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Pre-rut behavioural changes in farmed red deer with reference to atmospheric conditions

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Abstract

Red deer (*Cervus elaphus*) exhibit specific behaviour during the rutting season, which may have an impact on the safety on cervid farms, both due to aggressive interactions between animals and the safety of people staying there, such as staff and tourists. This issue applies especially to stags whose behaviour changes radically, and the correct interpretation of the observed changes is very important. Therefore, the aim of the study was to analyse the pre-rut behaviour of stags and to show the influence of atmospheric conditions on vocalization and other elements of their behaviour, which facilitate determination of the onset of the rutting season. The observations were conducted in August and September of 2017 and 2018. It was shown that lower temperatures, declines in air humidity, increasing atmospheric pressure, and transition of the moon phase towards the full moon resulted in intensification of the vocalization activity in the red deer in the pre-rutting season, which may accelerate the rutting period in the deer males. The number of vocalizations varied between the years and depended on the mean temperature, air humidity, atmospheric pressure, and moon phase in the pre-rutting and rutting seasons. Through observation of the changing weather conditions, it is possible to predict the time of increased activity of stags and the onset of the rutting period. Predicting the date of mating season in farm breeding, based on daily observations of changes in the behaviour of stags, can be helpful in planning veterinary treatments or selecting the composition of the hinds to be covered by specific stags, which can also contribute to the improvement of their welfare.

Keywords: *Cervus elaphus*, mating season, vocalization, temperature, rainfall, air pressure
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Introduction

Sounds made by animals convey species- and specimen-specific information. Natural selection and evolution have increased the importance of individual signals through ritualization (Rogers & Kaplan, 2002). As in most mammals characterized by sexual dimorphism, the reproductive success of male red deer depends on the competition with other males for access to females (Bartoš, 1986; McComb, 1991). Giving off a full and strong roar by a stag requires good individual quality and appropriate age, which is associated with the development of the vocal apparatus (Fitch & Reby, 2001; Feighny *et al*., 2006; Riede & Titze, 2008; Frey *et al*., 2012; Frey & Riede, 2013). During the rutting period, red deer (*Cervus elaphus* L., 1758) vocalize to get females and to form harems, which is the most important function of male vocalization: to attract females to their territories and discourage

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competitors from fighting (Garcia *et al*., 2013). Vocalizations in the rutting period are part of courtship, as they can accelerate ovulation in the hinds (McComb, 1987). Vocalization is used by females to find a mate and contributes to accelerated rutting and may prevent fights and unnecessary energy expenditure in competing males (Clutton-Brock *et al*., 1979; Reby & McComb, 2003; Reby *et al*. 2005). It is also worth emphasizing that most hinds conceive at the first ovulation (Guinness *et al*., 1971); therefore, usually at the onset of the mating season, the stag must be ready to fertilize the largest number of females at the beginning of the rutting season to be successful in transferring genes to the largest number of offspring. As shown by Reby & McComb (2003), stags with the highest number of matings initiated their vocal activity at the onset of the rutting season and continued the vocalization over most of the following days of the rutting period. The females therefore chose the male based on their long-term investment in vocal activity. The pre-rutting period and the effort made by the male at that time are probably more important and exert an impact on the number of fertilized females. Additionally, previous intense efforts, which may be manifested in changes in the stag behaviour, can lead to success in forming a larger harem (Reby & McComb 2003).

Vocal activity is an important part of advertising male reproductive potential in red deer (Volodin *et al*., 2016). It has been shown that older and larger males producing lower-frequency sounds were preferred by females. In this way, hinds ensure their safety during mating and have the prospect of better offspring (Charlton *et al*., 2007). The mating behaviour of *Cervus elaphus* males is rather associated with the defence of their harem (Struhsaker, 1967; Clutton-Brock *et al*., 1982), i.e., usually mobile groupings in which females are tracked and defended by males. The vocal activity of stags varies depending on the season of the year, time of the day, or age of the animal (Volodin *et al*., 2016). Additionally, climate change, rising temperatures, changing rainfall, and wind can affect animal activity (Walther *et al*., 2002; Bowler *et al*., 2017). It was confirmed in Spain that a decrease in rainfall was associated with a delayed rutting season and decreased rutting intensity, but appeared to favour a higher degree of polygyny and opportunity for sexual selection (Post *et al*., 1997; Millán *et al*., 2021). The mating season in red deer has been well described by researchers; however, the time preceding the season, preparation, and behaviour of animals before the rut have been insufficiently explored. It is especially important in farm breeding where deer retain much of the wild characteristics, especially males during rut (Bartoš, 1986). In farmed cervids, it is beneficial for females to get pregnant as soon as possible and at the same time because fawns will be born earlier, which will provide them with better early growth and a proper body weight, which is very important for surviving winter. However, hinds need to have a certain body condition to enter oestrus and the males should be ready for rutting or the following oestrus will take 20 days. Moreover, it is also important in male management that they are replaced once they get exhausted, and to ensure that hinds not pregnant after first cycle will be in the second cycle (Haigh & Hudson, 1993; Mulley, 2007). Predicting the date of the rutting period in farm breeding, based on daily observations of changes in the behaviour of stags, would be of great cognitive and practical importance. Appropriate analysis of behavioural changes by deer breeders can be helpful in determining the date of separating males into separate pastures, planning veterinary treatments or selecting the composition of the hinds to be covered by specific stags, which can also contribute to the improvement of their welfare (Janiszewski *et al*., 2016; Dziki-Michalska *et al*., 2021).

