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Spatio-temporal analyses on roe deer activity (Capreolus capreolus L.) in areas with and without wolf (Canis lupus L.) presence

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Abstract. In 2021 in north-western Bulgaria, on the territory of State Forestry "Midzhur", West Stara Planina Mtn, we analysed the temporal and spatial activity of the roe deer (*Capreolus capreolus*) in an area with scarce other large ungulates. In the locations where both wolf and roe deer were recorded a significant (75%) temporal overlap between the two species was found (Δ = 0 75, range 0.62 - 0.96 at CI 95). Although the overlap between the activity of the roe deer in locations with and without wolf registrations was high (Δ = 0.72, range 0.58 - 0.92 at CI 95), the activity had two clearly different main peaks - around 18:00 in locations without wolves and around 05:00 h in locations with wolves. The results of the time-spacing analysis showed that the average time for a roe deer to appear after the presence of a wolf (min = 8:17 h) was greater than the time needed for the wolf to appear after a roe deer (min = 1:35 h). The difference in the spatial distribution of roe deer in areas with and without wolf presence was not statistically significant; yet the highest detection rate of roe deer was recorded in locations with wolf registrations. This allowed us to conclude that the roe deer as a potential main prey species of the wolf in the region was not avoiding the predator spatially but temporarily while the wolf the strategy of the wolf was to synchronize its circadian activity with that of the roe deer.

Key words: activity overlap; time-spacing; avoidance; protective strategy; predator-prey relationship.

Introduction

The wolf (*Canis lupus* Linnaeus, 1758) is one of the most important carnivores and keystone species, both in Europe and in many other parts of the world (Beschta & Ripple, 2016; Mech & Boitani, 2003). This predator shapes the population size, behaviour, spatial distribution, and physiological state of its prey (Klich et al., 2020; Kuijper et al., 2015; Mattisson et al., 2016; Okarma, 1995; Ripple & Beschta, 2012). In general, although many species and taxa may shape the wolf food spectrum the ungulates, mainly the wild boar *Sus scrofa*, red deer *Cervus elaphus* and roe deer *Capreolus capreolus*, are its primary prey (Newsome et al., 2016; Okarma, 1995; Sidorovich et al., 2017; Zlatanova et al., 2014). The two most important variables in the wolf-ungulate relationship are the number of ungulate

species available for the predator and the specific selectivity towards each of them. These variables can be affected by many factors - sedentariness of the wolves in the area (Nowak et al., 2005), breeding status, behaviour and activity of prey, human activity or even weather conditions. When a prey species is persistently present in the wolf's diet, for example, the wild boar which forms an essential part of the wolf food spectrum in Europe and Bulgaria in particular (Dolapchiev et al., 2022; Mattioli et al., 2004; Emiliano Mori et al., 2017), the reductions of its population density due to overhunting or disease like African swine fever (ASF) may cause significant changes in food preferences (Murdoch & Oaten, 1975) and a switch to other ungulates of the deer family or livestock (Gazzola et al., 2007; Klich et al., 2021; Emiliano Mori et al., 2017; Valdmann & Saarma, 2020).

In State Forestry "Midzhur" in Bulgaria, the situation is similar. According to the 2021 annual census, the wild boar numbers decreased by 69.2% (168 individuals) in comparison with the 2019 census carried out before the outbreak of ASF in the region (544 individuals). The red deer in the region is present with relatively low numbers – 141 - 201 individuals for the period 2019 - 2021. The low numbers of the wild boar and red deer were also confirmed in our study with a very low registration rate (one for the wild boar and six for the red deer), even much lower than these of the wolf. This gave us a reason to assume that the roe deer in this area are subjected to high hunting pressure by the wolf. This is expected to influence its activity and spatial distribution as a part of its anti-predatory behaviour.

