ECOLOGIA BALKANICA

2024, Vol. 16, Issue 2 December 2024 pp. 70-79

Spatial and temporal relationships between predators in the „Sinite Kamani" Nature Park, Bulgaria

Nikolay Dolapchiev[1,2,*], Elitsa Popova[3], Milen Chanev[2]

[1]Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 2 Gagarin Str., 1113 Sofia, BULGARIA; e-mail: ndolapchiev@gmail.com

[2]Bulgarian Academy of Sciences, Space Research and Technology Institute, Sofia 1113 Acad. Georgy Bonchev Str., bl. 1, BULGARIA; e-mail: m_apiaster@abv.bg

[3]Department of Zoology and Anthropology, Faculty of Biology, Sofia University "St. Kliment Ohridski", 8 Dragan Tsankov Blvd., 1164 Sofia, BULGARIA; e-mail: elitsa.popova@uni-sofia.bg

*Corresponding author: ndolapchiev@gmail.com

Abstract. In the period 2023-2024, on the territory of the "Sinite Kamani" Nature Park, Eastern Stara Planina, Bulgaria, the circadian and spatial activity overlap of selected predator mammals was analyzed. The aim of the study is to determine whether niche segregations are observed in the spatial and temporal relationships between mutually competing predators inhabiting the same habitats. The red fox and the badger showed the highest degree of temporal overlap - 85%. The fox and the *Martes* sp. showed 75% of temporal overlap, while the red fox and *Felis* sp. showed a lower degree overlap - 62 %. The golden jackal and the *Felis* sp. showed the lowest interspecific temporal overlap too - 62%. The *Felis* sp. and *Martes* sp. showed 63% temporal overlap. The *Felis* sp. and the badger showed 61% temporal overlap. The temporal overlap between the jackal with the red fox and the badger showed similarity temporal overlap - 71% with red fox and 74% with the badger. The golden jackal and the *Martes* sp. showed 68 % the of temporal overlap. The badger and the *Martes* sp. showed 77 % the of temporal overlap. Similar to diurnal activity, a high degree of overlap was found in spatial activity, and avoidance of one predator species to another was not found. In the conducted research, no niche segregation was found in the spatial and temporal ecological niche in the predator species with a similar food spectrum. These results provided insights for the better management of the species in the protected areas.

Key words: *Canis aureus*, *Meles meles*, *Vulpes vulpes*, interspecific competition, predators.

Introduction

Interspecific interactions between predators have major ecological consequences in shaping ecological webs and food webs in ecosystems (Polis et al., 1989). These processes are crucial for the spatial and temporal distribution of predator species (Korpimaki, 1996; Salo et al., 2008). As a result of strong competition and predation among predators, competitively weaker species are often pushed into suboptimal habitats or forced to change their temporal activity to accommodate that of competitively stronger species (Creel et al., 2001; Ritchie & Johnson, 2009).

A number of studies have described competition between predators inhabiting the same habitats. Heldin et al. (2006) described strong predation pressure by the Eurasian lynx, *Lynx lynx* (L., 1758), on the red fox, *Vulpes vulpes* (L., 1758). Berger & Gese (2007) in their research found that the presence of wolves, *Canis lupus* L., 1758, significantly reduced the abundance of coyotes, *Canis latrans* Say, 1823. Fedriani et al. (2000) found that gray foxes, *Urocyon cinereoargenteus* S., 1775, spatially avoided coyotes, which the authors found to be one of the main factors in fox mortality.

Similar examples can be cited for the influence of the Ural owl (*Strix uralensis* Pallas, 1771) having a negative impact on the spatial distribution of the smaller forest owl (*Strix aluco* L., 1758) (Korpimaki, 1996). Creel et al. (2001) found that cheetahs (*Acinonyx jubatus*) spatially avoid lions (*Panthera leo*) in their habitat.

It is because of these relationships between predators that ecologists in their scientific works argue that the segregation of ecological niches serves to reduce competition and thus facilitates the coexistence of similar species (Pianka, 1978). Increasingly, however, emphasis is placed on the role of intra-guild predation (Polis et al., 1989) and on the segregation of ecological niches as a consequence of the anti-predator behavior of prey species at risk of predation (Sih et al., 1985).

The sharing of limited resources, including for rearing offspring and food resources, is expected to induce competition between species occupying similar niches (Boer & Groningen, 1990). Physiological and behavioral adaptations would promote niche partitioning, thereby favoring coexistence between species using very similar food resources (Razgour et al., 2011; Torretta et al., 2017).

Space and time are two major components of an ecological niche. Interspecific overlap in spatiotemporal behavior may suggest interspecific competition, for example through direct interference or resource exploitation (Kronfeld-Schor & Dayan, 2003; Merson et al., 2019).

In the present study, we investigated the interaction between predators that occur in the "Sinite kamani" Nature Park. More specifically, we investigated the spatial-temporal segregation of the niches leading to the coexistence of the golden jackal (*Canis aureus*), the red fox (*Vulpes vulpes*), the badger (*Meles meles*), the pine marten (*Martes martes*) and the stone marten (*Martes foina*).

