



Daily Activity, Sex- and Age-Structure of the Herds of Ungulate Species (Artiodactyla): a Case Study in the Rositsa State Hunting Enterprise, Stara Planina Mountain, Bulgaria*

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Abstract: The present study aimed to elucidate patterns of the daily activity, sex and age structure of the herds of red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) registered by camera traps on the territory of the Rositsa State Hunting Enterprise in Central Stara Planina Mountain. The study is carried out between July 2017 and June 2019. We used 38 camera traps, which stayed in the field for 5279 days. From the collected photos and videos, 5001 independent registrations were identified: 2551 for red deer, 1266 for roe deer and 1184 for wild boar. We defined five groups to study the sex and age structure of the herds: F – female adult individuals; M – male adults individuals; S – young up to 2 years; FJS – females with offspring and young and mixed – individuals by both sex and different age. We found that all three species are more active at night in autumn. We observed higher daytime activity for red deer in spring, for roe deer in winter, and for wild boar in summer. The overlap of their daily activities is greatest in summer and least in spring. A different frequency of occurrence of the five types of herds was found in the studied ungulates during the various seasons, as well as a difference in diurnal activity mainly between the herds with females and the other herds. The lowest percentage of mixed herds in winter we registered in herds of red deer compared to those of roe deer and wild boar. This study shows that the activity patterns of the three ungulates are significantly influenced by species-specific features, season and anthropogenic activity. The greater nocturnal activity of the studied ungulates in autumn is due to the hunting season and the accompanying increased restlessness of the animals. The present research may benefit the sustainable management and protection of game populations in the future.

Key words: red deer, roe deer, wild boar, activity patterns, camera traps

Introduction

The activity of animals is related to their circadian rhythms. However, they may be influenced by various abiotic (KAMLER et al. 2007, ENSING et al. 2014,

IKEDA et al. 2015, HOFMANN et al. 2016, CARAVAGGI et al. 2018, ZHOU et al. 2022) and biotic (BROWN et al. 2012, VAN DOORMAAL et al. 2015, CARAVAGGI et al. 2018, RAMIREZ et al. 2021) factors. In more cases, the ungulate activity is usually determined by

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light/dark cycles and often coincides with sunrise and sunset (GEORGII 1981, GEORGII & SCHRODER 1983). On the other hand, the differing needs of both sexes of ungulates as well as the variability in size and social structure of their herds in seasons also determine different activity rhythms (PAGON et al. 2013, PEKSA & CIACH 2018). E.g., lactating females expend more energy during the rearing period of their fawns, which they compensate for by devoting more time for feeding and rumination (HAMEL & CÔTÉ 2008). In the past, due to the difficulty in observing species at night, studies on their activity have only covered the daylight hours. The advent of technology, and especially camera traps, as a method of ecological research over the last decade, provides great opportunities. They have been used for monitoring, population density estimation and biodiversity assessment, and in recent years for the study of activity rhythms (O'CONNELL et al. 2011).

In this study, we investigate the activity of red deer, roe deer and wild boar, which often inhabit the same areas in Bulgaria. We also determine the sex and age structure of registered herds, which has not been done before using camera trap data. Depending on the season, the structure and size of herds in all three ungulates varies (DZIĘCIOŁOWSKI 1979, FERNÁNDEZ-LLARIO et al. 1996). The main types of herds observed in the species studied are mixed herds including individuals of both sexes and any age; herds of females with their offspring; herds of juveniles up to two-years old, herds of females over two-years old and herds of males over two-years old. The aim of this work is to elucidate the activity patterns of the three species studied and to test whether there is a difference in their activity according to herd type.

Materials and Methods

Study area

The study was conducted on the territory of the Rositsa State Hunting Enterprise (SHE Rositsa) located on the northern slopes of the Stara Planina Mountain (42°48'44 "N 25°06'42 "E) (Fig. 1). The area is characterised by a strongly folded topography cut by numerous river valleys. Mountainous terrains predominate, with most of the forests at altitudes of 500 to 800 m. The lowest point is at altitude of 250 m and the highest at 1430 m. This range determines the formation of different micro-regions with snow cover depths between 25 cm and 100 cm. The growing season is about 6 months, with an average annual temperature of 8–9°C. Days with temperatures above 10°C are between 160 and 190. Precipitation ranges from 560 to 680 mm/m² (GEORGIEV 1985). The most

widely represented is the European beech (*Fagus sylvatica*) with an accompanying species of common hornbeam (*Carpinus betulus*). Also occur scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), silver fir (*Abies alba*), black pine (*Pinus nigra*), sessile oak (*Quercus petraea*), Hungarian oak (*Quercus frainetto*) and Turkey oak (*Quercus cerris*). Among the wild ungulate species inhabiting the territory of the SHE Rositsa, red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*) and fallow deer (*Dama dama*) were present. Predators were represented by brown bear (*Ursus arctus*), grey wolf (*Canis lupus*), golden jackal (*Canis aureus*), red fox (*Vulpes vulpes*), European badger (*Meles meles*) and beech marten (*Martes foina*). The SHE Rositsa borders the Central Balkan National Park to the south-west where hunting is prohibited.

