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Activity Overlap and Time-spacing between the Wolf *Canis lupus* L. (Carnivora: Canidae) and its Ungulate Prey in Osogovo Mtn., Bulgaria

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Abstract: The spatial and temporal avoidance of the predator is of the highest importance for the survival of the prey. In habitats where spatial avoidance is impossible, the differences in the temporal presence play a significant role in the survival strategy of the prey. As this behaviour is still understudied in Bulgaria, we used two types of camera trap analyses – an activity overlap and time-spacing to investigate the spatio-temporal avoidance of the wolf in Osogovo Mountain by its ungulate prey – the wild boar (*Sus scrofa* L.) and roe deer (*Capreolus capreolus* L.). The results of the activity overlap showed that the wild boar and the roe deer had a high degree of activity overlap (Δ = 0.70). The wolf and the roe deer activity overlap was higher (Δ = 0.61) than that of the wolf and wild boar (Δ = 0.57). Time-spacing results further showed that it took a longer time for the wild boar to appear after the wolf (min = 14:24 h) than after the roe deer (min = 3:56 h). On the other hand, the wolf appeared sooner after a wild boar (min = 7:54 h) than after the roe deer (min = 11:19 h). Having in mind, that the wild boar prevailed in the wolf diet in Osogovo Mtn, the temporal analyses confirmed the hypothesis that the smaller wild boar-wolf activity overlap and the longer time required for the appearance of the wild boar after the wolf in the same place are part of the wild boar protective strategy to avoid the predator when present in the same areas. Unlike the wild boar, the roe deer is hunted by the wolf only if it is encountered by chance, which resulted in lower avoidance behaviour.

Key words: circadian activity; spatiotemporal avoidance; protective strategy; *Sus scrofa; Capreolus capreolus*

Introduction

The grey wolf *Canis lupus* L., 1758 and humans interacted and have lived in close proximity for tens of thousands of years (Germonpré et al. 2009). After the drastic decline in wolf numbers in Europe in the XX century, this predator has gradually restored its population across most of the continent (Chapron et al. 2014). Due to its important role in human existence, directly or indirectly (through its impact on other species), the wolf is one of the most studied predators in Europe. Still, some aspects of the wolf's ecology, such as the spatiotemporal interaction with its ungulate prey, are understudied, especially in the human-dominated environment.

Part of the relationship between predator and prey is expressed in predator hunting strategies (Dawkins & Krebs 1979, Matter & Mannan 2005), which leads to different adaptations in the predators' behaviour and this of their prey (Ste-

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phens & Peterson 1984). One of these adaptations is the shift of the prey's diurnal activity model in response to that of the predator (Nelson & Vance 1979, Overdorff 1988) and *vice versa*. Usually, predators change their diurnal activity towards the period when their prey is active (Jenny & Zuberbühler 2005) to exploit a better window of opportunity to encounter prey. This period, and hence, the activity of both predator and prey may be influenced by several factors – abiotic (e.g., different weather conditions, terrain ruggedness, forest visibility), biotic (inter- or intraspecies competition) as well as anthropogenic. The identification of the range and specificity of the diurnal activity of the predator-prey complex and the degree of overlap in the activity of the predator and its prey is a serious challenge, especially for predators with large home ranges and high mobility like the wolf.

The main wolf's ungulate prey species in Osogovo Mountain are wild boar (*Sus scrofa* L.) and roe deer (*Capreolus capreolus* L.) (Stancheva 2004, Dolapchiev 2022). Currently, the wild boar is prevailing in the wolf's diet, the roe deer has dominated in some periods in the past.

The circadian activity of the wolf, wild boar and roe deer was studied by many authors so far – wolf (Kolenosky & Johnston 1967, Vila et al. 1995, Fancy & Ballard 1995, Ciucci et al. 1997, Theuerkauf et al. 2003b, 2007, Kusak et al. 2005, Eggermann et al. 2009, Mengüllüoğlu & Bilgin 2010, Eriksen et al. 2011, Akbaba & Ayaş 2012, Karamanlidis et al. 2017, Oliveira 2017) wild boar (Boitani et al. 1994, Russo et al. 1997, Cahill et al. 2003, Akbaba & Ayaş 2012, Liu et al. 2013, Stolle et al. 2015, Sporek 2017, Caruso et al. 2018) and roe deer (Turner 1979, Cederlund 1989, Jeppesen 1989, Wallach et al. 2010, Pagon et al. 2013). Yet, comparison of wolf's activity overlap with that of its main ungulate prey has been relatively rare (Mengüllüoğlu & Bilgin 2010, Eriksen et al. 2011, Mori et al. 2020, Rossa et al. 2021, Petridou et al. 2023).

