activity was substantially higher at night-time (14.14 ± 31.01 calls/h) than at daytime (3.54 ± 6.13 calls/h). Stags produced the contact calls and bellows more often at night-time than at daytime (contact calls: 13.33 ± 30.63 vs 1.54 ± 5.04 calls/h; bellows: 0.61 ± 1.27 vs 0.04 ± 0.20 calls/h respectively). In contrast, stags produced the roars more rarely at night-time than at daytime (0.19 ± 0.67 vs 1.95 ± 3.54 calls/h).

In summer 2011, the single stag that produced the roars (Stag 1) was the highest-rank (dominant) stag in the group of six males. The Stag 1 approached researchers standing behind the paddock gate and threatened them by aggressive head movements. This dominant stag produced the roars and displayed simultaneously aggressive behaviour towards unfamiliar researchers, but never vocalised or behaved aggressively towards familiar keepers.

Discussion

This study presented a description of three different call types, including the roars, produced by male red deer out of the rutting period. We identified two call types (contact calls and bellows) that have not previously been identified for males of this species. The differences in the acoustics of the roars, contact calls and bellows were well distinguishable and allowed to reliable identify these call types. This study also showed that use of automated recording devices is important for identifying the complete vocal repertoires in farmed animals.

Stag roars during and out of the rutting period

The non-rutting roars examined in this study in summer 2011 and in winter 2018 were spectrographically very similar to each other. As we had audio recordings from only one stag in summer 2011 and from four stags in winter 2018, the observed differences in the roars could be primarily determined by individual rather than seasonal differences. Compared to the roar acoustics out of the rut, the roars of three Iberian red deer stags recorded by the authors in a previous study on the same farm during the rutting period had a higher maximum fundamental frequency (270.2 Hz) and a shorter duration (2.53 s; Volodin *et al.* 2015). However, the maximum fundamental frequency of the roars recorded in this study out of the rut was surprisingly similar to those of the roars of the Iberian red deer stags produced during the rutting period in the wild (223 Hz, Frey *et al.* 2012; Volodin *et al.* 2015). At the same time, the duration of the roars recorded in this study out of the rut was substantially longer than that during the rut in the wild (1.96–2.49 s, Frey *et al.* 2012; Volodin *et al.* 2015). In addition, out of the rut, all roars were produced as single calls, not being organised in bouts, whereas during the rut in the wild, Iberian red deer stags produce only 34.4% of their roars singly and all the remaining roars are emitted in bouts of 2–12 roars (Frey *et al.* 2012; Passilongo *et al.* 2013). Emission of the roars in bouts during the rut is also typical for other European subspecies of red deer in the wild (Reby and McComb 2003; Volodin *et al.* 2019*a*; Golosova *et al.* 2021).

The discrepancy between the acoustics of the roars produced within and out of the rutting periods on the same farm may be explained by the elevated emotional arousal of farmed stags during the rut. On the farm, the rutting stags could see and hear the neighbouring stags with their harems through wire mesh but could not drive them away. The increased call maximum fundamental frequency in farmed stags in the rutting period may be therefore related to their higher emotional arousal (Watts and Stookey 1999; Manteuffel *et al.* 2004; Briefer 2012). In captivity, the close proximity of people may increase the emotional arousal, resulting in shifts to higher-frequency vocalisation in animals of different species (Gogoleva *et al.* 2010; Briefer 2012). This effect was previously reported for the roars of red deer stags on the study farm in the rutting period (Volodin *et al.* 2015). The same effect was reported for semi-captive Siberian wapiti stags in the rutting period (Golosova *et al.* 2017). The increase of f0max has also been shown for the rutting groans of fallow deer, *Dama dama*, bucks in vicinity of females and actively vocalising rival males (Charlton and Reby 2011).

Another reason of the higher-frequency roars in farmed stags during the rut is that, on the farm, only the mature breeding stags with harems were recorded. At the same time, in the wild, bachelor and younger stags without harems can also emit the lower-frequency roars in addition to the mature males (Clutton-Brock and Albon 1979; Reby and McComb 2003). So, the average fundamental frequency taken in total for harem-holding and non-harem-holding stags can be lower than in the farm. However, it remains unclear why the roars produced out of the rut by moderately aroused stags towards people or towards rival stags are indistinguishable in fundamental frequency from the roars produced by wild-living rutting males and are much longer than all other roars. Further research with more captive and wild populations is necessary to elucidate this question.

Stag roaring outside the rutting period is not obligatorily related to mating, but can be provoked by the presence of other stags in the same paddock or by presence by people on the farm and thus indicate dominance of the roaring stag over potential rivals. Producing mating calls (roars or bugles) out of the rutting period is related to plasticity of the time window of the rut in red deer and wapiti. In zoos and in farmed conditions, where stags have access to females, red deer and wapiti mate far outside the rutting period (e.g. in December), which results in the appearance of calves at inappropriate time (e.g. during the winter; I.A.V., E.V.V., pers. obs.). So, management of captive herds often includes pre-winter separation of sex and age classes (e.g. Sibiryakova *et al.* 2018). The plasticity of breeding season timing and mating behaviour, including the roaring, might be evolutionarily advantageous. The red deer might shift the breeding season accordingly to natural changes in the environment (e.g. Ababaikeri *et al.* 2020; Rusin *et al.* 2021) and in response to human translocation to southern hemisphere (to New Zealand: McComb 1988; to Argentina: Hurtado *et al.* 2012).

