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RESEARCH PAPER

Patterns of spatial distribution and diel activity in carnivore guilds (Carnivora)

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Abstract. In mammalian carnivore guilds (order Carnivora), spatiotemporal partitions play a major role in reducing competitive confrontations and facilitating successful sympatry. Using camera-trapping techniques, the present study aimed to elucidate patterns of spatial distribution and diel activities among medium- and large-sized carnivore species across central Bulgaria. We obtained 3,364 images of nine focal carnivores from 13,988 camera-trapping days between 2015 and 2020. Our findings indicated that the spatial distribution of the focal carnivore guilds varied with changes in altitudinal gradient, ruggedness, and forest-agricultural landscape changes. Specifically, the two largest species, the grey wolf (*Canis lupus* Linnaeus, 1758) and the brown bear (*Ursus arctos* Linnaeus, 1758), were found only in the Balkan Mountains, whereas the largest mesocarnivore, the golden jackal (*Canis aureus* Linnaeus, 1758), was mainly distributed agricultural lowlands. The European wildcat (*Felis sylvestris* Schreber, 1777) was found in forests inside protected areas, and other mesocarnivores were distributed at intermediate levels between wooded-mountains and agricultural lowlands. Brown bear, golden jackal, and domestic dog (*Canis lupus familiaris* Linnaeus, 1758) showed cathemeral, crepuscular, and diurnal activity, respectively, whereas the remaining six carnivores showed nocturnal activity in synchrony with their main prey. Our findings indicated that anthropogenic landscape modifications and potential interspecific competition resulted in patterns of spatial distribution and temporal activity in this carnivore guild.

Key words: competition, daily activities, intraguild, landscape modifications, niche partitioning

Introduction

Mammalian carnivores typically occupy higher trophic levels and broadly affect ecosystem dynamics through trophic cascades (Ripple et al. 2014), understanding their community structure is fundamental to the development of conservation planning (Ritchie & Johnson 2009). In terrestrial carnivore guilds, both direct interference (e.g. killing and harassment) and resource competition among sympatric carnivores constrain the survival, fecundity, and eco-behavioural patterns of each

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species, affecting population dynamics as well as shaping community structure (Linnell & Strand 2000, Ritchie & Johnson 2009). According to the theory of competitive exclusion (Hardin 1960) and the niche variation hypothesis (Bolnick et al. 2007), competitive species need to partition their ecological niches to achieve sympatry in an environment. Partitioning of niches for food, use of space, and activity time in predator guilds is fundamental for the coexistence of multiple species (Schoener 1974, Amarasekare 2003). However, sympatric mammalian carnivores show substantial overlap in their trophic niches and share common resources (Manlick & Pauli 2020, Lanszki et al. 1999). Thus, spatial and temporal partitions play major roles in reducing competitive confrontations and facilitating successful sympatry (Monterroso et al. 2014, Karanth et al. 2017, Tsunoda et al. 2020).

Niche partitioning within a carnivore guild is affected by the availability of regional resources, landscape structure, and anthropogenic disturbances (Seveque et al. 2020, Manlick & Pauli 2020). For example, seasonal scarcity of food resources increases trophic overlap among competitive mesocarnivores, facilitating their spatiotemporal partitioning (Tsunoda et al. 2020). Further, anthropogenic landscape modifications decrease large canid and felid predators and allow dominance of superior competitors or introduced species, altering the spatiotemporal partitioning among the subordinate mesocarnivores (Wang et al. 2015, Tsunoda et al. 2018, Carricondo-Sanchez et al. 2019). Anthropogenic landscape alterations are major drivers of the depletion of available resources and eco-behavioural modification in wild animals (Bateman & Fleming 2012). Therefore, regional scale assessment of spatiotemporal patterns and intraguild interactions in carnivore guilds associated with environmental and landscape gradients is a central interest for conserving regional biodiversity (Ritchie & Johnson 2009).