Our hypothesis was that the spatiotemporal distribution of the studied species would give rise to niche segregation, which would lead to a reduction in intrigued competition. We expected human presence in the protected area to act as a disturbance and an additional factor serving to shape niche segregation within the guild.

The obtained results will support the better management of the studied species.

Materials and methods

Study area

The "Sinite Kamani" Nature Park is located in the eastern part of Stara Planina Mtn, Bulgaria (Fig. 1), stretching in an area of 11380.1 ha (113.8 km^2). The highest peak is Bulgarka (1181 m). The climate is temperate-continental with characteristic and frequent winds from the Mediterranean region. The amplitude in absolute temperatures varies between +41°C to -20°C. In the summer, it is cool in the higher parts, and dry and hot in the lower parts. In some areas of the park in winter, snow often lingers. The maximum rainfall is in May and the minimum is in August (Dolapchiev et al., 2024).

Deciduous forests (9,000 ha) occupy most of the park's territory, and over 600 ha are occupied by conifers. Forests are characterized as monodominant and mixed. The most common are the Common beech (*Fagus silvatica*), Cornish oak (*Quercus petraea*), common hornbeam (*Carpinus betulus*), Turkish oak (*Q. cerris*), Hungarian oak (*Q. frainetto*), sycamore (*Acer pseudoplatanus*), Oriental hornbeam (*C. orientalis*), Silver lime (*Tilia tomentosa*), etc. 38 species of mammals are registered on the territory of the park, of which 24 are protected by the Bulgarian Biodiversity Act. In the areas around settlements, especially in the northern part of the town of Sliven, bordering the park a frequent presence of domestic or stray cats and free-ranging and stray dogs is detected (Dolapchiev et al., 2024).

Collection and processing of data

The data was collected in the period 7 April 2023 – 18 April 2024. Seven camera traps (Moultrie MCG 13331, Scoutguard, Sunteк) were placed opportunistically in forested areas on animal trails to maximize animal detection (Fig. 1). The total number of trap days of operational camera traps was 1781. The average altitude of the camera traps was 785 m a.s.l (lowest point 585 m and highest 1022 m). 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 Base1.6 (Tobler, 2015), modified and translated into Bulgarian. 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. This was done to deal with the overrepresentation of the same individual in multiple photos, leaving only the independent events (entries in front of the camera).

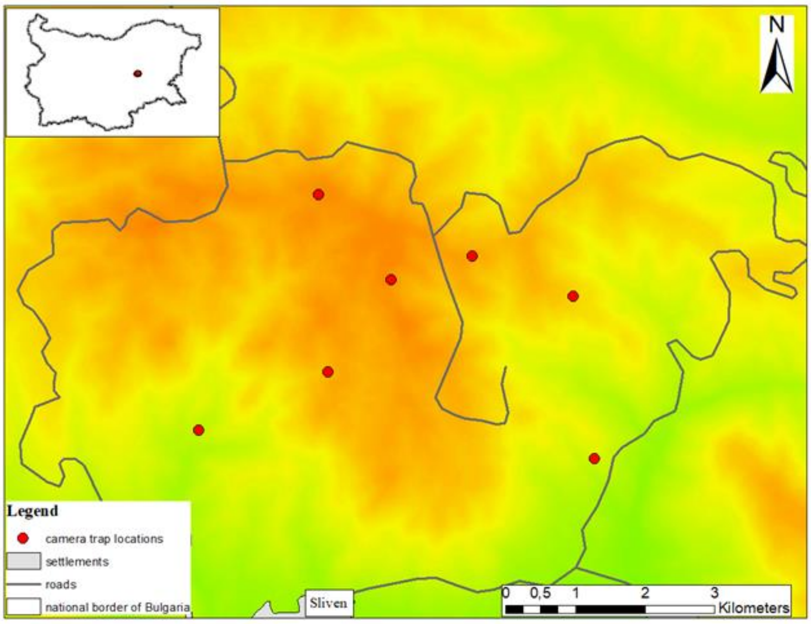

Fig. 1 Location of the „Sinite kamani" Nature Park and position of the camera traps.

Analyses

During the study period, 11334 photos and videos were collected and analyzed. Five species of predator mammals were identified (n = 3201). The total number of independent registrations of the species found was 273 (Table 1). The stone marten and pine marten live and share identical habitats (> 1000 m above sea level) in the Central and Eastern Stara Planina (Popov, 2007) To avoid the risk of misidentification of the two species (Raichev, 2018) in this study they were considered on a genus level - *Martes* sp. Similar to the procedure with the stone marten and pine marten, in order to avoid the risk of misidentification of the wild cat (*Felis silvestris*) and its hybrid form, in this study they are considered at the genus level - *Felis* sp.