Data collection

The recording of the ungulates species was performed using 38 camera traps of 4 models (SG DTC-565V, KG 680V, Ltl Acorn 5210, Ltl Acorn 5310). Devices were placed on paths and dirt roads at a height of approximately 1 m from the ground between July 2017 and June 2019 at a minimum distance of 1 km from each other (ROWCLIFFE et al. 2008). Camera traps stayed on the terrain for 5279 trap days (Fig. 2). They were set according to the methodology described of POPOVA et al. (2019).

Data analysis

The information from the camera traps (time, date, location, species, sex and age of the recorded individuals and their number) was filled into a table. To avoid pseudo replications (MEREDITH & RIDOUT 2014) we considered as an independent event all registrations of the same individual made by one camera within 30 min (LINKIE & RIDOUT 2011). We obtained 12173 photos and videos of the target species. From them we identified 5001 independent registrations: 2551 for red deer, 1266 for roe deer and 1184 for wild boar. There were 159 registrations for fallow deer, 151 of which were collected over the summer. Due to its few registrations in other seasons, this species was excluded from the analyses. For the three studied ungulate species, we identified five herd types: F – female adult individuals; M – male adult individuals; S – young up to 2 years; FJS – females with offspring and young and Mixed – individuals by both sex and different age. We used a chi-square test of independence (2x2) to test whether there was a difference in the frequency of occurrence of herd types between seasons. Furthermore, the identification of all registered individuals was performed by

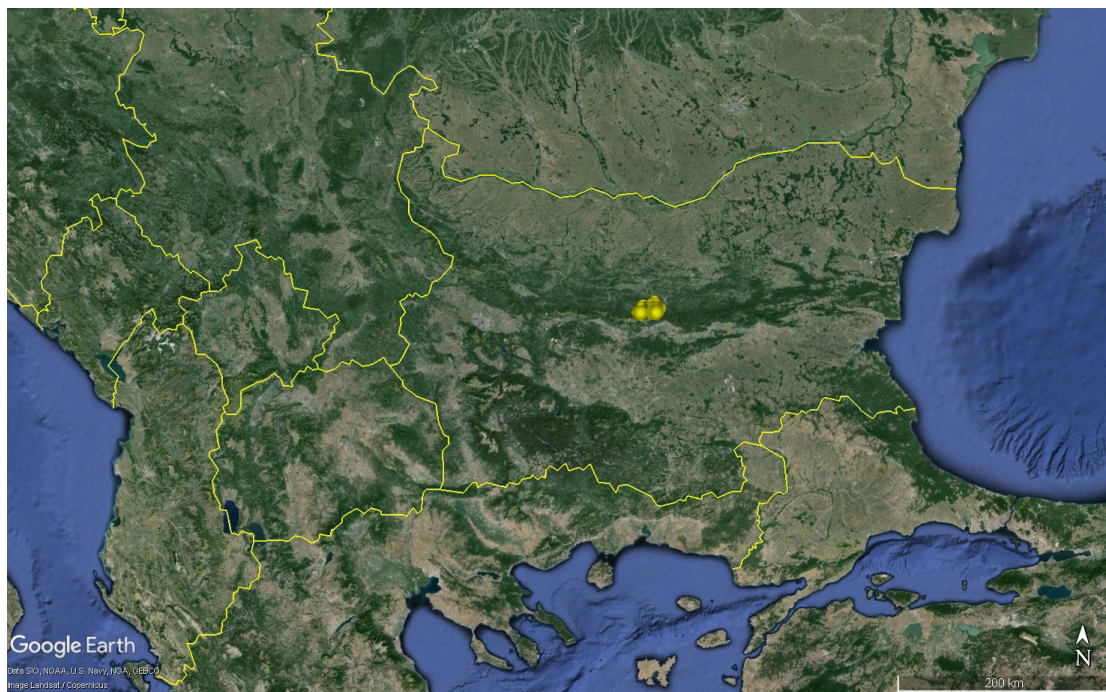


Fig. 1. Map of Bulgaria and the study area.