Therefore, the aim of the research was to analyse changes in pre-rut behaviour of stags and show the impact of weather conditions on vocalization and other behavioural elements in farmed male red deer that facilitate recognition of the onset of the mating season.

Material and method

Experimental design

The research was carried out at the Research Station of the Institute of Parasitology, Polish Academy of Sciences, Kosewo Górne (Region of Warmia and Mazury; Poland; N: 53°48'; E: 21°23'). In the first year of the study (2017), seven red deer stags aged 2 to 9 years were observed (named: Dziki, 9 years old; Niko, 6 years old; Hubert, 4 years old; Florek and Jasiek, 3 years old; Neo and C12, 2 years old). In the second year (2018), the observations involved the same five stags (except C12 and Jasiek). Stags in both years were kept in summer paddocks in contact with a herd of 40–45 hinds. The breeding system consisted of rotational access to pasture in the paddocks with a density and nutritional scheme recommended by FEDFA (2020) and Mattiello (2009). In 2017, the herd was monitored in terms of mating behaviour. In 2017 and 2018, the frequency and duration of vocalization as well as weather conditions were recorded. At the beginning of the study, the deer were observed for 24 h to establish the time of day with the highest intensity of the vocal activity of the stags. This indicated that the observations should be carried out for one hour in the morning and three hours in the evening. The study was conducted for two months (August, September) in 2017 and 2018 from 05:00 to 06:00 and from 20:00 to 23:00 every other day. A ZOOM H6 sound recorder, a Nikon D70s camera, binoculars,

and a Night Vision Scope NV5x60 devices were used to record the sounds produced by the stags and observe their behaviour. The weather conditions were recorded using a thermometer with a hygrometer and weather maps from a nearby meteorological station (Institute of Meteorology and Water Management; Maritime Department; Meteorological station). At the beginning of the study, the herd was accustomed to the presence of the observer. The observations were made at a distance of 2–10 m from the animal group; after 20 min, the animals ignored the presence of the observer. The numbers on the ear tags and diagrams of stags' antlers were used to identify the individual specimens (Fig. 1).

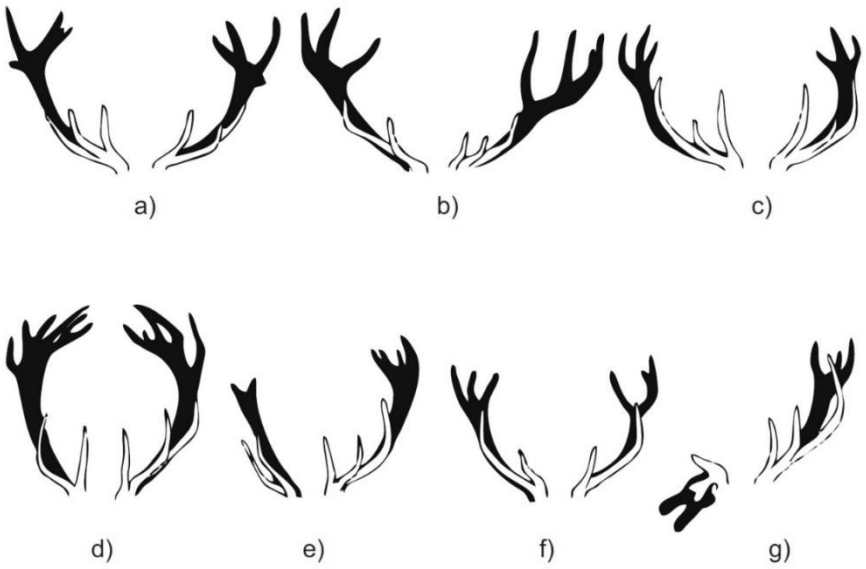

Figure 1 Scheme of the antler shape in the stags.

During the observations, all behaviours of the stags were recorded. These included vocalization, i.e., a single roar or few roars per event, being in a male group, stag fights, fighting against vegetation with antlers, chasing the hinds, flehmen response, urinating on the lower abdomen, and other behaviours, which are listed and described in the ethogram (Table 1).

To carry out statistical analyses, the observation period was divided into two terms: pre-rut and early rut. The two periods were delimited by a sudden increase in the number of vocalizations indicating the onset of the rutting period. The most frequent behaviours of the stags (Table 1) were selected for the analysis: vocalization, flehmen response, attempts to fight, staying in a group of males, thrashing the vegetation, and chasing the hinds.

Statistical analysis

The results are expressed as the mean value and standard deviation. The Shapiro–Wilk test was used for the analysis of the distribution of the studied variables. A mixed linear model (GLMmix procedure of SAS software; Statistical Analysis System, 9.4, 2013) was used, in which the following factors were used as constant factors: year, time, and also as regressors: temperature, air humidity, rainfall, atmospheric pressure, wind speed, and moon phase as affecting vocalization. The introduction to the linear model of the day as a random factor and the interaction of the year and time due to the large number of null solutions caused problems with the matrix inversion and, consequently, the singularity of the model.

The Mann–Whitney test were used to compare the vocalizations between the years, and the Student's *t*-test was used to compare the atmospheric conditions between the years. The simple correlations between the number of vocalizations and other behaviours and the atmospheric conditions were assessed using the r-Pearson correlation coefficient and the Spearman rank correlation coefficient. All relationships were evaluated at the significance level of $P < 0.05$. The statistical analyses were performed using Statistica 9.1 software (StatSoft, Poland).