The R programming language (v.4.1.1), the R Studio software, and the R package overlap were used to analyze the circadian activity and the level of its overlap (Meredith, 2022) based on non-parametric kernel density estimation (KDE) of the independent registrations. The result of this analysis is a coefficient for the degree of overlap ranging 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.

In order to account for the spatial interaction between the studied predator species, the relative frequency of registration (Detection Rate - DR) of the camera trap species was compared. Relative frequency represents the standardized number of target species recorded by camera traps, taking into account the difference in survey duration and recalculating them for 100 camera trap days. Thus, DR is calculated using the following formula (O'Brien et al., 2003):

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

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.

Table 1. Number of independent registrations from the camera traps (7 April 2023 – 18 April 2024**).**

Species	**Independent registrations**
Golden jackal *Canis aureus*	32
Red fox *Vulpes vulpes*	131
Martens *Martes* sp. (*M. martes* and *M. foina*)	57
Badger *Meles meles*	26
Cats *Felis* sp. *(Felis silvestris* and hybrids form of *Felis silvestris)*	27
Total	273

Results

Interspecific temporal relationships

The red fox and the badger (Fig. 2 C) showed the highest degree of temporal overlap - 85% (Δ = 0.85, confidence interval 0.79 – 0.95). The fox and the *Martes* sp. (Fig. 2 D) showed 75% (Δ = 0.75, confidence interval 0.66 – 0.89) of temporal overlap, while the red fox and *Felis* sp. (Fig. 2 A) showed a lower degree overlap 62% (Δ = 0.62, confidence interval 0.35 – 0.72). The golden jackal and the *Felis* sp. (Fig. 2 F) showed the lowest interspecific temporal overlap too - 62% (Δ = 0.62, confidence interval 0.35 – 0.73). The *Felis* sp. and *Martes* sp. (Fig. 2 J) showed 63% temporal overlap (Δ = 0.64, confidence interval 0.39 – 0.74). The *Felis* sp. and the badger (Fig.2 B) showed 61% temporal overlap (Δ = 61, confidence interval 0.32 – 0.67).

The temporal overlap between the jackal with the red fox and the badger showed similarity - temporal overlap 71% with red fox (Fig. 2 G) (Δ = 0.71, confidence interval 0.63 – 0.93) and 74% with the badger (Fig. 2 E) (Δ = 0.70, confidence interval 0.50 – 0.78). The golden jackal and the *Martes* sp. (Fig. 2 H) showed 68% the of temporal overlap (Δ = 0.68, confidence interval 0.56 – 0.88). The badger and the *Martes* sp. (Fig. 2 I) showed 77 % the of temporal overlap (Δ = 0.68, confidence interval 0.66 – 0.84).

Detection Rate (DR)

The detection rate amplitudes between red fox and badger calculated for each camera trap had different values. The highest are at the camera traps with the names Dolapite (Fig. 3 D) and Dragieva cheshma (Fig. 3 F). At the Dolapite camera trap (Fig. 3 D), the highest value was 54.85 for the badger and 2.99 for the red fox, at the Dragieva cheshma camera trap (Fig. 3 F), however, the red fox was 31.05 and the badger 6.21.

The detection rate between the red fox and *Martes* sp. showed the highest indicators for the red fox at the camera trap Dragieva chesma (Fig. 3 F) - 31.05 and respectively 4.14 for *Martes* sp. For *Martes* sp. the highest indicators were shown at the camera trap Mecha polyana - 92.87, as far as the red fox was 2.51 (Fig. 3 A).

The highest detection rate between the golden jackal and *Felis* sp. for the golden jackal was recorded at the camera trap Dragieva cheshma (Fig. 3 F) 22.57 and 10.35 respectively for *Felis* sp. The indicator for *Felis* sp. for this camera trap was also the highest of all others.

For the red fox and *Felis* sp., the highest spatial overlap value for the red fox was 31.05 at the Dragieva cheshma (Fig. 3 F), and 10.35 for the red fox at the same camera trap. Accordingly, this was the highest indicator of *Felis* sp. for all camera traps.

In the spatial relationships between *Felis* sp. and *Martes* sp., the highest values for *Martes* sp. were observed in the Mecha polqna camera trap (Fig. 3 A) - 92.87, and 2.51 respectively for *Felis* sp. Highest indicators for *Felis* sp. is reported at the camera trap Dragieva cheshma (Fig. 3 F) - 10.35 and 4.14 for *Martes* sp.

For *Felis* sp. and badger, as we have already mentioned above, the highest value was 10.35 for *Felis* sp. at the camera trap Dragieva chesma (Fig. 3 F), and for badger - 6.21. Accordingly, the highest value for the badger was at the Dolapite (Fig. 3 D) camera trap - 54.85, and for *Felis* sp. - 0.37.

Regarding the spatial relationships between the golden jackal and the red fox, for both species the highest values were at the Dragieva cheshma (Fig. 3 F) camera trap, with 22.57 for the golden jackal and 31.05 for the red fox.