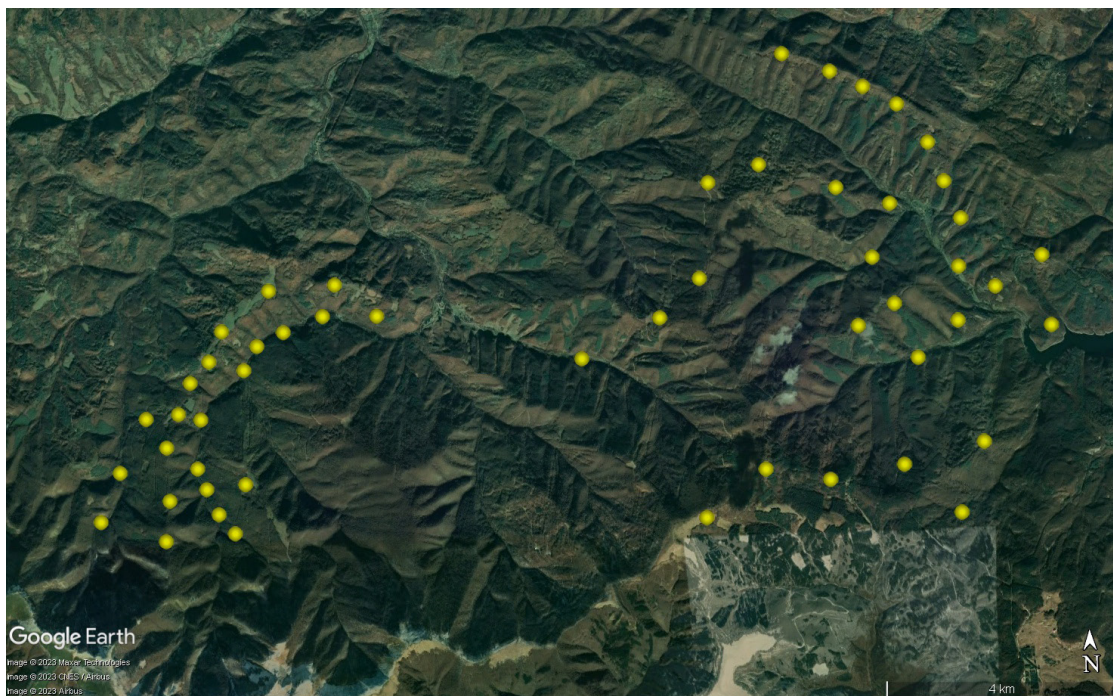


Fig. 2. Map of camera traps location.

one person (A. Ahmed). Also, registrations of individuals that could not be clearly identified by sex and age (e.g., only part of the animal's body was photographed) but could be identified as red deer, roe deer, or wild boar were recorded as unknown and these were not included in the herd analysis.

Temporal activity overlaps

For the temporal overlap analysis, we assumed each individual was recorded with camera traps were treated as a separate observation. For each capture by camera traps, we converted the time into radians (MEREDITH & RIDOUT 2014, ROWCLIFFE et al. 2014). Similar to ZANNI et al. (2021), for each species, we estimated seasonal activity patterns using the *fitact* function in the activity package in R (ROWCLIFFE 2016). Then us-

Table 1. Estimates of the proportion of active time during daylight hours and the percentage of active time during the 24-hour cycle over the four seasons in SHE Rositsa.

Species	Seasons	N	Prop. diurnal	Activity level	SE	CI
Red deer	Winter	302	44%	0.51	±0.06	0.40-0.63
	Spring	229	52%	0.61	±0.07	0.47-0.74
	Summer	1643	39%	0.46	±0.02	0.41-0.51
	Autumn	377	32%	0.66	±0.05	0.54-0.72
Roe deer	Winter	268	62%	0.52	±0.04	0.39-0.56
	Spring	152	54%	0.36	±0.05	0.26-0.47
	Summer	733	40%	0.46	±0.04	0.39-0.54
	Autumn	113	38%	0.64	±0.09	0.39-0.75
Wild boar	Winter	153	25%	0.41	±0.05	0.32-0.50
	Spring	58	23%	0.34	±0.05	0.24-0.42
	Summer	834	49%	0.57	±0.04	0.49-0.64
	Autumn	139	22%	0.45	±0.05	0.35-0.55

ing the *densityPlot* function in the *overlap* package, we calculated the percentage of activity time during daylight hours for the three species, by taking into consideration sunrise and sunset times for the study area (taken from Astronomical calendar 2017, 2018, 2019 of IA-BAS). To compare the activity levels of each species across seasons and the activity levels of the herd types of each species on an annual basis, we used the *compareAct* function with the Wald test.

The temporal overlap of species activity pairwise was estimated by nonparametrically calculating the overlap coefficient, Δ , which ranges from 0 to 1 (LINKIE & RIDOUT 2011). We used the coefficient Δ_1 when the sample size was less than 75 and Δ_4 when the sample size was greater than 75 (RIDOUT & LINKIE 2009). We also calculated the 95% confidence intervals of the overlap coefficients as percentile intervals from 999 bootstrap samples (MEREDITH & RIDOUT 2014).

Results

The three target species showed different levels of activity across seasons (Tables 1 and 2). Red deer were more active in autumn and spring than in winter and in the summer. In winter and spring, they used light and dark hours almost equally, whereas in summer and autumn the species had mostly nocturnal activity (Tables 1 and 2). Throughout the year, red deer are most active around sunset, with two other distinct peaks at sunrise and at night (except in summer, where they are not as distinct) (Fig. S1).