Table 1 Ethogram of farmed deer reproductive behaviour in the pre-rutting period and early rutting

Subcategory of behaviour	Types of behaviour	Description	The number of individual behaviours [%]
preparation for the rutting season	flehmen response	tilting the upper lip upwards with the neck stretched out to capture the female's scent	11.3
	urinating on the lower abdomen	passing urine in the lower abdomen, standing	2
	distribution of urine with antlers	digging up the places where you have previously urinated with antlers	0.2
	detachment of velvet from the antlers with the help of vegetation	rubbing with antlers against grassy vegetation as well as bushes and trees growing in the grazing area	11.2
	fighting against vegetation with antlers	hitting the grass with antlers as well as bushes and trees growing in the grazing quarters	
	demonstration of potential by stags	moving slowly with head held high, teardrops open, and antler demonstration	0.2
social behaviour	being in a mixed group	presence of a given stag in a grouping with other males and females	-
	being in a male group	presence of a given stag in a group with other males	5
	disconnecting from the herd	departure of a given stag from the grouping	-
stag vocalization	attempts to roar	first short sung sounds	55.5
	single roar	singing of one roar	
	few roars	singing a few roars in succession	
agonistic behaviour	march to judge the opponent	a slow march of two males with the presentation of the silhouette and antlers, which is the stage of selecting the dominant	0.3
	stags power tests	short-term pushing through with antlers	9.3
	stags fight	pushing and hitting antlers between two stags	
competition for females	drive out younger males	aggressive behaviour of the stag towards younger males, combined with an antler attack	0.2
	drive out hinds	driving the doe away by the bull showing signs of aggressive behaviour	0.2
	taking a hind from another stags' group	the male doe is driven away from another stag's group and joins his group	4
	creating a harem	the formation and guarding of a group of hinds by a stag	0.1
copulation	mating stag–stag	the stag jumping onto the back of another male, imitating copulation	0.1
	mating attempt	jumping on the back of the doe to cover it	0.1
	mating a stag–doe	copulation with a doe	0.3

Results

Inter-year differences

During the observations in the pre-rutting period, the average air temperature was 15.61 ^{o}C, i.e., almost five degrees higher than in the mating season; similar to the average air humidity. The average precipitation rate was substantially higher in the pre-rutting period than during the mating season. The average atmospheric pressure and wind force were similar in both observation periods (Table 2).

The comparison of the observations carried out in 2017 and 2018 demonstrated that the air temperature fluctuated largely in the first year of the study. A marked decrease was observed at the beginning of September, which resulted in the acceleration and increase in the frequency of vocalization by almost two days. In mid-September 2017, the air temperature decreased again, which also contributed to intensification of the roaring activity of the stags (Fig. 2).

Table 2 Mean number of farmed deer vocalizations and data on the weather conditions during the pre-rutting and early rutting seasons

Analysed variable				Pre-rutting season		Early rutting season	
				M	SD	M	SD
temperature	average			15.61	3.803	10.78	4.313
	morning	05:00–06:00	°C	15.76	4.039	12.65	5.678
		20:00–21:00		17.24	4.657	10.94	4.507
	evening	21:00–22:00		15.42	4.062	10.12	4.314
		22:00–23:00		13.61	3.631	9.41	4.139
air humidity	average			76.95	4.230	71.32	5.871
	morning		%	76.24	5.449	70.53	8.285
	evening			77.36	6.523	72.12	6.518
rainfall	average		mm/3h	0.788	1.452	0.059	0.243
atmospheric pressure	average		hPa	1006.49	8.322	1007.52	8.092
wind speed	average		km/h	12.61	5.272	12.50	7.238
phase of the moon			%	49.84	36.273	59.12	35.524
vocalization number	sum morning + evening			21.73	31.569	693.06	472.458
	morning	05:00–06:00		5.06	7.810	170.24	123.486
	evening	20:00–21:00		4.91	10.357	165.71	133.337
		21:00–22:00		5.24	10.932	187.18	137.510
		22:00–23:00		6.58	11.911	169.94	125.862
		sum		16.73	29.891	522.82	363.485
average length of a single vocalization			seconds	1.67	0.953	2.47	0.557

M, mean; SD, standard deviation

The number of vocalizations in 2017 and 2018 was compared with reference to the weather conditions in the pre-rutting period. The vocalization emitted by the stags and the average length of a single roar in the pre-rutting period did not differ substantially between the years (Table 3). However, there were substantial differences between 2017 and 2018 in the sum of single vocalizations, the number of morning and evening vocalizations at 20:00–21:00 and 22:00–23:00, and the sum of evening vocalizations during the early rutting season (P <0.05) (Table 3).