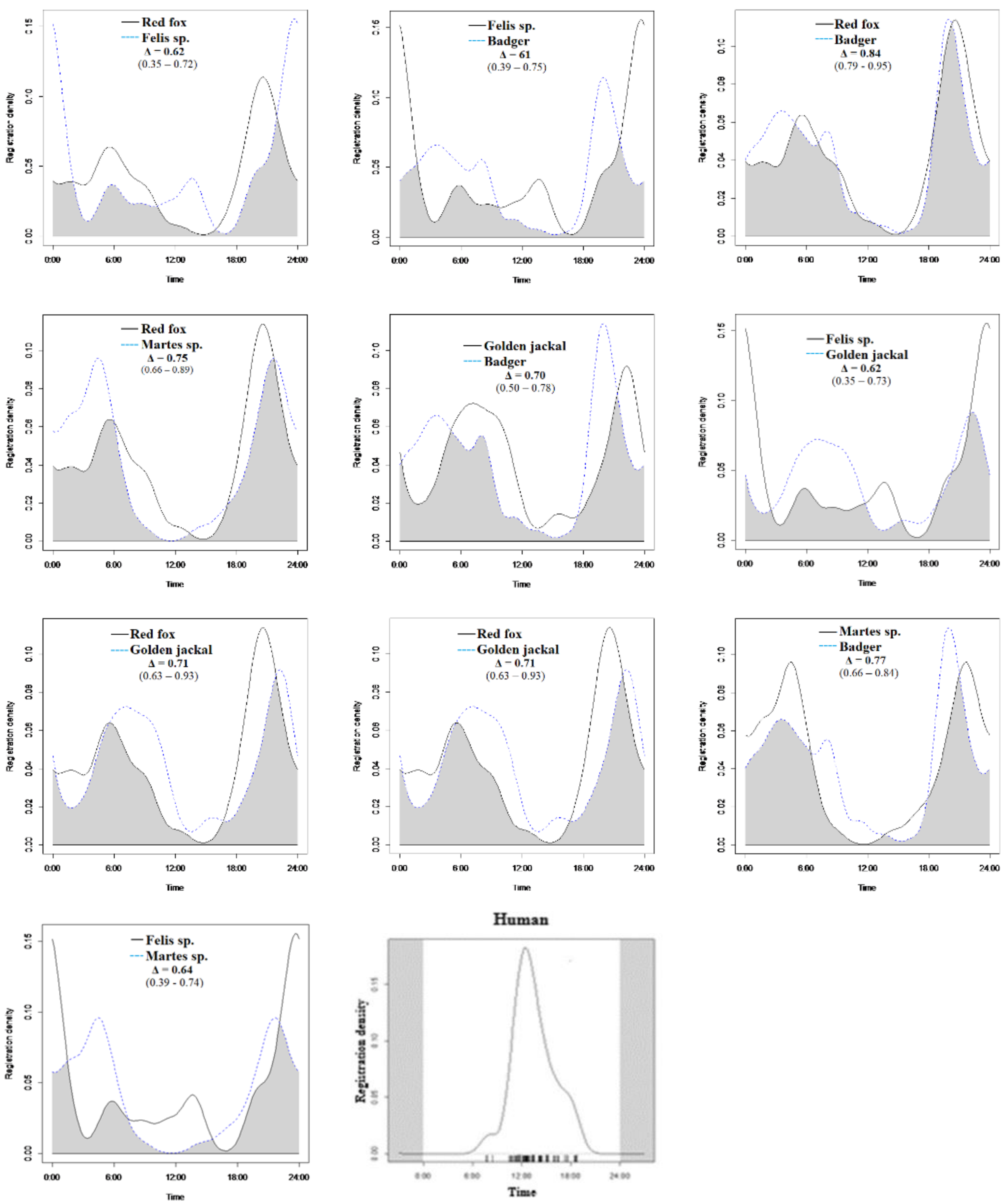

Fig. 2. Comparison of diurnal activity between different carnivore species.
A. Red fox vs *Felis* sp.; **B.** *Felis* sp. vs Badger.; **C.** Red fox vs Badger; **D.** Red fox vs *Martes* sp.; **E.** Golden jackal vs Badger; **F.** *Felis* sp. vs Golden jackal; **G.** Red fox vs. Golden jackal; **H.** Golden jackal vs *Martes* sp.; **I.** *Martes* sp. vs Badger; **J.** *Felis* sp. Vs *Martes* sp.; **K.** Human

Regarding the spatial relationships between the golden jackal and the badger, for the golden jackal the highest indicators were reported at Dragieva cheshma (Fig. 3 F) camera trap - 22.57, and for the badger - 6.21. For the badger, the highest values were reported for the Dolapite (Fig. 3 D) - 54.85, and respectively for the golden jackal of the same camera trap - 0.37.