Wolves, wild boars and roe deer adjust their activity patterns to some factors, especially those which alleviate the hunting pressure for the prey or enhance the hunting success of the predator. This is especially important in areas where the number of prey species is low (1–3), thus the wolf pressure per species is expected to be high. According to various studies, human activity, breeding status, presence and activity of prey or the weather conditions are the major factors that shape wolf activity (Kolenosky & Johnston 1967, Harrington & Mech 1982, Fancy & Ballard 1995, Ciucci et al. 1997, Theuerkauf et al. 2003b, 2007, Kusak et al. 2005, Chavez & Gese 2006). The impact of these factors on wolf activity is highly variable and is determined by habitat characteristics (including prey) and human impact. This explains the different outcomes for the wolf activity patterns published across countries and latitudinal/longitudinal gradients. Another reasonable explanation for the great variability of activity patterns of wolves is their adaptability to respond quickly to the different gradients of their ecological niche (Packard 2003).

The spatiotemporal activity of the wolf and its prey is not studied so far in Bulgaria. To fill this gap, we used the camera trap data from Osogovo Mtn. with two main objectives: 1) identification of the wolf circadian activity range and the degree of its overlap with the activity of its ungulate prey (wild boar and roe deer); 2) identification of the chance for spatiotemporal interactions of the three species at a same location via time-spacing analyses.

Two hypotheses were formulated: 1) the species that experiences the strongest pressure from the wolf (prevailing in its diet) will avoid it in space and time more than the prey less present in the diet; 2) the activity of the species that experiences less hunting pressure from the wolf will not be significantly affected by wolf activity.

Materials and Methods

Study area

Osogovo Mountain, located in southwest Bulgaria, is a trans-border mountain shared between Bulgaria and North Macedonia. The total area of the mountain is 4223 km^2, of which 996 km^2 is in Bulgaria. The highest peak is Ruen (2251 m a. s. l.). Osogovo Mtn falls in the European-continental climatic region with average July temperatures of 18-24°C and relatively cold winter (-6 to -8°C), with significant winter precipitation and stable snow cover (Sabev & Stanev 1963). The habitats are mainly forested, consisting of beech (*Fagus sylvatica* L.), oak (*Quercus robur* L.) and Hornbeam (*Carpinus* sp.). Almost everywhere the beech outlines the upper border of the forest. The high parts of the mountain (over 1800 m) are covered by mountain pastures with spreads of Juniper bushes (*Juniperus* sp.). Because of its location (protected border area), Osogovo has relatively well-preserved habitats. On the other hand, the strict border control until the end of the 1980s defined Osogovo as one of the least studied mountains in Bulgaria. The whole study area lies within the management of the State Hunting Enterprise Osogovo, where hunting is organised on a small scale for individual hunters and

Fig. 1. Bulgarian part of the Osogovo Mountain and location of the camera traps used.

supplementary feeding for the ungulate game (the wild boar and the roe deer) is provided. The Bulgarian part of the mountain is protected as a Natura 2000 area. Totally, 36 species of mammals (excluding bats) have been recorded in the mountain (Zlatanova et al. 2005, 2018). The wild boar and the roe deer are abundant and present in significant numbers (Table 1). There were also herds of semi-free-ranging horses (*Equus ferus caballus* L., 1758) extensively grazed and bred in large enclosures with electric fences at an altitude of about 2000 m. No other livestock has been grazed in the study area since 2012.

Unlike other parts of Bulgaria, the wolf has continuously been present in the mountain (Genov & Kostava 1993) containing data on wolf attacks on domestic animals were used (Table 1). In 2003, two small (up to 4 individuals) wolf packs were registered along transects (Zlatanova et al. 2005). Between 2016 and 2018, two packs were recorded with camera traps in the same region – one of eight and one of four individuals (Popova et al. 2019). The larger pack has maintained integrity through 2020 and beyond.