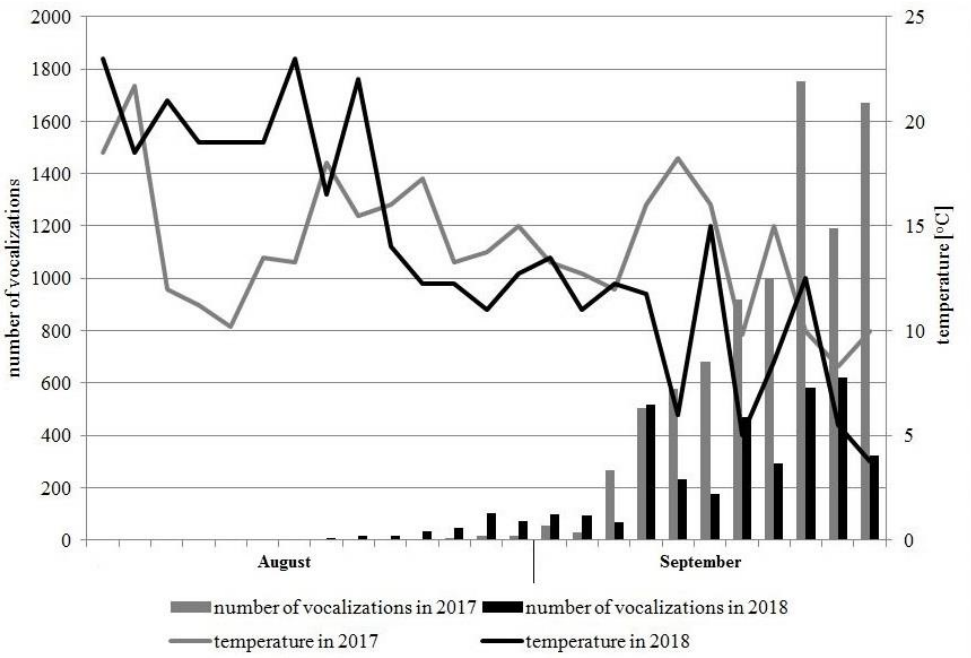

Figure 2 Number of vocalizations from farmed male red deer in 2017 and 2018 vs. air temperature in the regions of Warmia and Mazury, Poland

The pre-rutting period differed between 2017 and 2018 in terms of the mean temperature (lower mean temperature recorded in 2017), air humidity in the evening, atmospheric pressure, and wind speed (P <0.05). The mean temperature, atmospheric pressure, and wind force were lower in 2017, and only air humidity in the evening hours was higher than in 2018 (Table 4).

The early mating season differed between 2017 and 2018 in terms of the mean temperature, morning temperature, average humidity, the amount of rainfall, atmospheric pressure, wind strength, and precipitation (P <0.05). The mean temperature, morning temperature, average humidity, and rainfall were higher in 2017, and only the values of atmospheric pressure, wind force, and precipitation were lower than in 2018 (Table 4).

Pre-rutting and rutting period differences

The mean number of vocalizations was almost thirty times higher in the mating season than during the pre-rutting period. In both periods, the stags vocalized more often in the evening than in the morning. Moreover, single roars were almost 1.5 times longer during the rutting season than in the pre-rutting period (Table 2). The number of stag vocalizations was compared with reference to the weather conditions prevailing in the pre-rutting period and during the mating season (Table 5, 6, 7). The influence of the year, temperature, air humidity, atmospheric pressure, and moon phase were evident on the vocalization of farmed deer (P <0.05, Table 5).

Table 5 The probability of the influence of given factors on the vocalization of farmed deer

Parameter evaluation				
Effect	Estimate	SD	F	*P*
Intercept	691.750	78.199	8.85	<0.0001*
year	45.745	13.059	12.27	<0.0001*
time	11,906	16,726	0.30	0.825
temperature	-5.729	1.265	20.49	<0.0001*
air humidity	-4.072	0.981	17.22	<0.0001*
rainfall	-1.434	5.262	0.07	0.786
atmospheric pressure	-0.279	0.051	29.53	<0.0001*
wind speed	-1.856	1.039	3.19	0.076
phase of the moon	0.474	0.176	7.29	0.008*

SD, standard deviation; *statistically significant values at P <0.05

The mean number of vocalizations in the morning and evening hours was correlated with the mean temperature at the time of observation (P <0.05) in the pre-rutting period. Moreover, the sum of deer vocalizations increased with a decline in air temperature (P <0.05). A negative correlation was found between the mean temperature and the number of vocalizations between 05:00 and 06:00, between 20:00 and 21:00, and between 21:00 and 22:00 (P <0.05). The sum of evening vocalizations increased with the decrease in the average temperature and at 20:00–21:00 and 21:00–22:00 in the pre-rutting period (P <0.05). There was also a negative correlation of the average air humidity with the sum of vocalizations and the number of sounds produced in the evening (P <0.05). Furthermore, the average air humidity had an impact on the average length of a single vocalization in the pre-rutting period (P <0.05). The average air humidity in the evening had an impact on the number of vocalizations at 20:00–21:00 and 21:00–22:00 and on the average length of a single vocalization of the animals in the pre-rutting period (P <0.05). The mean atmospheric pressure had a positive effect on the number of vocalizations at 20:00–21:00 and 21:00–22:00 in the pre-rutting period (P <0.05). The moon phase exerted a positive effect on the number of vocalizations in the morning and evening hours, the sum of sounds produced in the evening, and the average length of single roars produced by the stags in the pre-rutting period (P <0.05). The precipitation sum and average wind force did not have an impact on the number of sounds produced by the stags in the pre-rutting period (Table 6).

Table 3 Comparison of vocalizations between 2017 and 2018 in the pre-rutting period and during the early rutting season

Analysed variable			Pre-rutting season				U	*P*	Early rutting season				t^a/U^b	*P*
			1.08-5.09.2017		1.08-7.09.2018				6.09-30.09.2017		8.09-30.09.2018			
			M	SD	M	SD			M	SD	M	SD		
vocalization number	sum morning + evening		9.375	14.509	33.353	38.726	96.500	0.156	951.667	512.024	402.125	166.938	3.043[a]	0.012*
	morning	05:00–06:00	4.875	8.106	5.235	7.766	119.000	0.557	242.556	131.047	88.875	30.624	3.414[a]	0.007*
	evening	20:00–21:00	1.250	5.000	8.353	12.849	88.500	0.087	229.444	148.504	94.000	65.831	2.476[a]	0.030*
		21:00–22:00	0.875	3.500	9.353	13.802	87.000	0.081	239.000	161.909	128.875	76.965	1.822[a]	0.094
		22:00–23:00	2.375	4.256	10.529	15.248	105.500	0.276	240.667	118.428	90.375	80.706	10.000[b]	0.011*
		sum	4.500	8.922	28.235	37.712	104.000	0.260	709.111	393.118	313.250	174.808	2.732[a]	0.019*
	average length of a single vocalization		1.637	0.913	1.694	1.017	134.000	0.957	1.637	2.638	2.38	0.517	2.288[b]	0.574