Numerous authors have worked on the circadian activity of the two species targeted in our study – the wolf (Akbaba & Ayaş, 2012; Ciucci et al., 1997; Eggermann et al., 2009; Eriksen et al., 2011; Fancy & Ballard, 1995; Karamanlidis et al., 2017; Kolenosky & Johnston, 1967; Kusak et al., 2005; Mengüllüoğlu & Bilgin, 2010; Mori et al., 2020; Oliveira, 2017; Petridou et al., 2023; Rossa et al., 2021; Theuerkauf et al., 2003, 2007; Vila et al., 1995) and the roe deer (Cederlund, 1989; Jeppesen, 1989; Mori et al., 2020; Pagon et al., 2013; Petridou et al., 2023; Rossa et al., 2021; Turner, 1979; Wallach et al., 2010). Yet, analysis of the overlap of the wolf activity with this of its prey in cohabitation was made relatively less (Eriksen et al., 2011; Mengüllüoğlu & Bilgin, 2010; Mori et al., 2020; Petridou et al., 2023; Rossa et al., 2021), with only one study in Bulgaria - in Osogovo Mtn where the main prey is the wild boar (Dolapchiev, 2022) supplemented by the roe deer.

To analyze the functional response of the roe deer towards the hunting pressure of the wolf we conducted a camera trap study in West Stara Planina Mtn (State Forestry "Midzhur"). We formulated three hypotheses about the adaptive spatiotemporal strategy of the roe deer and wolves: (1) The relative frequency of roe deer registrations will be significantly lower in locations with wolf registrations than in locations without them – e.g., roe deer will tend to avoid areas with increased wolf presence; (2) Both the predator (wolf) and the prey (roe deer) adopted an activity pattern that benefitted their survival strategy - providing a window for hunting opportunities for the wolf and avoidance for the predator for the roe deer. (3) There are no differences in the minimum and average time in the appearance of the wolf and the roe deer at the same location (time-spacing analysis).

Materials and Methods

Study area

The research was conducted on the territory of the State Forestry (SF) "Midzhur" (397.8 km²) located in the West Stara Planina Mtn along the border with the Republic of Serbia. The entire Forestry is a Natura 2000 site with high biodiversity. It covers a rugged terrain (highest peak - Midzhur 2169 m) with a high density of rivers, part of the Danube River catchment basin. The vegetation consists predominantly of broad-leaved forests: oak (*Quercus robur*), beech (*Fagus sylvatica*), cerris (*Quercus cerris*), complemented by black pine (*Pinus nigra*), scots pine (*Pinus*

sylvestris), spruce (*Picea abies*), fir (*Abies alba*), mountain peony (*Trollius europaeus*), etc.

The most important mammal species are the brown bear (*Ursus arctos*), red deer, wild boar, roe deer, wolf, red fox (*Vulpes vulpes*), stone (*Martes foina*) and pine (*Martes martes*) martens, badger (*Meles meles*), etc. A few chamois (*Rupicapra rupicapra*) individuals are also present due to a reintroduction attempt in the past.

Nearby our study area is the "Chuprene" biosphere reserve, declared in 1973, which is one of the few areas in Bulgaria where the wolf never went through extinction. There is recent, still unconfirmed official data for the presence of another large carnivore – the lynx (*Lynx lynx*).

The official game census data of the SF "Midzhur" for the wolf, roe deer, wild boar and red deer are presented in Table 1.

Field data collection

The data was collected with camera traps which are proven to be a useful tool for studying the behaviour of large mammals (Silveira et al., 2003; Tobler et al., 2008; Yasuda, 2004). The research was conducted in the period from 11 February 2021 to 26 June 2021 (135 days in total). Eight camera traps (Moultrie MCG 13331) were placed opportunistically in forested areas on animal trails to maximize animal detection. To cover a bigger area but still account for the smaller home ranges of the prey and to obtain a big enough sample size of registrations, the camera traps we set in two groups far apart about four km, with about 400 m between camera traps in each group (Fig. 1). The average altitude of the camera traps was 1227 m a.s.l.

Table 1. Official game census of the SF "Midzhur" (Juparov, 2019; Petrov, 2021).

year	*Canis lupus*		*Capreolus capreolus*		*Sus scrofa*		*Cervus elaphus*	
	Individuals	hunting bag	Individuals	hunting bag	Individuals	hunting bag	Individuals	hunting bag
2018	61	4	843	0	501	158	133	0
2019	67	0	1054	2	544	224	141	0
2020	36	1	1257	6	271	217	167	2
2021	28	4	1114	31	168	20	201	1
2022	45	3	1147	25	200	34	224	1