For the golden jackal and *Martes* sp. spatial relationships, for the golden jackal the highest indicators were recorded at Dragieva cheshma (Fig. 3 F) - 22.57, and for *Martes* sp. - 4.14. For *Martes* sp., the highest values were reported at Mecha polyana - 92.87 (Fig. 3 A), and respectively for the golden jackal at the same camera trap - 2.51. Regarding the spatial relationships between the badger and *Martes* sp., the highest indicators for the badger were recorded at the camera trap Dolapite (Fig. 3 D) - 54.85, and for *Martes* sp. - 3.73. Accordingly, the highest index for *Martes* sp. was reported for Mecha Polyana (Fig. 3 A) camera trap - 92.87, and for the badger - 42.67.

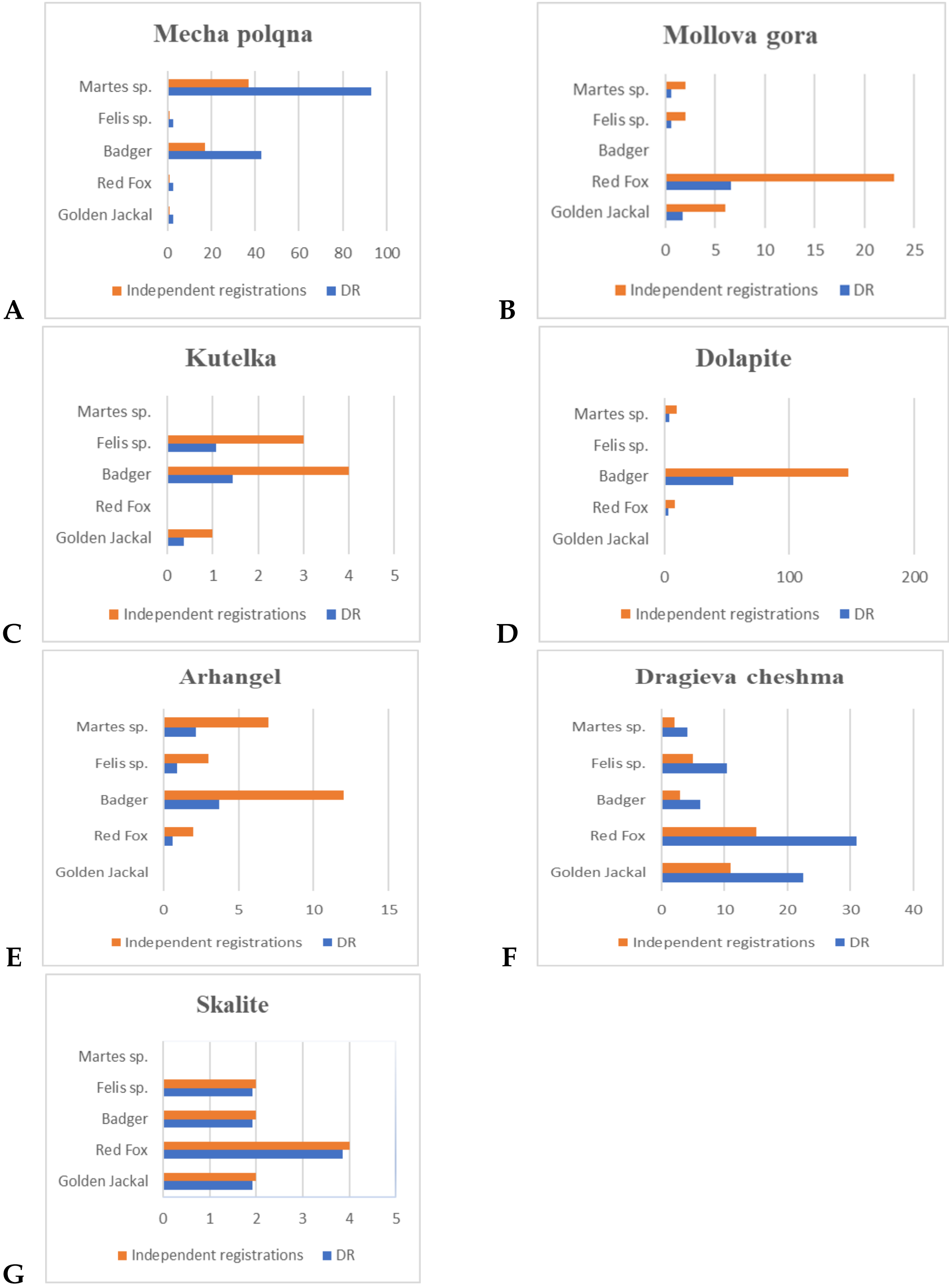

Fig. 3. DR comparison for each camera trap.

Discussion

The camera trap method is a valuable tool for objectively recording interactions between large or medium predators. Cross-sectional analyzes of the overlap of spatial and temporal activity of species help to better understand the processes that occur between them.