M, mean; SD, standard deviation; U, Mann–Whitney test results; t^a, the Student's *t*-test result; U^b, Mann–Whitney test results, *statistically significant values at *P* <0.05

Table 4 Comparison of the weather conditions between 2017 and 2018 in the pre-rutting period and during the early rutting season

Analysed variable			Pre-rutting season				t	*P*	Early rutting season				t	*P*
			2017		2018				2017		2018			
			M	SD	M	SD			M	SD	M	SD		
temperature	average	°C	14.703	3.004	16.471	4.343	-1.366	0.021*	12.833	3.535	8.469	4.087	2.362	0.032*
	morning		16.250	3.890	15.294	4.239	0.674	0.505	16.222	4.381	8.625	4.104	3.675	0.002*
	evening		14.187	3.584	16.588	4.142	-1.775	0.085	11.704	3.397	8.417	4.676	1.673	0.115
air humidity	average	%	78.187	4.215	75.794	4.023	1.668	0.105	72.000	7.754	70.563	2.969	0.515	0.025*
	morning		76.375	7.209	76.118	3.257	0.133	0.895	71.111	10.576	69.875	5.303	0.298	0.769
	evening		80.000	5.739	74.882	6.382	2.417	0.022*	72.889	8.223	71.250	4.268	0.505	0.621
rainfall		mm/3h	0.813	0.982	0.765	1.821	0.093	0.926	0.813	0.000	0.765	0.354	-1.000	0.025*
atmospheric pressure		hPa	999.521	4.752	1013.058	4.792	-8.143	<0.001*	1001.249	2.016	1014.564	6.146	-6.159	<0.001*
wind speed		km/h	11.875	3.673	13.309	6.471	-0.788	0.033*	9.139	3.018	16.281	8.858	-2.171	0.023*
phase of the moon		%	38.437	38.553	60.588	31.391	-1.815	0.079	69111	27.926	47.875	41.478	1.252	0.229

M, mean; SD, standard deviation; *t*, Student's *t*-test result; *statistically significant values at *P* <0.05

During the mating season, the number of deer vocalizations exhibited a negative correlation with the mean atmospheric pressure in the morning and evening hours (P <0.05). In turn, the phase of the moon had a positive effect on the sum of sounds emitted by the stags and on the number of deer vocalizations at 05:00–06:00 and 21:00 and 22:00 (P <0.05). The number of deer vocalizations during the rutting season was not correlated with the ambient temperature, air humidity, rainfall sum, and wind strength (P< 0.05) (Table 7).

Characterization of pre-rutting and early rutting behaviour

During the observation in the pre-rutting period, behaviours such as mating stag–doe, driving out the opponent, driving out hinds, chasing the hinds, detachment of velvet from the antlers with the help of vegetation, fighting against vegetation with antlers, flehmen response, urinating on the lower abdomen, being in a male group, stag fights, and a single roar or few roars per event were recorded (Table 1). The most frequently repeated behaviour was a single roar or few roars per event (55.5%). Flehmen response (11.3%), thrashing the vegetation with antlers (11.2%), and stag fights (9.3%) were quite frequently repeated as well. The rare types of behaviour included urinating on the lower abdomen (2%), taking a hind from another stag's group (4%), mating stag–doe (which was recorded on the last day of the observations) (0.3%), and driving out younger males (0.2%) (Table 1). The hinds were not chased until the beginning of September, and this behaviour was observed more frequently as the rut approached. Except for vocalizations, these behaviours were shown by the stags more often in the morning than in the evening. The relationship between the most common behaviours and weather conditions was assessed. It was shown that flehmen response, attempted fights, staying in a group, thrashing the vegetation, or chasing of the hinds by the stags did not depend on the weather conditions. Only the chasing of the hinds was negatively correlated with the mean evening temperature (P <0.05) (Table 8).

The frequency and intensity of the behaviours exhibited by the stags varied, depending on their age. The highest activity was observed in the case of 'Dziki', who was the oldest stag in the herd, whereas 'C12', one of the youngest animals, was the least active. 'Dziki' vocalized most often and the average length of the roar produced by this stag was 1.7 seconds. An exception was 'Hubert' (4 years old), whose activity was more intense than the average value. There was a positive correlation between the age of the animals and their activity. The intensity of the analysed behaviours increased with the age of the stags.

Table 6 Relationship between the number of farmed deer vocalizations and data on the weather conditions in the pre-rutting period