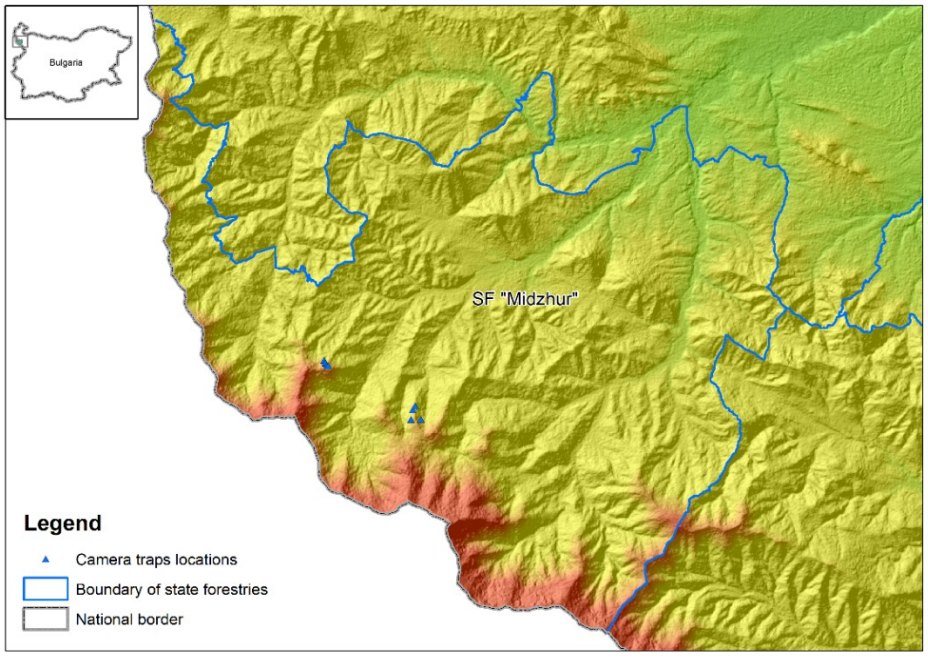

Fig. 1. Locations of the camera traps within SF "Midzhur".

The camera traps were set up to take three consecutive pictures, five seconds apart. The next series of photos could be taken one minute after the previous triggering. A standard form was filled for each camera trap, recording location, and describing habitat characteristics. A common database was filled in Camera Base 1.6 (Tobler, 2015), modified and translated into Bulgarian (Zlatanova, unpublished). Photos showing the prolonged stay of the same individual/s in front of the camera trap were considered as one independent registration to avoid overrepresentation of the species.

Analyses

The data set included 1072 camera trap working days and 318 independent registrations, 302 of which were of 10 wild mammal species (Appendix 1). The roe deer was the most frequently recorded (n = 112), followed by the wolf (n = 52), red deer (n = 6), brown bear (n = 4), and wild boar (n = 1).

The camera trap locations and respective data were divided into two groups: Groups A - locations without wolves (n = 4) and Groups B - locations with wolves. 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 detection data from camera traps. Three types of camera trap analyses were performed for the wolf and its ungulate prey the wild boar and roe deer:

1). To account for the presence of the wolf on the spatial distribution of the roe deer, the relative frequency of registration (Detection Rate - DR) was compared for the data from the two groups - locations with and without wolf registrations. Relative frequency represents a standardized number of target species registrations from camera traps, considering the difference in survey duration and recalculating them per 100 camera trap days. Thus, DR was calculated using the following formula (O'Brien et al., 2003:

$$\mathbf{DR} = \frac{\mathbf{n} \times \mathbf{100}}{\mathbf{ctd}}$$

where: DR – relative registration frequency; n – number of independent registrations of the target species; ctd – number of traps days.

T-test was used to compare the two groups' average DR, applied at a significance level of 0.05 applied to a 95.0% confidence interval.

2). The R programming language (v.4.1.1), RStudio software, and the overlap package (Meredith, 2022) were used to analyse the circadian activity of the wolf and roe deer and its level of overlap between species and between the activity of roe deer in locations with and without wolves. This package uses the non-parametric kernel density estimation (KDE) method for estimating the density of registrations. The result of this assessment is a coefficient for the degree of overlap in the circadian activity of the studied species. The coefficient ranges from 0 (complete activity divergence) to 1 (complete overlap) (Ridout & Linkie, 2009). The results were interpreted by hours only, given the differences in the length of the day during different parts of the year, which shifts the twilight periods.