Resource utilization is critical for the coexistence of sympatric species or species with very close food niches (Racheva et al., 2012; Ripple et al., 2014; Kamler et al., 2003; Lanszki et al., 2016; Farkas et al., 2017; Tsunoda et al., 2020, 2022). Studies have found a separation (Fedriani et al., 1999; Scheinin et al., 2006; Kamler et al., 2003) and spatiotemporal niches (Arjo & Pletscher, 1999; Scheinin et al., 2006; Mori et al., 2020) of sympatric competing canids.

The studies of spatial interactions between the golden jackal and the red fox clearly show the tendency of the red fox to avoid the golden jackal (Scheinin et al., 2006), which was confirmed by another study (Tsunoda et al., 2020). Both studies were conducted in areas with increased human presence. In the second study, an activity overlap analysis was carried out, resulting in a 79% temporal overlap between the two species. The temporal avoidance is additionally straitened by human activity during the day shortening the strips of active time by the forced, predominantly nocturnal circadian way of life.

This also is comparable with our results - 71% (Fig. 2 G). The high levels of temporal overlap add to the high levels of food niche overlap (Scheinin et al., 2006; Farkas et al., 2017), leaving only one option for alleviating the competition - differences in spatial niches (the golden jackal's established spatial avoidance of the red fox side) (Scheinin et al., 2006; Tsunoda et al., 2020). These results differ from ours, where the golden jackal showed a lower spatial presence in front of the camera traps compared to the red fox. At four of the seven camera traps set, the red fox had higher spatial indices than the golden jackal (Fig. 3). The golden jackal showed a higher degree of spatial presence than the red fox in only one camera trap (Fig. 3).

Such a high temporal overlap (68%) was also noted in our study for the golden jackals and *Martes* sp. (Fig. 2 H). This high overlap registered in our study was not confirmed by other studies in Bulgaria (Tsunoda et al., 2020, 2022), where was demonstrated that the clear alleviation of the competition was done through spatial separation. Higher spatial but not an increase in the temporal overlap was noted only during cold seasons. In the spatial relationships in the present study, the golden jackal showed higher values in DR. In four of the seven camera traps set, the golden jackal did not show distinctly higher values than the *Martes* sp., which had a higher value than the golden jackal in three of them (Fig. 3).

Previous studies looking at red fox and pine marten relationships have described increases in pine marten density following epidemics of red fox disease, which clearly suppresses the spread of the species (Smedshaug et al., 1999; Lindstrom et al., 2018). In terms of space and time, our study did not show a distinct spatial avoidance or dominance of one of the two species over the other. In an equal number of camera traps (three each), both species had a higher DR than the other (Fig. 3). The results reflecting their day-to-day activity showed a high degree of attachment - 75% (Fig. 2 D).

A previous study conducted in southern Italy showed a high degree of overlap in the diurnal activity of the red fox and badger at 77% (Mori et al., 2020). Our research results showed an even higher degree of overlap of 84% (Fig. 2 C). Our results did not clearly show a spatial dominance of either species. The badger has a higher DR coefficient in four camera traps and the red fox in three camera traps (Fig. 3).

A previous study looking at the overlap between diurnal activity of wild cats and badgers found 61% (Mori et al., 2020). Our data showed a slightly lower value of 71% (Fig. 2 B). In the spatial activity at four of the seven camera traps set, the badger had a higher DR coefficient ~~compared to *Felis* sp.,~~ in contrast to *Felis* sp., which it had at two (Fig. 3).

The results of the overlap of diurnal activity of the *Felis* sp. and red fox species in a previous study showed 81% (Mori et al. 2020). 20% lower indicators showed the results we obtained (Fig. 2 A).

The results obtained from the spatial overlap of the two species did not show significant dominance or avoidance of one of the two species. The red fox had a higher value of DR in four of the camera trap traps, and *Felis* sp. - in three of them (Fig. 3).

In a previous study conducted in Bulgaria, the golden jackal and the badger showed 59% overlap in diurnal activity (Tsunoda et al., 2018). Our results are 11 points higher than these results (Fig. 2 E). Spatially, both species performed equally well. Both the golden jackal and the badger were present in more than three camera traps, where they had higher DR values (Fig. 3). The results clearly showed a lack of spatial avoidance in either species.

The results obtained in a previous study carried out on the territory of Bulgaria showed almost identical results in the overlapping of the daily activity of the golden jackal and the wild cat - 62% (Tsunoda et al., 2020), as ours showed 61% (Fig. 2 F). Spatially, the two species did not show avoidance or displacement of each other at the observed camera traps. Both species had significantly more registrations than each other in two camera traps (Fig. 3).

The overlap in the diurnal activity of the *Martes* sp. and the badger was 77% (Fig. 2 I). A 7% higher value is obtained in other research conducted in Bulgaria - 84% (Tsunoda et al., 2020). Spatially, the badger showed clearly higher values of DR compared to the *Martes* sp. in five of the seven photo traps placed (Fig. 3).

Diurnal activity of the target species for the study was mainly concentrated in the dark hours of the day, which led to a high degree of overlap.