Analysed variable				**vocalization number**						**average length of a single vocalization**
				sum morning and evening	**morning**	**evening**				
					05:00–06:00	20:00–21:00	21:00–22:00	22:00–23:00	sum	seconds
temperature	average		°C	R=-0.518 p=0.001*	R=-0.351 p=0.045*	R=-0.537 p=0.001*	R=-0.558 p<0.001*	R=-0.389 p=0.025*	R=-0.488 p=0.003*	R=-0.264 p=0.137
	morning	05:00–06:00		R=-0.550 p<0.001*	R=-0.480 p=0.004*	-	-	-	-	R=-0.189 p=0.292
		20:00–21:00		R=-0.468 p=0.005*	-	R=-0.450 p=0.008*	-	-	R=-0.463 p=0.006*	R=-0.238 p=0.182
	evening	21:00–22:00		R=-0.439 p=0.011*	-	-	R=-0.449 p=0.008*	-	R=-0.486 p=0.004*	R=-0.228 p=0.201
		22:00–23:00		R=-0.350 p=0.045*	-	-	-	R=-0.284 p=0.109	R=-0.341 p=0.052	R=-0.230 p=0.197
air humidity	average		%	R=-0.504 p=0.002*	R=-0.307 p=0.082	R=-0.368 p=0.035*	R=-0.361 p=0.039*	R=-0.169 p=0.347*	R=-0.255 p=0.152*	R=-0.459 p=0.007*
	morning			R=-0.152 p=0.398	R=-0.016 p=0.927	-	-	-	-	R=-0.172 p=0.337
	evening			R=-0.451 p=0.008*	-	R=-0.445 p=0.009*	R=-0.439 p=0.011*	R=-0.050 p=0.781	R=-0.216 p=0.228	R=-0.463 p=0.006*
rainfall	average		mm/3h	R=-0.253 p=0.155	R=-0.151 p=0.399	R=-0.316 p=0.073	R=-0.327 p=0.06	R=-0.137 p=0.446	R=-0.137 p=0.449	R=-0.105 p=0.559
atmospheric pressure	average		hPa	R=0.262 p=0.14	R=0.158 p=0.377	R=0.473 p=0.005*	R=0.473 p=0.005*	R=0.107 p=0.554	R=0.152 p=0.397	R=0.022 p=0.902
wind speed	average		km/h	R=0.064 p=0.722	R=-0.019 p=0.915	R=0.042 p=0.815	R=0.070 p=0.697	R=0.097 p=0.589	R=0.125 p=0.487	R=0.071 p=0.695
phase of the moon			%	R=0.238 p=0.181	R=0.144 p=0.422*	R=0.136 p=0.450*	R=0.112 p=0.535*	R=0.253 p=0.156*	R=0.173 p=0.334*	R=0.158 p=0.381*

R, Spearman rank-order correlations; *statistically significant values at $P < 0.05$

Table 7 Relationship between the number of farmed deer vocalizations and the weather conditions in the early rutting period

Analysed variable				**vocalization number**						**average length of a single vocalization**
				sum morning and evening	**morning**	**evening**				
					05:00–06:00	20:00–21:00	21:00–22:00	22:00–23:00	sum	seconds
		average		r=0.029 p=0.912	r=0.167 p=0.523	r=-0.047 p=0.858	r=-0.175 p=0.501	r=0.187 p=0.473	r=-0.019 p=0.943	r=0.236 p=0.363
	morning	05:00–06:00		r=0.078 p=0.766	r=0.182 p=0.484	-	-	-	-	r=0.287 p=0.264
temperature		20:00–21:00	°C	r=-0.038 p=0.885	-	r=-0.149 p=0.569	-	-	r=-0.083 p=0.752	r=0.164 p=0.530
	evening	21:00–22:00		r=0.027 p=0.916	-	-	r=-0.133 p=0.611	-	r=-0.021 p=0.937	r=0.199 p=0.444
		22:00–23:00		r=0.026 p=0.919	-	-	-	r=0.151 p=0.564	r=-0.021 p=0.937	r=0.203 p=0.435
		average		r=-0.408 p=0.104	r=-0.347 p=0.172	r=-0.349 p=0.169	r=-0.418 p=0.094	r=-0.363 p=0.152	r=-0.413 p=0.100	r=-0.128 p=0.624
air humidity		morning	%	r=-0.362 p=0.153	r=-0.313 p=0.222	-	-	-	-	r=-0.031 p=0.907
		evening		r=-0.275 p=0.285	-	r=-0.124 p=0.636	r=-0.272 p=0.291	r=-0.379 p=0.133	r=-0.279 p=0.277	r=-0.191 p=0.461
rainfall		average	mm/3h	R=0.102 p=0.696	R=-0.255 p=0.323	R=-0.102 p=0.696	r=0.045 p=0.865	r=0.135 p=0.605	R=0.153 p=0.557	r=0.012 p=0.963
atmospheric pressure		average	hPa	r=-0.620 p=0.008*	r=-0.604 p=0.010*	r=-0.547 p=0.023*	r=-0.433 p=0.082	r=-0.684 p=0.002*	r=-0.601 p=0.011*	r=-0.308 p=0.228
wind speed		average	km/h	R=-0.153 p=0.556	R=-0.045 p=0.862	R=-0.394 p=0.117	r=-0.067 p=0.798	r=-0.296 p=0.248	R=-0.116 p=0.655	r=-0.183 p=0.483
phase of the moon			%	R=0.238 p=0.181	r=0.5540 p=0.021*	r=0.5124 p=0.035*	r=0.431 p=0.084	r=0.604 p=0.010*	r=0.461 p=0.063	r=0.546 p=0.023*

r, Pearson r correlation; R, Spearman rank-order correlation; *statistically significant values at P <0.05

Table 8 Relationship between the number of the most common behaviours of the stags and the weather conditions