Roe deer activity level also varied with the seasons and twenty-four hours. They were most active during autumn and winter, mostly at night in

autumn and during the day in winter. The lowest activity they were in spring when roe deer used almost equally the light and dark hours of the twenty-four hours (Tables 1 and 2). There are two distinct peaks after sunrise and before sunset as well as a smaller one at night in winter. In spring and autumn, they were most active around sunrise, and in summer, around sunset (Fig. S1).

Wild boar was most active in summer, with an equal distribution in the light and dark part of the diurnal period. Only in summer did it have bimodal activity during around sunrise and sunset. In the other three seasons, there was exclusively nocturnally active (Table 1 and 2), more pronounced around and after sunset (Fig. S1).

We found the greatest temporal overlap in diurnal activity of all three species in summer (range of mean $\Delta_4 = 0.89-0.93$) and the least in spring (range of mean $\Delta_4 = 0.49-0.76$). As expected, in all four seasons, the greatest overlap was between red deer and roe deer (range of mean $\Delta_4 = 0.76-0.93$), with less overlap with wild boar (red-boar, $\Delta_4 = 0.64-0.89$; roe-boar, $\Delta_4 = 0.49-0.89$). Although roe deer and wild boar showed the smallest temporal overlap, Wald's test showed no statistical difference in their activity levels across the seasons. For the red deer-wild boar pair there was a significant statistical difference in spring ($w = 10.36$, $p = 0.001$), summer ($w = 5.22$, $p = 0.02$) and autumn ($w = 9.24$, $p = 0.002$), and for the red deer-roe deer pair only in spring ($w = 9.22$, $p = 0.002$) (Table 3, Fig. S1).

In all three species, we found a significant statistical difference in the frequency of recording of the various herd types across seasons (for red deer: $\chi^2=240.39$, $df=3$, $p<0.001$; for roe deer: $\chi^2=150.73$,

Table 2. Comparison of the activity levels of each species in SHE Rositsa during four seasons with the Wald test.

Species	Seasons	Difference	SE	W	P
Red deer	Winter vs Spring	-0.10	0.09	1.37	0.24
	Winter vs Summer	0.05	0.06	0.57	0.45
	Winter vs Autumn	-0.15	0.07	4.47	0.03
	Spring vs Summer	0.15	0.07	4.30	0.04
	Spring vs Autumn	-0.05	0.08	0.37	0.54
	Summer vs Autumn	-0.20	0.05	14.98	<0.000
Roe deer	Winter vs Spring	0.17	0.07	5.93	0.01
	Winter vs Summer	0.06	0.06	1.07	0.30
	Winter vs Autumn	-0.11	0.10	1.19	0.28
	Spring vs Summer	-0.11	0.06	2.78	0.10
	Spring vs Autumn	-0.28	0.11	6.84	0.01
	Summer vs Autumn	-0.17	0.10	2.96	0.09
Wild boar	Winter vs Spring	0.08	0.07	1.34	0.25
	Winter vs Summer	-0.16	0.06	6.75	0.01
	Winter vs Autumn	-0.04	0.07	0.27	0.60
	Spring vs Summer	-0.23	0.06	14.07	<0.000
	Spring vs Autumn	-0.11	0.07	2.44	0.12
	Summer vs Autumn	0.12	0.07	3.10	0.08

Table 3. Overlap of the daily activity of the three ungulate species between seasons in SHE Rositsa.

Species couples	Seasons	λ^4	CI lower	CI upper	Difference	SE	W	P
Red-Roe	Winter	0.81	0.75	0.88	-0.02	0.08	0.05	0.83
	Spring	0.76	0.68	0.84	0.25	0.08	9.22	0.002
	Summer	0.93	0.90	0.96	-0.003	0.04	0.004	0.95
	Autumn	0.85	0.76	0.93	0.02	0.10	0.05	0.82
Red-Boar	Winter	0.72	0.65	0.79	0.09	0.07	1.57	0.21
	Spring	0.64	0.52	0.75	0.27	0.08	10.36	0.001
	Summer	0.89	0.85	0.92	-0.11	0.05	5.22	0.02
	Autumn	0.84	0.76	0.91	0.21	0.07	9.24	0.002
Roe-Boar	Winter	0.60	0.52	0.67	0.11	0.07	2.82	0.09
	Spring	0.49	0.37	0.60	0.02	0.07	0.07	0.79
	Summer	0.89	0.86	0.92	-0.11	0.05	3.91	0.05
	Autumn	0.71	0.61	0.81	0.19	0.11	2.91	0.09

df=3, $p < 0.001$; for wild boar: $\chi^2 = 132.37$, df=3, $p < 0.001$). We also found a difference in daily activity, particularly among herds of females and the other herd types (Tables 4 and 5).

Discussion

The high values of temporal overlap in the diurnal activity of the three ungulate species indicate that they do not avoid each other. The exceptions are roe deer and wild boar in spring, where the lowest temporal overlap was recorded. Our results are consistent

with those of ZANNI et al. (2021). According to the authors, the differences in activity patterns of roe deer and wild boar are due to two important factors influencing roe deer behaviour during this season: fawn birth and mating season. The authors suggest that the change in roe deer activity may be a defensive strategy adopted by them to avoid encounters with wild boars to protect their young. The wild boar is thought to be an opportunistic omnivore species that has been found to show predatory tendencies even towards mammalian young (WILCOX & VAN VUREN 2009).