The main reason for this is the human factor in the studied region, expressing in an increased tourist flow concentrated mainly in the daylight part of the day (Dolapchiev et al., 2024).

In the present study, no niche segregation was found in the studied species. The results of a previous study in the same region showed that human presence during daylight hours is the leading factor in shaping the circadian activity of mammal species in the "Sinite kamani" Nature Park (Dolapchiev et al., 2024). Both in the previous and in the present study, the diurnal activity of the species is mainly concentrated in the dark part of the day (Fig. 2). Human activity is cyclical (Fig. 2 K) (only in one time range - the light part of the day) and clearly therefore, in an effort to avoid man when he is not active, carnivores are active in the dark part of the day. As a consequence, no temporal niche segregation of species with a close food spectrum could be observed. No temporal avoidance of one predator to another was observed. As a result, the temporal overlap between different carnivore species was over 60%, ranging from 61% between *Felis* sp. and the badger (Fig. 2 B) up to 84% between the red fox and the badger (Fig. 2 C).

Niche segregation was also not observed in the spatial relationships of the studied predators. Spatial avoidance was not detected in the predators towards each other.

Our hypothesis of segregation of the spatial and temporal ecological niches of the studied species was not confirmed. None of the studied species showed avoidance or dominance over other species, both temporally and spatially. The collected information will serve for a better management of the studied species on the territory of the "Sinite kamani" Nature Park.

Conclusions

The results of our study gave reason to reject the hypothesis of segregation of the ecological niches of predators inhabiting the same habitats in the "Sinite kamani" Nature Park.. When studying the temporal activity, no clear avoidance of one predator species towards another was noted. The results of the analysis of spatial activity were similar. It is planned to study the nutritional ecological niche of predator species with a similar nutritional spectrum in the next stage of our study.

Acknowledgments

This work was partially supported by the Bulgarian Ministry of Education and Science under the National Research Programme "Young scientists and postdoctoral students -2" approved by DCM 206 / 07.04.2022

References

Arjo, W., & Pletscher, D. (1999). Behavioral responses of coyotes to wolf recolonization in northwestern Montana. *Canadian Journal of Zoology*, 77(12), 1919–1927. doi: 10.1139/z99-177

Berger, K., & Gese, E. (2007). Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology*, 76(6), 1075–1085. doi: 10.1111/j.1365-2656.2007.01287.x

De Boer, W., & Groningen, R. (1990). Large herbivores that strive mightily but eat and drink as friends. *Oecologia*, 82(2), 264–274, doi: 10.1007/BF00323544

Creel, S., Spong, G., & Creel, N. (2001). Interspecific competition and the population biology of extinction-prone carnivores. In: Gittleman, J.L., Funk, S.M., Macdonald, D., & Wayne, R.K. (eds.) *Carnivore conservation*. Cambridge University Press, 35–60.

Dolapchiev, N., Zlatanova, D., Georgiev, D., & Popova, E., (2024). Human Presence as a Factor Determining the Circadian Activity of Mammal Species in the Sinite Kamani Nature Park. *Acta Zoologica Bulgarica*, 76(2), 187-196.

Farkas, A., Jánoska, F., Fodor, J., & Náhlik, A. (2017). The high level of nutritional niche overlap between red fox (*Vulpes vulpes*) and sympatric golden jackal (*Canis aureus*) affects the body weight of juvenile foxes. *European Journal of Wildlife Research*, 63(3), 46, doi: 10.1007/s10344-017-1101-x

Fedriani, J., Fuller, T., Sauvajot, R., & York, E. C. (2000). Competition and intraguild predation among three sympatric carnivores. *Oecologia*, 125(2), 258–270. doi: 10.1007/s004420000448

Fedriani, J., Palomares, F., & Delibes, M. (1999). Niche relations among three sympatric Mediterranean carnivores. *Oecologia*, 121(1), 138–148. doi: 10.1007/s004420050915

Helldin, J., Liberg, O., & Glöersen, G. (2006). Lynx (*Lynx lynx*) killing red foxes (*Vulpes vulpes*) in boreal Sweden - Frequency and population effects. Journal of Zoology, 270(4), 657–663. doi: 10.1111/j.1469-7998.2006.00172.x

Kamler, J., Ballard, W., Gilliland, R., Lemons II, P.R., & Mote, K. (2003). Impacts of Coyotes on Swift Foxes in Northwestern Texas. *The Journal of Wildlife Management*, 67(2), 317–323. doi: 10.2307/3802773

Hakkarainen, H., & Korpimaki, E. (1996). Competitive and predatory interactions among raptors: an observational and experimental study. *Ecology*, 77(4), 1134-1142. doi: 10.2307/2265582

Kronfeld-Schor, N., & Dayan, T. (2003). Partitioning of Time as an Ecological Resource. *Annual Review of Ecology, Evolution, and Systematics*, 34, 153–181. doi: 10.1146/annurev.ecolsys.34.011802.132435

Lanszki, J., Kurys A., Szabó, L., Nagyapáti, N., Porter, L., & Heltai, M. (2016). Diet composition of the golden jackal and the sympatric red fox in an agricultural area (Hungary). *Folia Zoologica*, 65(4), 310–322, doi: 10.25225/fozo.v65.i4.a3.2016

Lindström, E., Brainerd, S.M., Helldin, J.O., & Overskaug, K. (1995). Pine marten — red fox interactions : a case of intraguild predation ? *Annales Zoologici Fennici*, 32(1), 123-130.