Contact calls of stags and hinds

Previously, stag contact calls have been investigated bioacoustically only in the Siberian wapiti (Volodin *et al.* 2016). These calls were indistinguishable from the contact calls of Siberian wapiti hinds in the maximum fundamental frequency and duration (Volodin *et al.* 2016). Our study is the first finding of stag contact calls in European red deer. In contrast to wapiti, stag contact calls of the Iberian red deer were strongly different from the contact calls of hinds, recorded previously on the same farm (Sibiryakova *et al.* 2015; Volodin *et al.* 2015, 2018*a*, 2018*b*). Hind contact calls were about three times longer (0.65–0.79 s) and higher in the maximum fundamental frequency (173–209 Hz; Sibiryakova *et al.* 2015; Volodin *et al.* 2015, 2018*a*). It remains unclear why such prominent acoustic differences between stag and hind contact calls exist in red deer but not in wapiti. Further research is necessary to highlight the potential reasons of this discrepancy, such as, for example, the effect of differences in sexual size dimorphism in red deer and wapiti (Geist and Bayer 1988) or the effect of difference in sound production mechanism of contact calls (Reby *et al.* 2016) and the related differences in vocal fold elasticity (Riede *et al.* 2010).

Bellows of red deer stags and other artiodactyls

The low-frequency bellows of our subject Iberian red deer stags were very similar in the acoustics to the domestic cattle bull bellows. However, they were shorter in duration and lower in fundamental frequency than those of bull bellows of the Chillingham cattle breed (*Bos taurus*) (duration = 1.5 s, f0max = 150–170 Hz, Hall *et al.* 1988), bellows of yearling bulls and cows during sham branding (duration = 1.5 s, f0max = 142 Hz, Watts and Stookey 1999) and bellows of free-ranging mature crossbred Brahman × European cattle bulls (*Bos taurus taurus* × *Bos taurus indicus*; duration = 1.45 s, f0max = 114 Hz, Volodin *et al.* 2017). Bellows of the Iberian red deer stags were also slightly shorter and lower in fundamental frequency than are bellows of the American bison *Bison bison* bulls (duration = 2.05 s, f0max = 230 Hz, Gunderson and Mahan 1980).

Aside from cattle bulls, another artiodactyl producing the bellow-like 'humming' calls is giraffe (Baotic *et al.* 2015). As for cattle bull bellows, these calls are also comparable with red deer bellows in fundamental frequency (92.01 ± 25.78 Hz) and duration, varying from a minimum 0.41 s to a maximum of 4.17 s. The similarity with red deer bellows is increased in that this call type of giraffe was recorded only during the nocturnal recording with the automated devices in captive conditions of three different zoos (Baotic *et al.* 2015). As in the study of giraffes, automated recording of red deer calls in our study prevented identifying the context of vocal emissions; however, as the recording device was attached to the feeder, we can reasonably propose that most of the faint calls (contact calls and bellows) were produced in the vicinity of the feeder and were friendly or neutral communicative exchanges emitted during or between the rounds of feeding of the stags.

Nocturnal and diurnal vocalising

Farmed Iberian red deer stags in the non-rutting period produced the roars primarily at daytime, whereas the contact calls and bellows were primarily produced at night-time. Thus, some call types are produced by red deer stags only out of the working hours. The contact calls and bellows were emitted by the stags nearly exclusively at nights, so even the keepers and managers did not suspect that the stags on their farm produced such calls. This effect of 'secretive life of farmed animals' should be taken into account for further research of vocal behaviour of farmed deer both during and out of the rutting periods. The apparently 'secretive' night calling may outcome from the functions of the contact calls and bellows. Whereas there are no evident reasons why to call during the day, calling at night may aim to check the status of other group members when animals cannot see their conspecifics. It would be expected that an attack by a predator would elicit a 'warning call', but if an animal dies silently (because of disease, heart attack, extreme cold, etc.), the only way to notice it would be that such animal would not answer to these contact calls. Therefore, the function of contact calls in male red deer groups can be in maintaining group cohesion and spatial proximity. This is similar to the function of contact calls in groups of a few females with young in red deer (Kidjo *et al.* 2008; Sibiryakova *et al.* 2015) and other ungulates (Padilla de la Torre *et al.* 2015, 2016; Volodin *et al.* 2019*b*).

In spite of the fact that farmed Iberian red deer stags roared in the light time of day, they rarely addressed the roars toward the permanent farm staff. Probably, subject stags direct their aggression and roaring selectively to unfamiliar researchers, as Stag 1 did this in 2011. We conclude that the registration of the full set of call types produced by farmed red deer is only possible with automated recorders. In contrast, the collection of all acoustic data only manually by researchers visible for animals can result in a distorted picture. So, the automated bioacoustic recording is proving to be a useful tool for animal welfare monitoring on the farms (Bishop *et al.* 2019; Mcloughlin *et al.* 2019; Laurijs *et al.* 2021).

Applied in this study, automated method of audio recording was the only appropriate approach for collecting calls from red deer stags vocalising in a tight group, when animals communicate neck-to-neck around the feeder, primarily with a closed mouth and head down. Limitation of automated recording in animal groups is that calls cannot be assigned to particular individuals. However, using stationary video cameras does not allow identifying particular callers, as the animals often block the view of each other or can vocalise with their backs to the camera. Using collar-mounted individual microphones for recording calls on an individual basis is appropriate only for the solitary animals, as chipmunks (Couchoux *et al.* 2015) or lynxes (Studd *et al.* 2021). On red deer farm, collar-mounted individual microphones cannot help record calls on an individual basis, as they would record the calls of neighbouring stags with the same as or even the higher intensity than calls of the focal callers.

Supplementary material

Supplementary material is available online.

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

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