In spring, due to the mating period of roe deer,

Table 4. Number of herd types for the three ungulate species recorded during the four different seasons in SHE Rositsa.

Species	Seasons	FJS	Female	Male	Mixed	Subadult	Unknown	Total
Red deer	Winter	86	111	49	1	33	22	302
	Spring	39	57	77	1	29	26	229
	Summer	513	493	184	31	286	136	1643
	Autumn	97	80	111	39	40	10	377
Roe deer	Winter	34	104	64	7	22	37	268
	Spring	8	52	62	3	9	18	152
	Summer	28	185	199	9	203	109	733
	Autumn	23	43	14	3	12	18	113
Wild boar	Winter	19	6	45	20	12	51	153
	Spring	9	2	17	1	5	25	59
	Summer	237	91	173	7	127	199	834
	Autumn	34	1	42	8	6	48	139

Table 5. Comparison of the activity levels of the type herds of the three ungulate species in all year in SHE Rositsa with the Wald test.

Species	Herd type	Difference	SE	W	P
Red deer	<i>F vs M</i>	0.05	0.06	0.66	0.41
	<i>F vs S</i>	0.11	0.07	2.48	0.12
	<i>F vs FJS</i>	0.11	0.06	2.84	0.09
	<i>F vs Mix</i>	0.20	0.09	4.59	0.03
	<i>M vs S</i>	0.06	0.07	0.96	0.33
	<i>M vs FJS</i>	0.06	0.06	1.08	0.30
	<i>M vs Mix</i>	0.15	0.09	2.89	0.09
	<i>S vs FJS</i>	-0.01	0.07	0.01	0.94
	<i>S vs Mix</i>	0.08	0.09	0.77	0.38
	<i>FJS vs Mix</i>	0.09	0.09	1.00	0.32
Roe deer	<i>F vs M</i>	0.09	0.10	0.91	0.34
	<i>F vs S</i>	0.19	0.09	4.31	0.04
	<i>F vs FJS</i>	0.19	0.10	3.30	0.07
	<i>F vs Mix</i>	0.08	0.13	0.38	0.54
	<i>M vs S</i>	0.10	0.09	1.09	0.30
	<i>M vs FJS</i>	0.10	0.11	0.82	0.36
	<i>M vs Mix</i>	-0.01	0.13	0.01	0.91
	<i>S vs FJS</i>	0.00	0.10	0.00	0.98
	<i>S vs Mix</i>	-0.11	0.12	0.81	0.37
	<i>FJS vs Mix</i>	-0.11	0.13	0.68	0.41
Wild boar	<i>F vs M</i>	0.04	0.08	0.21	0.64
	<i>F vs S</i>	-0.19	0.09	4.36	0.04
	<i>F vs FJS</i>	0.04	0.08	0.20	0.66
	<i>F vs Mix</i>	0.00	0.11	0.00	0.98
	<i>M vs S</i>	-0.15	0.08	3.76	0.05
	<i>M vs FJS</i>	0.07	0.06	1.29	0.26
	<i>M vs Mix</i>	0.04	0.10	0.11	0.74
	<i>S vs FJS</i>	0.23	0.08	8.77	0.003
	<i>S vs Mix</i>	0.19	0.11	2.86	0.09
	<i>FJS vs Mix</i>	-0.04	0.10	0.14	0.71

in addition to males becoming territorial, there is a similarity in the activity of the two sexes (Fig. S2). The low activity levels during this season appear to be a consequence of the territoriality of males and the lower mobility of females, due to them remaining close to their young in the first days after birth. The high activity levels found in roe deer in autumn and winter coincide with the recording of greater herd diversity (Fig. S3). In autumn, however, roe deer are mostly nocturnally active, which we assume is a consequence of the restlessness of the hunting season during this period. In winter, when temperatures are low at night, we found that the roe deer are mostly daily active (PAGON et al. 2013, ZANNI et al. 2021).

Red deer showed high values of temporal overlap of diurnal activity with both roe and wild boar throughout the year. The overlap in summer with roe deer reached almost 1 – full overlap ($\Delta 4 = 0.93$), indicating the close species-specific requirements of the two species. Like roe deer, red deer were also most active in autumn, with a predominance of nocturnal activity. This is the season of the mating season for red deer, but unlike roe deer, they do not show a similarity in the activity of the two sexes (Fig. S2). Observed peaks of female activity were at sunrise and sunset, while males were most active after sunset and at night. These differences are likely due to different courtship patterns. Whereas in roe deer males guard only their territories and females choose which male to mate with, in red deer the formation of harems and their protection from competing intruders leads to fighting between opponents and a dynamic social structure of herds during this period (JęDRZEJEWSKI et al. 2006). Therefore, the herd structure of the two deer species was quite different during their mating periods (Fig. S3). We observed a similar pattern of activity in both sexes of red deer during the summer (Fig. S2), which contrasts with that found by the KAMLER et al. (2007) in Białowieża National Park. On the one hand, our results may be due to the studied territory being a hunting area, which may affect deer activity rhythms. On the other hand, the observed activity patterns may be due to warmer summer daytime temperatures. This suggestion is supported by the greatest similarity we found in the activity patterns of the three target species during this season (Fig. S1). Other authors have also found a significant influence of temperature on the activity of wild animals (MALONEY et al. 2005, PAGON et al. 2013, BRIVIO et al. 2016).