Analysed variable			flehmen response	attempts to fight between stags	staying in a group of males	thrashing the vegetation with antlers	chasing away the hinds
M			2.520	2.000	1.040	2.360	1.800
SD			2.632	1.915	1.059	1.934	1.893
temperature	average	°C	r=-0.073 p=0.727	r=-0.307 p=0.136	r=-0.166 p=0.428	r=-0.079 p=0.706	r=-0.380 p=0.061
	morning		r=-0.223 p=0.284	r=-0.175 p=0.403	r=-0.121 p=0.565	r=0.178 p=0.395	r=-0.082 p=0.697
	evening		r=-0.006 p=0.976	r=-0.302 p=0.143	r=-0.154 p=0.463	r=-0.159 p=0.448	r=-0.423 p=0.035*
air humidity	average	%	r=0.156 p=0.457	r=0.183 p=0.380	r=0.109 p=0.605	r=-0.197 p=0.345	r=-0.231 p=0.266
	morning		r=0.172 p=0.412	r=0.142 p=0.499	r=0.074 p=0.724	r=0.029 p=0.891	r=-0.082 p=0.696
	evening		r=0.065 p=0.759	r=0.146 p=0.485	r=0.098 p=0.641	r=-0.371 p=0.068	r=-0.299 p=0.147
rainfall		mm/3h	U=62.000 p=0.597	U=66.500 p=0.760	U=70.500 p=0.933	U=48.500 p=0.187	U=54.000 p=0.328
atmospheric pressure		hPa	r=0.221 p=0.289	r=0.290 p=0.159	r=0.021 p=0.922	r=0.253 p=0.222	r=0.139 p=0.507
wind speed		km/h	r=0.009 p=0.964	r=0.052 p=0.804	r=0.001 p=0.996	r=-0.238 p=0.252	r=-0.174 p=0.405
phase of the moon		%	r=-0.098 p=0.641	r=0.076 p=0.717	r=0.293 p=0.155	r=0.135 p=0.520	r=-0.062 p=0.769

M, mean; SD, standard deviation; r, Pearson r correlations; U, Mann–Whitney test results; *statistically significant values at $P < 0.05$

Discussion

It is assumed that the rutting period in the study area begins in mid-September and lasts until mid-October. However, the mating season depends largely on climatic conditions (Coulson *et al*., 2003). The weather affected the pre-rut behaviour. However, once the animals enter the rut, the weather is not important but there is a year effect: in the year with "autumn-like" pre-rut (lower temperature), the vocalizing behaviour is more intense. The number of vocalizations in 2017 and 2018 was compared and it was shown that there were two large decreases in the temperature in September in the first year of observations, which resulted in acceleration of vocalization by two days, but the average temperature during the early rutting period in 2017 was higher than in 2018. Similar results were also reported in a deer population in Scotland, where there was a 10-day shift in the onset of the rutting season caused by global warming over a 30-year period (Coulson *et al*., 2003). There is a general tendency for deer to start the mating season earlier than in the past. The rutting season in Europe begins earlier in the western than in the eastern parts, which is usually explained by the continental climate of the eastern part of the continent. Through comparison of the reproductive phenology of deer in France and Norway, Loe *et al*. (2005) concluded that the temperature and the associated spring vegetation development were crucial for the timing and synchronization of the rutting period (Langvatn *et al*., 2004; Pettorelli *et al*., 2005; Macháček *et al*., 2014; Paoli *et al*., 2018).

Male vocalization is usually most pronounced when females reach their oestrus peak and lasts 4–5 weeks (Clutton-Brock & Albon, 1979). During the rut, day and night general activity of the stags is intensified as well (Kamler *et al*., 2008; Pépin *et al*., 2009). Similar observations were recorded in farmed deer, and the behaviour in the analysed animals was consistent with the Bützler (1974) ethogram; moreover, the behaviour related to chasing the hinds was observed only during the early rutting season.

At the beginning of the rutting season, the most intensified activity is usually exhibited by young stags at ~5 y (Pépin, 2001); however, it declines with the duration of the period or is inconsistent, which is confirmed by the present observations of farmed deer. Younger, free-living males tend to be more

mobile but they move in areas where older males are present (Smith-Flueck & Flueck, 2006). Interestingly, the animal with the lowest activity was the youngest in the herd and had distorted antlers limiting the vision in his right eye. In the pre-rutting period, the stag was increasingly being pushed away from the herd. Consequently, at the end of the observation period, the stag stayed alone and did not show any typical pre-rutting behaviour. In their research, Topiński (1974); Clutton-Brock *et al*. (1982); Bartoš & Bahbouh (2006); Bartoš *et al*. (2007); Janiszewski *et al*. (2008); and Veiberg *et al*. (2004) showed that, at the peak of the rutting season, the male's breeding status was influenced by the body weight and antler size. Therefore, the size and shape of antlers is the main condition for achieving dominance in the herd. The condition of antlers depends on the health status of stags, which is reflected in the length of vocalization. It has been shown that males with poor health status produce shorter roars and their mating season is shorter too. Importantly, the extension of the rutting period may induce the occurrence of repeated oestrus in females (Volodin *et al*., 2016). The possibility of predicting such phenomena is extremely important in deer farming practice.

Previous analyses showed that middle-aged males (8 years old) started to vocalize earlier (Yoccoz *et al*., 2002), as in the studies of the red deer in the Isle of Rum, Scotland (Clutton-Brock *et al*., 1982) and reindeer (*Rangifer tarandus*) (Espmark, 1964). In the study of the farmed deer, the 9-year-old stag (Dziki) showed the most intense and earliest vocal activity, and the average length of its single roar was quite long, although the size and condition of the antlers were similar to those of three other younger males (Niko, Jasiek, Neo). Therefore, it can be concluded that the experience and behaviour displayed before the rutting period is more important. In their longer-lasting influence on females, they contribute to faster ovulation and greater success in fertilization and, consequently, transmission of their genes (Reby & McComb, 2003).