3). The time interval between successive registrations of species (time-spacing - ts) was calculated, considering who visited the place first (species A visits the site first followed by species B and vice versa) using this formula:

$$\mathbf{ts} = \mathbf{time}_{\mathbf{beginningB}} - \mathbf{time}_{\mathbf{endA}}$$

where ts is the time interval between successive visits of the two species; $time_{beginningB}$ - the time (in hh:mm:ss), when the animal of type B was observed for the first time on a photo/clip (ie. 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/clip (ie. end of independent registration).

Results

Detection Rate (DR)

The detection rate of the two species calculated for each camera trap varied between 0 - 21.37 for the wolf, and 0 - 25.9 for the roe deer. The comparison for the two groups A and B (Fig. 2) showed that the range and the mean DR value were generally higher for roe deer in camera traps with a higher presence of wolves, yet the difference in the average DR between the two groups is not significant ($t = 0.330$, 6 d. f., $p = 0.753$).

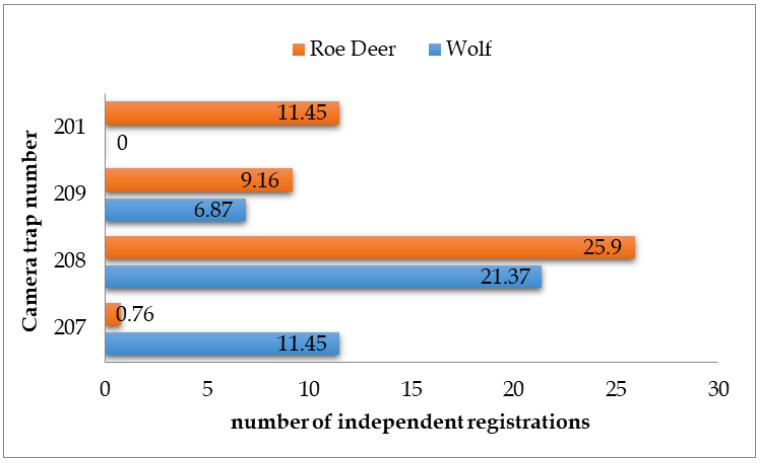

Fig. 2. DR comparison for each camera trap in Group B.

Circadian activity

The results of the circadian activity of roe deer from Group A (n=50), in which no wolves were recorded, showed a peak of its activity between 18:00 and 24:00 h, with a much smaller peak in morning hours, while for the roe deer in Group B, the main peak was in the morning hours around 6:00 h. (Fig. 3A). At the same time in Group B the wolf was trying to synchronise its peaks of activity with the roe deer (Fig. 3B), as its bigger peak was in the evening hours. Common to both species was the pronounced peak of activity during the dark hours of the day.

Both roe deer in the two Groups and the wolf and the roe deer in Group B showed similar and significant overlap in their circadian activity – 72 % (Δ = 0.72, range 0.58 - 0.92 at CI 95) for the former and 75% (Δ = 0.75, confidence interval 0.62 - 0.96) for the latter.