In our study, we found that wild boar was most active in the summer, when it used light and dark hours equally (ZANNI et al. 2021). During the other three seasons it was mostly nocturnally active, which is consistent with the research of some authors (BRIV-

IO et al. 2017, MORI et al. 2020), but contrasts with the results of others (RUSSO et al. 1997, GAUDIANO et al. 2022). The studied wild boars were least active in spring when the female boars had a smaller home range due to giving birth (GRAVES 1984). Nursing increases the energy needs of females, leading to a greater food requirement (RUSSO et al. 1997, KEULING et al. 2008) and explaining their daily activity in the summer (Fig. S2). Both sexes in wild boar had similar activity in autumn and winter (Fig. S2). Wild boars' mate in late autumn and males stay with females in mixed herds, so we observed primarily mixed herds during the winter (Fig. S3).

Conclusions

Our study found that species-specific features, seasons, and human activity influenced the activity patterns of the three ungulates. The observed nocturnal activity of all three species studied in autumn appears to be the result of disturbance from hunting pressure. However, the response of each species may be different. As they write CHASSAGNEUX et al. (2019) differences in response to hunting disturbance can be observed even at the individual level. According to some authors, species increase their vigilance (JAYAKODY et al. 2008), while others report lower levels of activity or negligible impact of hunting (KEULING et al. 2008, PAGON et al. 2013, BRIVIO et al. 2017). This supports the claim that species respond locally depending on the situation and environmental conditions. The observed seasonal changes are mostly related to sunrise and sunset, but also to temperature (ENSING et al. 2014). The influence of endogenous processes on the activity of the three studied species was greatest during their rutting season and offspring rearing periods. In our case, the feeding that occurs on the territory of SHE Rositsa during the year, especially in winter, probably also influences some of the influence. However, we need further research to determine the extent of this influence. The results of the present study may benefit the sustainable management and protection of game populations in the future.