The activity of the farmed deer was manifested mainly by the increased frequency of vocalization, especially during the mating season. Observations reported by Volodina *et al*. (2006) showed that stags vocalized most often between 05:00 and 06:00 and between 20:00 and 23:00 Additionally, the peak vocal activity of deer in Russia was recorded at 08:00–09:00 in Tver and at 07:00–09:00 and 16:00–18:00 in Kostroma (Volodin *et al*., 2016). In the Alpine deer population in Italy, the deer vocalized mainly at night and early in the morning, with a peak at 05:00–07:00 (Bocci *et al*., 2013). In turn, the stags in the population from the Isle of Rum population vocalized mainly during the day (Clutton-Brock & Albon, 1979), likewise farmed stags in France (Pepin *et al*., 2001). Many results confirm that deer exhibit the highest overall activity at sunrise and sunset (Feighny *et al*., 2006; Pépin *et al*., 2009), which was also observed in the case of the farmed deer in Poland.

In the pre-rutting period, the average length of a single roar produced by the stags was 1.67 s, which was similar to the results reported by Feighny *et al*. (2006) when analysing hinds from the Rocky Mountains (Canada), and over twice as long as the vocalization of red deer hinds or calves living in Spain during the rutting period (Volodina *et al*., 2006). The average length of a single roar in the early rutting period in the study on the farmed deer was 2.47 s. This value was higher than that reported by Feighny *et al*. (2006) and lower than in the study of farmed deer breeding conducted by Volodina *et al*. (2006) and similar to the value measured in wild stags. As shown by Frey *et al*. (2012), the duration of the roars of Iberian deer during fights was shorter, i.e., on average 1.90 s, and ranged between 0.83 and 3.86 s. In turn, in their study of Manchurian deer, Volodin *et al*. (2013) recorded a longer mean vocalization time of 3.07 ± 0.52 s. The frequency of vocalization of the farmed stags in the pre-rutting period was low, i.e., 5.45. During the early mating season, it increased to 173.26 s; nevertheless, it was lower than the value recorded in the deer from Tver but higher than the activity of the animals in Kostroma (central Russia) (Volodin *et al*., 2016). The differences may have been related to the different density and structure of the herd, as already demonstrated in many studies (Clutton-Brock & Albon, 1979; Bowyer and Kitchen, 1987; Clutton-Brock *et al*., 1997; Yoccoz *et al*., 2002), which was nevertheless similar to the conditions in Kostroma and in free-living animals (Clutton-Brock & Albon, 1979).

As mentioned in the Introduction, weather conditions may affect the mating season in red deer. The study carried out by Prebanić and Ugarković (2015) showed no correlation between the activity of deer and air temperatures in the pre-rutting period. In contrast, the present study of the farmed deer showed a relationship between the air temperature and vocalization in the pre-rutting period, whereas no such relationship was observed during the early mating season. Moreover, the average air temperature and atmospheric pressure influenced the sum of activities of the farmed stags in the morning hours, and the average temperature in the evening induced behaviour consisting of chasing of the hinds by the males. Douhard *et al*. (2013) showed a negative relationship between the temperature and the roaring count index, which can be explained by a reduction in animal activity accompanying a rise in the temperature. Similarly, the results presented by Volodin *et al*. (2013; 2015) revealed a

negative relationship between the number of roars and air temperature in Siberian and Far Eastern deer.

Interestingly, wind force has not been shown to influence vocalization or other deer behaviour, even though the wind affects sound dispersion, as well as the overall behaviour of many species (Ruzicka & Conover, 2011). Moreover, weather conditions, especially wind that have an impact on odour i.e., scents suspended in the air and odour plumes, should affect stag behaviour because it is the smell that indicates that the female is ready for copulation (Müller-Schwarze, 1971).

The moon phase also increased the frequency of vocalization in the farmed stags, not only during the rutting season (as shown by Prebanić & Ugarković, 2015), but also in the pre-rutting period. The lower air temperatures in the pre-rutting period and the transition towards the full moon increased the activity of the farmed deer in Poland. In contrast, Woodside (2010) showed that the moon phases, especially the full and new moon phases, have an inconsiderable effect on the activity and range of movement in Cervidae. The results reported by Bocci *et al*. (2013) indicate that the frequency of vocalization in red deer decreases with increasing humidity. A similar observation was recorded in the farmed deer in Poland in the described research.

Conclusion

In conclusion, lower temperatures, lower air humidity, increasing atmospheric pressure, and transition towards the full moon phase contribute to an increase in the vocal activity of deer in the pre-rutting period, which may accelerate the onset of the rutting period in males. The number of vocalizations varied in 2017 and 2018, and depended on the average temperature, air humidity, atmospheric pressure, and moon phase in the pre-rutting period and during the rutting season. Thus, by observing the changing weather conditions, it is possible to predict the time of increased activity of stags and the onset of rutting. Probably due to the experience gained with age, the older stags made greater investments in vocal activity earlier than the younger ones. Prediction of the mating behaviour of males has a huge impact on acceleration or repeatability of ovulation in hinds, which is particularly valuable information for deer breeders and wildlife managers.

Authors' Contributions

KT (ORCID 0000-0003-4725-9020) participated in designing the study, wrote the manuscript, was involved in drafting and revising the manuscript for intellectual content, carried out data analysis and interpretation, and was involved in the preparation and revision of the manuscript and supervision of the manuscript. PJ (ORCID 0000-0003-4654-7805) participated in designing the study. ŻSB (ORCID 0000-0001-6645-6172) contributed to the acquisition, analysis, and interpretation of data. FC (ORCID 0000-0001-9014-147X) was involved in the preparation and revision of the manuscript. All authors reviewed and approved the manuscript before it was submitted for publication.

Conflict of Interest

The authors declare that they have no conflict of interest.

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