Merson, S.D., Dollar, L.J., Tan, C.K.W., & Macdonald, D.W. (2019). Activity patterns of sympatric living exotic and endemic carnivores (the fosa) in Western Madagascar's deciduous forests. *Journal of Zoology*, 307(3), 186–194. doi: 10.1111/jzo.12630

Mori, E., Bagnato, S., Serroni P., Sangiuliano, A., Rotondaro, F., Marchianò, V., Cascini, V., Poerio, L., & Ferretti, F. (2020). Spatiotemporal mechanisms of coexistence in an European mammal community in a protected area of southern Italy. *Journal of Zoology*, 310(3), 232–245. doi: 10.1111/jzo.12743

Pianka, E. (1978). *Evolutionary Ecology*. Harper and Row, New York, Hagerstown, San Francisco, London, 398 p.

Polis, G.A., Myers, C.A., & Holt, R.D. (1989). The Ecology and Evolution of Intraguild Predation : Potential Competitors That Eat Each Other. *Annual Review of Ecology and Systematics*, 20, 297–330. doi: 10.1146/annurev.es.20.110189.001501

Racheva, V., Zlatanova, D., Peshev D., & Markova, E. (2012). Camera traps recorded use of sett sites by badgers (*Meles meles* L., Mammalia) in different habitats. *Acta Zoologica Bulgarica*, 64(2), 145–150.

Razgour, O., Korine, C., & Saltz, D. (2011). Does interspecific competition drive patterns of habitat use in desert bat communities? *Oecologia*, 167(2), 493–502. doi: 10.1007/s00442-011-1995-z

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., & Wirsing, A.J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, 343(6167), 1241484. doi: 10.1126/science.1241484

Ritchie, E.G., & Johnson, C.N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, 12(9), 982–998. doi: 10.1111/j.1461-0248.2009.01347.x

Salo, P., Nordström M., Thomson, R.L., & Korpimäki, E. (2008). Risk induced by a native top predator reduces alien mink movements. *Journal of Animal Ecology*, 77(6), 1092–1098. doi: 10.1111/j.1365-2656.2008.01430.x

Scheinin, S., Yom-Tov, Y., Motro, U., & Geffen, E. (2006). Behavioural responses of red foxes to an increase in the presence of golden jackals: A field experiment. Animal Behaviour, 71(3), 577–584. doi: 10.1016/j.anbehav.2005.05.022

Sih, A., Crowley, P., McPeek, M., Petranka, J., & Strohmeier, K. (1985). Predation, competition, and prey communities: a review of field experiments. *Annual Review of ecology and systematics*, 16, 269–311. doi: 10.1146/annurev.es.16.110185.001413

Smedshaug, C.A., Selås, V., Lund, S.E., & Sonerud, G. A. (1999). The effect of a natural reduction of red fox *Vulpes vulpes* on small game hunting bags in Norway. *Wildlife Biology*, 5(3), 157–166. doi: 10.2981/wlb.1999.020

Torretta, E., Mosini, A., Piana, M., Tirozzi, P., Serafini, M., Puopolo, F., Saino, N., & Balestrieri, A. (2017). Time partitioning in mesocarnivore communities from different habitats of NW Italy: Insights into martens' competitive abilities. *Behaviour*, 154(2), 241–266. doi: 10.1163/1568539X-00003420

Tsunoda, H., Ito, K., Peeva, S., Raichev, E., & Kaneko, Y. (2018). Spatial and temporal separation between the golden jackal and three sympatric carnivores in a human-modified landscape in central Bulgaria. *Zoology and Ecology*, 28(3), 172–179. doi: 10.1080/21658005.2018.1504406

Tsunoda, H., Newman, C., Peeva S., Raichev, E., Buesching, C. D., & Kaneko, Y. (2020). Spatio-temporal partitioning facilitates mesocarnivore sympatry in the Stara Planina Mountains, Bulgaria. *Zoology*, 141, 125801. doi: 10.1016/j.zool.2020.125801

Tsunoda, H., Peeva, S., Raichev, E., Kronawetter, T., Kirilov, K.B., Georgiev, D., & Kaneko, Y. (2022). Patterns of spatial distribution and diel activity in carnivore guilds (Carnivora). *Journal of Vertebrate Biology*, 71, 22018. doi: 10.25225/jvb.22018

Received: 07.08.2024
Accepted: 08.11.2024