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Supplementary materials

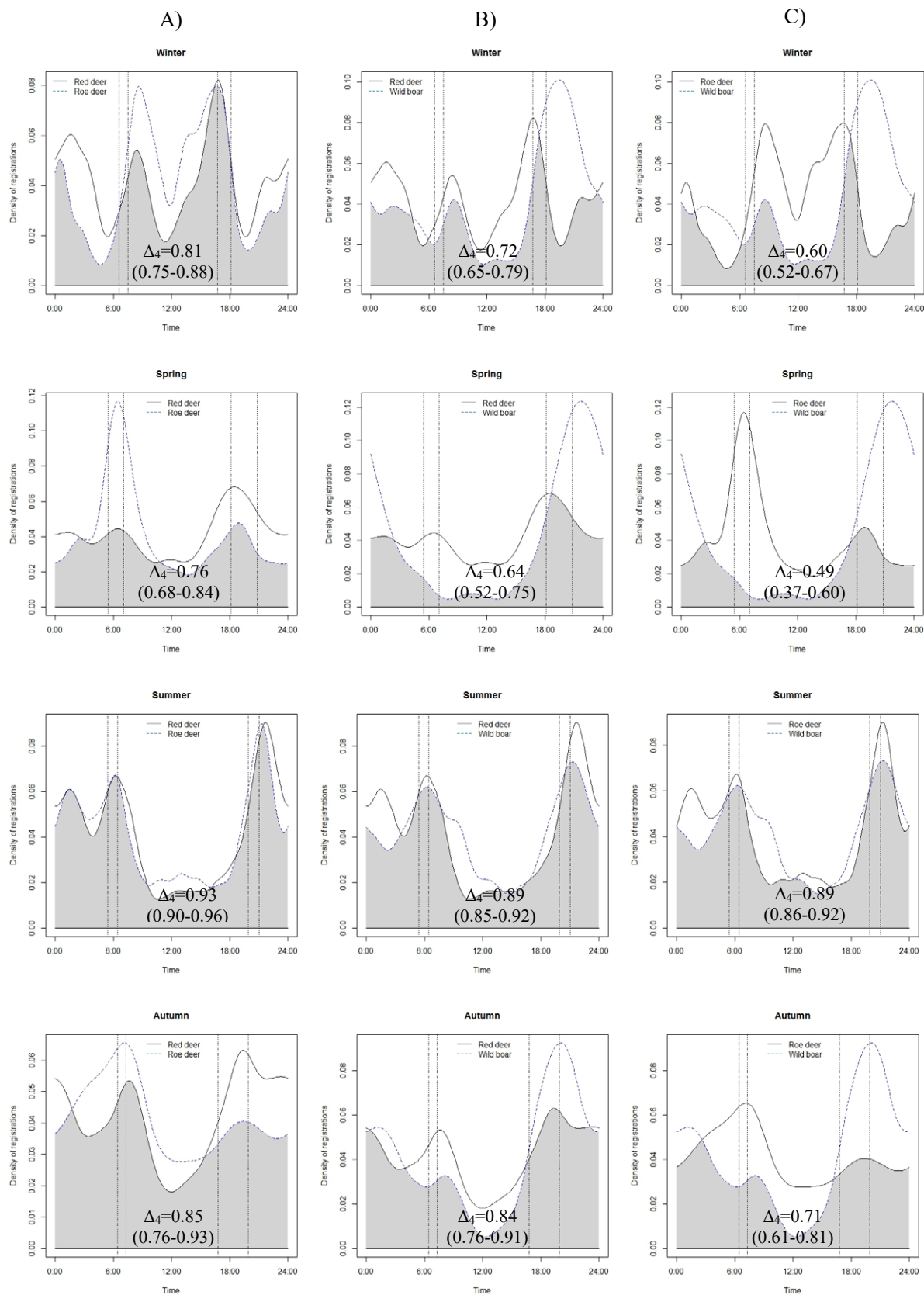


Fig. S1. Diurnal activity overlap of the three ungulates species during different seasons. A – between red deer and roe deer; B – between red deer and wild boar; C – between roe deer and wild boar. The vertical lines show the time of sunrise and sunset. Δ indicates the degree of overlap. The lower and upper values are given in brackets, respectively.