Collection and processing of data

In the period 28 September 2019 – 16 May 2020, 21 camera traps (WK5 A3, Bestguarder, Scoutguard, Ltl Acorn) were placed in three grid cells (Fig. 1), sized 1 x 1 km (7 camera traps per grid). The grid was selected to more or less match the size of the ungulate home range. The camera traps were set up opportunistically at sites chosen to maximize animal detection – on animal trails and away from attractants (like artificial feeding sites or water). The location of each camera trap was taken with a hand-held GPS device. All cameras were placed on trees, between 40 and 130 cm above the ground, operating in a continuous 24-hour cycle. The camera traps were set to shoot 3 photos (5 seconds apart) and a 10-second video to maximize the chances of capture. The next series of photos and a video could be taken one minute after the previous triggering. A standard form was filled out for each camera trap location, describing its habitat characteristics. The footage was processed in Camera Base v.1.7 (Tobler 2015). Photos and videos of prolonged stay (up to 5 min) of the same individual/individuals in front of the camera trap were considered as independent events to avoid overrepresentation of the species. The sample collected and analysed is presented in Table 2.

To assess the activity of the studied species we followed the approach of Rowcliffe et al. (2014) for quantifying the activity level from the time of camera trap detection. Three types of camera trap analyses were performed for the wolf the wild boar and the roe deer:

Relative frequency of registrations. To account for the wolf effect on the ungulate prey spatial distribution, we compared the wild boar and roe

Table 1. Wolf, roe deer and wild boar numbers, density and hunting bag, according to the official data of State Hunting Enterprise (SHE) Osogovo for a ten-year period (2011–2020) (Dolapchiev et al. 2022).

Year	Wolf			Roe deer			Wild boar		
	Census	Density	Hunting bag	Census	Density	Hunting bag	Census	Density	Hunting bag
2011	22	0.11	15	1246	6.31	8	1057	5.35	271
2012	19	0.10	11	1075	5.44	10	997	5.05	478
2013	21	0.11	16	1292	6.54	17	1014	5.13	369
2014	15	0.08	9	1354	6.85	19	1039	5.26	377
2015	17	0.09	8	1312	6.64	16	1033	5.23	328
2016	26	0.13	15	1371	6.94	10	1078	5.46	521
2017	15	0.08	9	672	3.40	20	503	2.55	446
2018	18	0.09	1	672	3.40	25	533	2.70	346
2019	16	0.08	3	678	3.43	35	462	2.34	365
2020	17	0.09	1	757	3.83	17	369	1.87	239

deer relative frequency of registrations (or hereafter Detection rate – DR) in locations without and with wolf registrations for the whole study period. The DR was calculated per 100 trap days by the following formula (O'Brien et al. 2003):

$$DR = \frac{(N \times 100)}{ctd}$$

where N is the number of independent registrations of the target species; ctd is the total number of camera trap days, calculated for each grid by the formula:

$$ctd = d_{i1} + d_{i2} + d_{i3} + \ldots d_{in}$$

where *ctd* is the number of trap days; *d* is the number of days during which trap *i* was active in the field.

Two statistical tests at 0.05 significance, within the 95.0 % confidence level were used in the comparison of the two groups (grid cells with and without wolves): t-test to compare means (for normally distributed data) and Mann-Whitney (Wilcoxon) W-test to compare medians (when significant departures from normality were observed).

An activity overlap analysis was performed with the R programming language (v. 4.1.1), the RStudio software, and the overlap package. They were used to analyse the circadian activity and the level of activity overlap (Meredith 2022) of the three species by the means of non-parametric kernel density estimation (KDE) of registrations on all camera trap data. The result of this assessment is a coefficient for the degree of overlap in the diurnal activity of the studied species. The coefficient ranges from 0 (complete activity divergence) to 1 (complete overlap) (Ridout & Linkie 2009). The obtained results were interpreted only by hours, given the differences in the length of the day during different parts of the year, which shift the twilight periods.