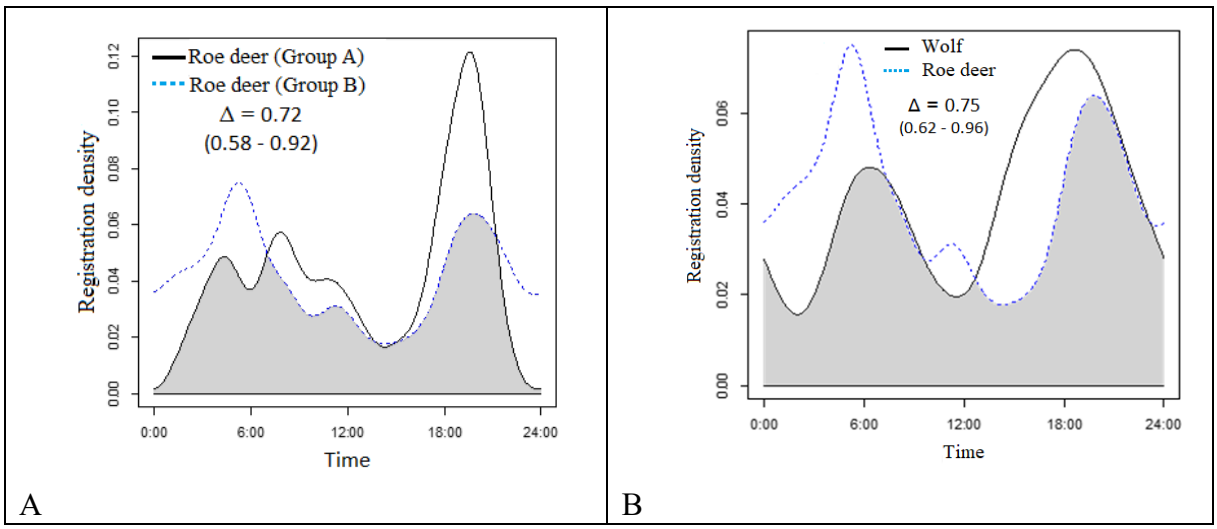

Fig. 3. Circadian activity and level of overlap between (A) Roe deer in Group A (without wolves) and Group B (with wolves) and (B) Wolf and roe deer in Group B.

Time-spacing

The minimum and the average time for a roe deer to appear at the same location after a presence of a wolf was greater (min = 8:17 h; $\bar{\chi}$ = 61:48 h.) than the time needed for the wolf to appear after a roe deer (min = 1:35 h; $\bar{\chi}$ = 49:13 h.).

Discussion

In many areas of Bulgaria, the wild boar is one of the leading prey species in the wolf diet. For example, in Osogovo Mtn it is the main prey while the roe deer forms an insignificant share (Dolapchiev et al., 2022). In the Rhodope Mountains

(Genov et al., 2008; Serafimov et al., 2008) the wild boar is second in importance, after a similarly large prey – the red deer. In our study, due to the ASF effect on the wild boar and the relatively low numbers of the red deer (also confirmed by us – Appendix 1), it is only logical to conclude that the roe deer would be of high importance for the wolf as a prey, as it is in many European countries (Newsome et al., 2016; Zlatanova et al., 2014).

The changes in the wild boar numbers happened recently, so it was expected that the wolf hunting pressure on the roe deer would be a recent turnover. In this case, the species needs a quick but effective spatial or temporal strategy to decrease the chances of predation. Such protective strategy can be influenced by several factors, including abiotic - e.g., topography (like elevation and slope) (Evcin et al., 2019; Franchini et al., 2023) and different weather conditions (Brivio et al., 2017), biotic – food base availability, inter- or intra-species competition, the influence of other predators (Torretta et al., 2017), as well as some anthropogenic factors (Gaynor et al., 2018; Kati et al., 2020). Ungulates, including the roe deer, can change their spatial and temporal activity patterns to avoid predation and other disturbances (Berger et al., 2002; Berger, 2007; Stephens & Peterson, 1984). Wolves, in their turn, to improve their hunting success, adjust their activity patterns to that of their prey (Fuller, 1991; Harrington & Paquet, 1983; Theuerkauf et al., 2003) which again affects the behaviour of their prey (Stephens & Peterson, 1984). As a result, the prey corrects its circadian activity model in response to that of the predator (Nelson & Vance, 1979; Overdorff, 1988) and vice versa. Predators usually change their activity towards the period when their prey is active (Jenny & Zuberbühler, 2005). Prey can also spatially avoid the predator by changing their habitat use in response to predation pressure (Bednekoff, 2006).

Interspecific relationships in ungulates can also be a factor reflecting their spatial and temporal activity (Latham, 1999; Bartos et al., 2002; Focardi et al., 2006; Dolman et al., 2008; Ferretti et al., 2011a,b; Franchini et al., 2023). Small number of records of red deer and wild boar in the present study do not allow an analysis of the effect of their relationship on their spatial and diurnal activity.

Our analyses in the current study showed that unlike Osogovo Mtn, where the roe deer circadian activity was clearly asynchronous to this of the wolf (Dolapchiev, 2022), in SF "Midzhur" the wolf managed to synchronise its activity to this of the roe deer when present in the same locations. This conclusion was also supported by the comparison of the roe deer activity in locations with and without wolves as in areas without wolves the roe deer main activity peaks were different.