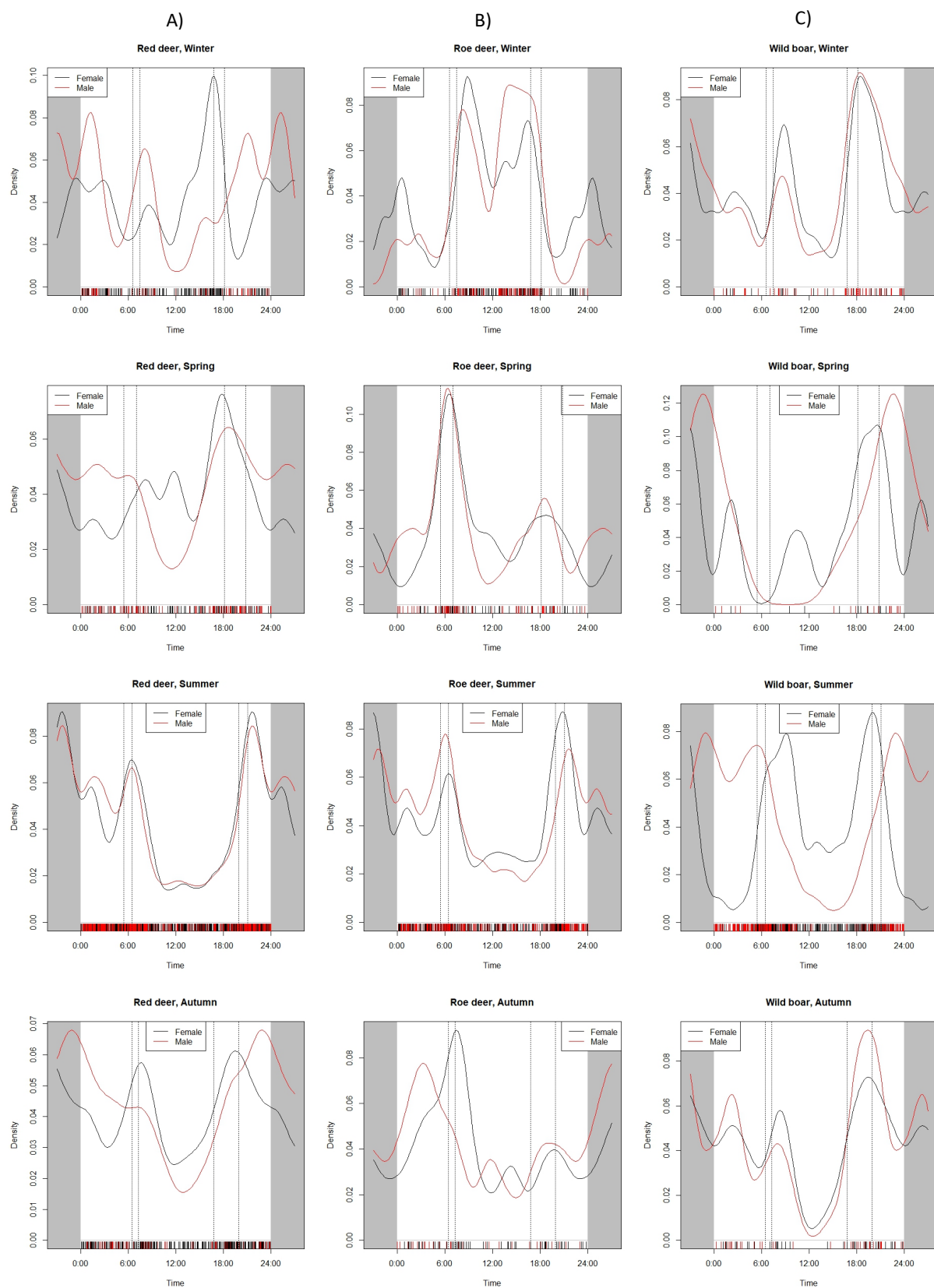


Fig. S2. Diurnal activity of female and male of the three ungulates species during different seasons. A – red deer’s female and male; B – roe deer’s female and male; C – wild boar’s female and male. The vertical lines show the time of sunrise and sunset.

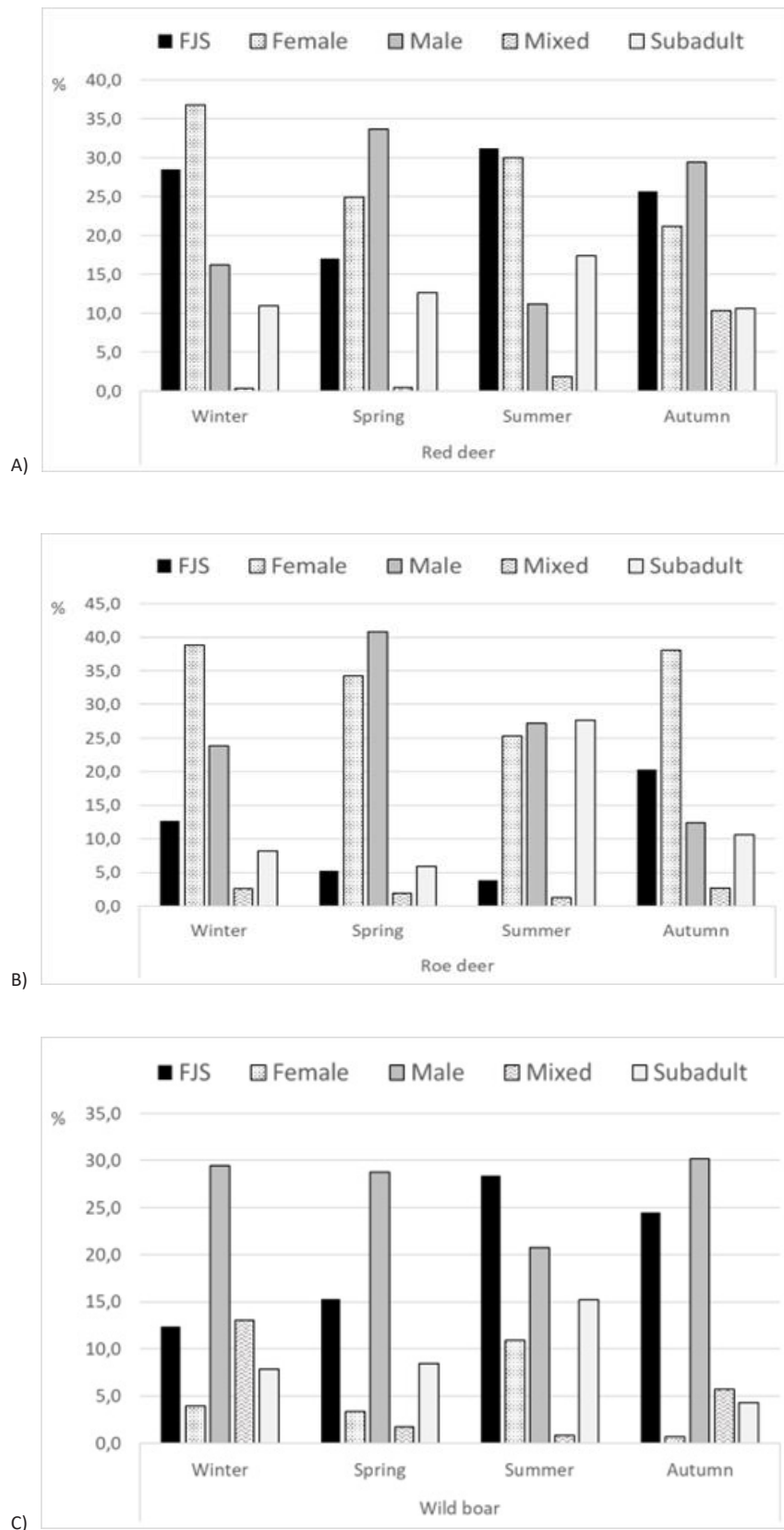


Fig. S3. Frequency of occurrence of observed herds in different seasons for the three ungulate species. A – red deer; B – roe deer; C – wild boar.