Table 2. Captures from camera traps (photos and videos) collected for the survey. Total – number of all target species documented; Ind. No – number of independent captures. Σ of Ind. – sum of all independent registrations of the three species.

Species	*Canis lupus*		*Capreolus capreolus*		*Sus scrofa*		Σ of Ind.
	Total	Ind. No	Total	Ind. No	Total	Ind. No	
No	43	23	2857	946	858	274	1243

In addition, the registrations of the three target species were divided and analysed into three groups – daytime, nocturnal and crepuscular (twilight) activity. The recognition of these three periods is part of the automated function of the Camera Base programming, which, based on the location of the camera traps and a built-in algorithm, calculates the time of sunrise and sunset for each registration and joins this registration to the corresponding group. Crepuscular (twilight) is defined as the period between half an hour before and half an hour after sunrise/sunset.

Time-spacing (ts) analysis was done on nine camera trap data, where the three species were recorded in the same locations. This is the time between consecutive registrations of the target species (species A appears first and species B second):

$$ts = time_{beginningB} - time_{endA}$$

where ts is the time interval between successive visits of 2 different species (species A visits the feeding place first, and species B – after it); $time_{beginningB}$ – the time (in hh:mm:ss) when the animal of type B was observed for the first time on a photo/clip (i.e., the beginning of the independent registration); $time_{endA}$ – the time (in hh:mm:ss) when the animal of species A was last observed in a photo/video (i.e., end of independent registration).

No human presence was recorded in the study, which could affect the registrations of the studied species.

Results

Spatial overlap

The detection rate in each grid cell ranged between 0.43 and 11.64 for the wild boar, 0.86–42.67 for the roe deer and 0 and 3.45 for the wolf (Fig. 2). The t-test on means / Mann-Whitney (Wilcoxon) W-test on medians showed no significant difference in the presence of wild boar or roe deer between locations with and without wolves (Fig. 2).

Circadian activity and overlap

The wild boar (n = 273) and the roe deer (n = 976) showed significant overlap (Fig.3A) in their activity (Δ = 0.70, confidence interval 0.64–0.75). The wolf (n = 23) and the roe deer (Fig. 3B) overlapped their activity more (Δ = 0.61, confidence interval 0.45–0.74) than the wolf and wild boar (Δ = 0.57, confidence interval 0.64–0.75) (Fig. 3C).

The wild boar showed mainly nocturnal activity (n=207) with less daytime (n=47) and crepuscular (n=27) registrations, while the roe deer spent almost an equal amount of time in the day and night-time activity (408 to 409 registrations respectively). The crepuscular activity of roe deer was almost twice as low as the day and night activity. Similar to the wild boar, pattern was observed in the wolf – nocturnal activity (n=16) and an almost equal number of daytime (n=4) and crepuscular activity (n=3).

Time-spacing

The results of the time-spacing analyses showed that it took a minimum of three times longer time for the wild boar to appear after the wolf (min = 14:24 h; $\bar{\chi}$ = 348:55 h.) than the same for the roe deer (min = 3:56 h; $\bar{\chi}$= 410:49 h). On the other hand, the wolf appeared sooner after a wild boar (min = 7:55 h; $\bar{\chi}$= 387:04 h.) than after the roe deer (min = 11:19 h; $\bar{\chi}$ = 262:33 h).

Discussion

Several authors found in their research that the wolf was active mostly at twilight (at dawn and dusk) when the prey was expected to be more vulnerable due to the low light (Theuerkauf et al. 2003a,