The comparison of the DR in Group A and B gave us the right to conclude that the roe deer avoidance was not spatial. This was also supported by a similar study in Osogovo Mtn (Dolapchiev, 2022), where the avoidance of the main wolf prey – the wild boar, was also not spatial but temporal. The elevated presence of roe deer in areas with a wolf can be explained with only one logical option - the wolf was most probably trying to be more frequent in areas with a higher probability to encounter its prey (Fig. 2).

The circadian activity of the wolf in our study, where the main peak was at dusk (around 18:00) was different from the results obtained in Norway (Eriksen et al., 2011), Poland (Eggermann et al., 2009; Theuerkauf et al., 2003, 2007) and Osogovo Mtn in Bulgaria (Dolapchiev, 2022), where the peak of wolf activity was at dawn. The wolf activity in Mediterranean countries was found to be mainly during the night (Akbaba & Ayaş, 2012; Blanco et al., 2005; Ciucci et al., 1997; Karamanlidis et al., 2017; Kusak et al., 2005; Mori et al., 2020; Petridou et al., 2023; Rossa et al., 2021; Vila et al., 1995). Similar results were reported for Romania (Oliveira, 2017).

The circadian activity of the roe deer in our study was mainly at twilight and nocturnal, unlike this in Osogovo Mnt. (Dolapchiev, 2022) and Greece (Petridou et al., 2023) where a significant part of it was during the day. Our results concurred with other studies in which the highest levels of roe deer activity were recorded within the same time range (Jeppesen, 1989; Wallach et al., 2010; Pagon et al., 2013; Cederlund, 2014; Mori et al., 2020; Rossa et al., 2021).

The comparison of the activity between the roe deer locations without and with wolves (Groups A and B) showed that although there was significant overlap, the wolf was having a serious impact on it, shifting the main peak of the roe deer activity from dusk (where the main peak of the wolf lied) to dawn. This could be considered an antipredatory strategy of the roe deer. On the other hand, the wolf was trying to compensate for

this shift in the twilight activity of its prey forming two peaks - larger at dusk and smaller at dawn) to be active within the active hours of its potential prey. This resulted in a significant overlap of the activity of both species (Δ = 0 75). A similarly high degree of overlap was obtained in a study in Italy (Δ = 0 71) (Mori et al., 2020).

In areas with rugged terrain and predominantly coniferous forests (as the one in our study), the visibility is generally low. Therefore, wolves and roe deer must rely on senses other than sight to detect each other's sound and smell (Mech & Boitani, 2003). Active animals make more noise than inactive ones, and it is logical to assume that the odour could be dispersed more efficiently by an animal that is moving than by an animal that is at rest (Peters & Mech, 1978). So from this point of view, for the sake of the wolf's hunting efficiency, this predator should try to synchronize its activity with this of the roe deer and at the same time avoiding hours when the humans would be active. The roe deer, on the other hand, should also avoid humans and predators, so full asynchronisation with the wolf activity was not possible and there was still some overlap of the peaks. One possible solution for the roe deer, in this case, was to increase its activity when the wolf activity was decreasing or to be active before the wolf's activity peaks. Such adaptations could be clearly seen in Fig. 3B.

The time-spacing analysis in the locations where both the wolf and the roe deer were present implied an active wolf interest in the roe deer as prey. At the same time, the roe deer was trying to avoid the predator temporarily. Similar avoidance behaviour of the main wolf prey in Osogovo Mtn (the wild boar) was found in a recent study (Dolapchiev, 2022), where it took three times longer 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 in Osogovo 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), which confirmed that the activity was formed by the active interest in the main prey.

Conclusions

The results of our study gave us a reason to reject the first hypothesis about the spatial avoidance of the wolf by the roe deer – the analyses of the DR clearly showed that there was no evidence to support this assumption. The second hypothesis can be fully accepted, since the temporal analyzes showed clear indications of the strategies of the two species: a) the roe deer seeks to temporally avoid the wolf; b) the wolf seeks to synchronize its temporal activity pattern with that of the roe deer in order to make a successful catch. The last hypothesis was also rejected in full – the differences in the results of the time-spacing analysis showed that, as a part of its anti-predatory behaviour, the roe deer was trying to delay its appearance in visited by wolves places, while the wolves were trying to shorten these time intervals to be able to find the prey.

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