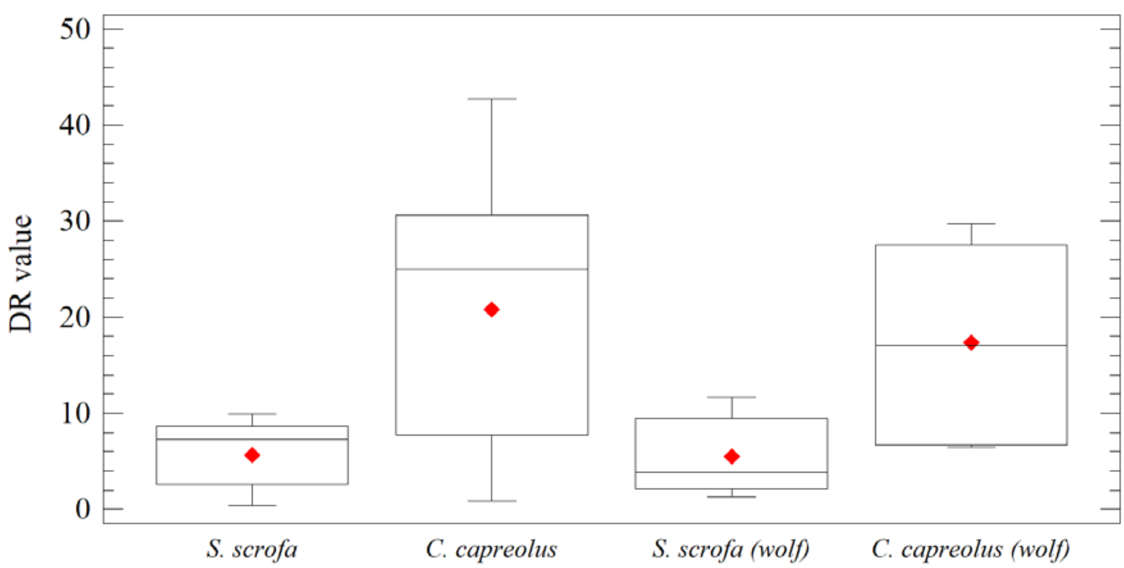

Fig. 2. Detection rate (DR) range compared between locations without wolf and with wolf. The single species names stand for locations without wolf registrations. The species names with (wolf) stand for locations with wolf registrations. Diamonds – average value, horizontal line – median value, box – interquartile range.

2007, Eggermann et al. 2009, Eriksen et al. 2011). In the current study on Osogovo Mountain, the wolf showed distinct nocturnal activity, with day and crepuscular activities of similarly low values (Fig. 4). This concurs with several other studies conducted in the Mediterranean region (Vila et al. 1995, Ciucci et al. 1997, Blanco et al. 2005, Kusak et al. 2005, Karamanlidis et al. 2017), Romania (Oliveira 2017) and Turkey (Akbaba & Ayaş 2012) where high nocturnal wolf activity was also registered. A possible explanation for this could be the nocturnal activity of the wild boar, which according to our recent research in Osogovo is the main wolf prey (Dolapchiev et al. 2022). Yet, although food availability is a key element for the predator, the overlap of the wolf's activity with its main prey (wild boar) is unexpectedly low – about 60 % (Δ = 0.57). This may be due to the counter-balancing antipredatory behaviour of the wild boar which showed a very distinctive peak of its activities, around 18:00 h in the evening, out of the wolf's main active period at dawn (around 6:00 h) (Fig.3C). Thus, although both species have distinct nocturnal activity time activity, there is a clear lack of overlap of its peaks. The reason for this might be found in various factors, one of which is the density of the main prey. Harrington & Mech (1982) found that the high density of the wolf combined with the low density of prey forced wolves to adapt much more accurately their activity to that of their prey. In a more saturated population of wolves and low prey density, any increase in efficiency would benefit the predator. Despite the current decrease in numbers recorded lately (Table 1), Osogovo Mtn. is one of the mountains in Bulgaria with a very stable and high-density wild boar population which, as recorded in our studies, can support bigger wolf packs with good hunting success. This most probably is the reason for the recorded less-than-expected overlap in the activity of the wolf and the wild boar. A similar hypothesis was made by Eriksen et al. (2011), according to whom the benefit of adjusting the predator's activity to the activity of the victim depends on the density of both species. A higher density of wolves or a lower density of prey would lead to greater competition between the former, which in turn would lead to a higher degree of synchronisation with the activity of the prey.

The comparison of our results to other studies in Bulgaria concerning wild boar activity showed that a similar outcome was found for Vitosha Nature Park where the wild boar was also extremely nocturnal (Doykin 2018). Studies in Poland (Sporek 2017) Canada (Stolle et al. 2015) Argentina (Caruso et al. 2018) and Italy (Boitani et al. 1994, Russo et al. 1997) provided similar results.

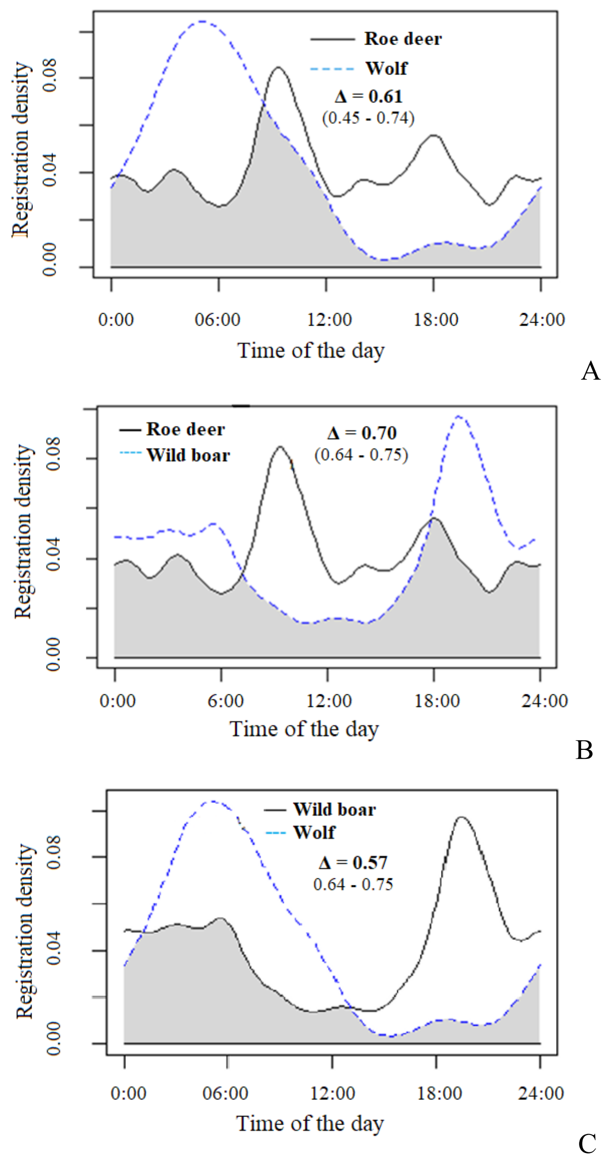

Fig. 3. Circadian activity, registration density and overlap level between the roe deer, wild boar and wolf during the period 28.09.2019 – 17.05.2020. A. Activity and overlap between roe deer and wild boar. B. Activity and overlap between roe deer and wolf. C. Activity and overlap between wild boar and wolf.

Apart from the hunting pressure from the wolf, the wild boar's activity and behaviour are shaped also by human impact. The wild boar is a main game species in many countries and is subject to serious hunting pressure (Table 1). Hunting happens during the daylight, which forces the wild boar to choose secluded places during the day and opt mainly for nocturnal activity. This is additional proof that the human factor is very important for shaping nocturnal activity in many species (Gaynor et al. 2018). The activity of the wolf in Osogovo Mtn. was most

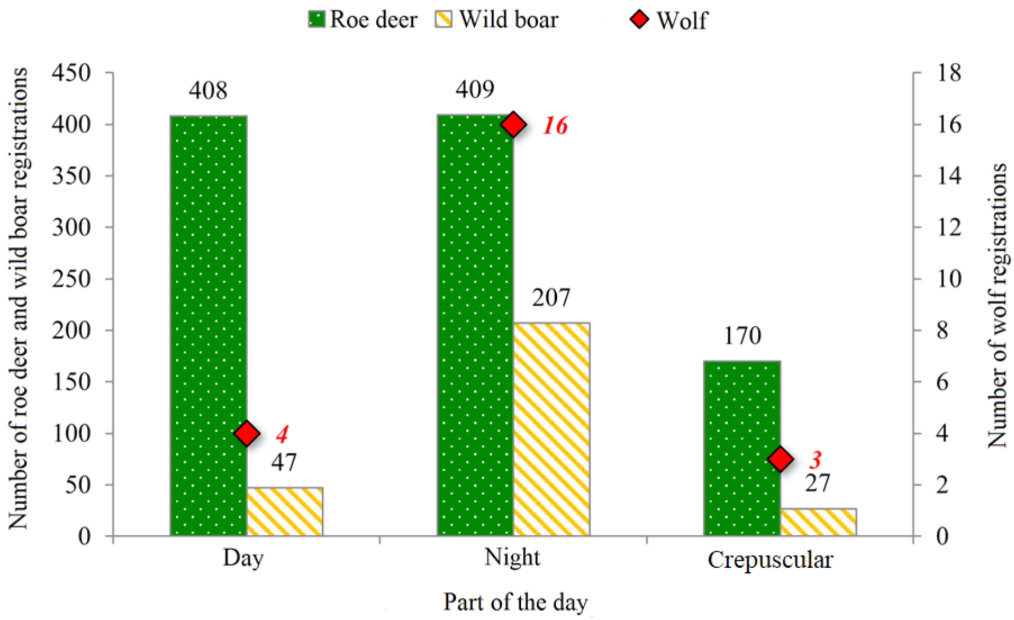

Fig. 4. Activity pattern (day, night and crepuscular) of the roe deer, wild boar and wolf (diamonds) in Osogovo Mtn.

probably also affected by the human factor but to a lesser extent than this of the wild boar (Fig. 3C).

The hunting bag in Osogovo Mtn has an insignificant impact on the second prey of the wolf – the roe deer (Table 1). Unlike the wild boar, the roe deer is usually hunted by the wolf only if it is encountered by chance (Mattioli et al. 2004). The low hunting pressure both from the wolf and from humans provided an opportunity for this species for an equal amount of day and night activity (Fig. 4) and for a well-pronounced peak in the morning hours (Fig. 3A) when the species can be frequently observed grazing on the sub-Alpine meadows near the forest edge. A second, smaller peak of the activity can be observed in similar hours of the wild boar evening peak. These hours are less active for the wolf and it seems that both ungulates benefit from this time frame. This is also the reason for the high overlap of the wild boar – roe dee activity (70 %).

The reported peak in the daylight activity of the roe deer in the morning hours (6:00-12:00) differed from the results of other published studies, where peaks in the circadian activity of the species were reported mainly for the twilight part of the day (dawn and dusk) (Cederlund 1989, Jeppesen 1989, Wallach et al. 2010, Pagon et al. 2013). Possible reasons for these differences, and especially for the high percentage of daylight activity, lie in the relatively low human disturbance in the mountain, compared to other regions of the country and the very low hunting pressure, both from the wolf and humans. This allowed for a slightly higher degree of overlap of the roe deer activity with this of the wolf, compared to that of the wild boar. The time-spacing analyses also confirmed the conclusions so far – the fact that it took three times longer time for wild boar to appear after a wolf (min = 14:24 h) in the same place than for the roe deer (min = 3:56 h) showed a clear anti-predatory mechanism in the wild boar behaviour. On the other hand, the wolf's appearance sooner after a wild boar (min = 7:54 h) than after the roe deer (min = 11:19 h) proved once more the wolf's active preference for the wild boar as its main prey. According to our knowledge, such time-spacing analyses for the wolf-wild boar and wolf-roe deer relationship were not carried out in other countries or studies, so the validity of this mechanism as a behaviour trait cannot be yet confirmed.

Conclusion

Following the results of the current study, we concluded that the first hypothesis "The species that experiences the strongest pressure from the wolf (prevailing in its diet) will avoid it in space and time more than the prey less present in the diet" – can be partially accepted. The wild boar, which is the main prey of the wolf, is not avoiding it spatially, but by an activity shift.

The second hypothesis "The activity of the species that experiences less hunting pressure from the wolf will not be significantly affected by wolf activity" is fully proven, as the roe deer, which forms an insignificant share of the wolf diet in Osogovo is not only significantly affected by the wolf activity but is also less affected by the human activity.

Camera traps are a valuable tool for studying the circadian activity of species and we recommend implementing it in any related study. Due to their non-invasiveness, they are effective and objective means for studying the relationships between numerous species. Yet, the data obtained by camera traps alone is not sufficient to explain all results, so cross-analysis with other methods (for example, diet analysis and hunting pressure) should be implemented in a complex study to provide a more objective picture for understanding the relationships between the studied species.

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