The present study aims to elucidate patterns in spatial distribution and diel activities among medium- and large-sized species in carnivore guilds across central Bulgaria. Although there have been some local-scale observations of spatiotemporal partitioning among mesocarnivores in this study region (Georgiev et al. 2015, Tsunoda et al. 2018, 2020), no previous assessment has been made at a regional scale. We hypothesized that spatial and temporal patterns in carnivore guilds might be associated with geo-environmental conditions, anthropogenic landscape modifications (e.g. less forested cover) as well as intraguild competition. To test our hypothesis, we investigated distributional patterns and diel activities among carnivores by analysing camera-trapping data from various altitudinal and landscape areas.

Study area

The study area is in central Bulgaria, including the Upper Thracian Plain and the three surrounding mountains, the Central Stara Planina, the Sredna Gora, and the Eastern Rhodopes (Fig. 1). The climate across the region is transitional between moderate-continental and continental-Mediterranean, but is cooler in high-altitude areas of the Central Stara Planina Mountains (> 1,000 m a.s.l) (Velikov & Stoyanova 2007). Vegetation and land use vary according to altitude. Lowland areas up to 500 m a.s.l. are a mosaic of agricultural fields, orchards, pastures, buildings, oriental hornbeam shrublands

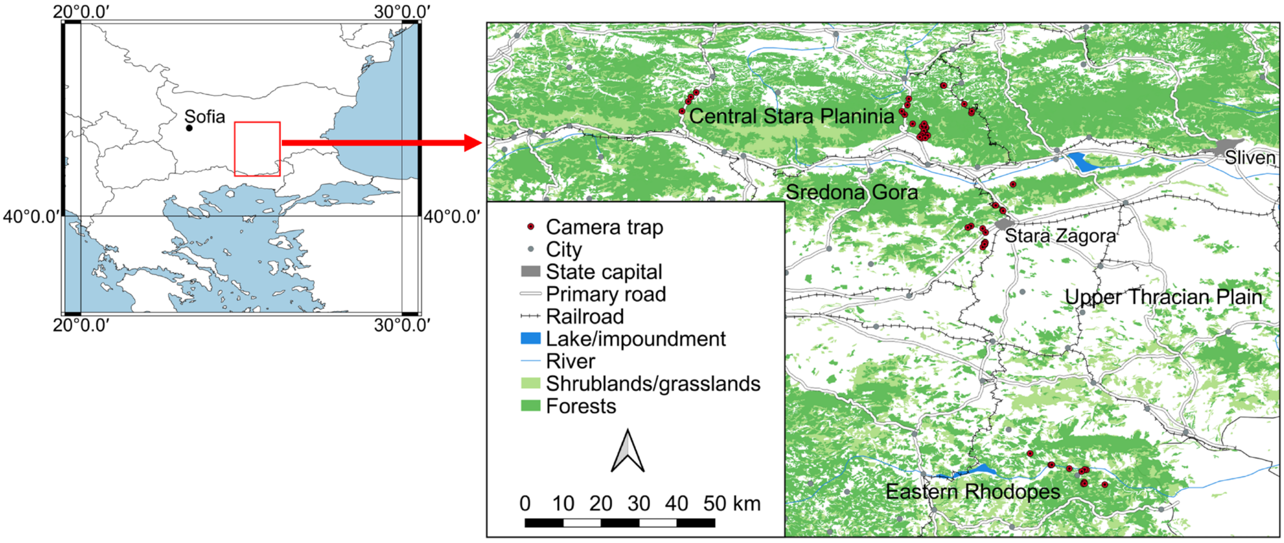

Fig. 1. Location of the study area and camera-trapping stations in central Bulgaria.

(*Carpinus orientalis* Mill.), and patches of oak (*Quercus dalechampii* Ten.) forest. Mountainous areas from 500 to 800 m a.s.l. are predominantly covered by secondary oak forests (*Quercus* spp.) and black pine (*Pinus nigra* J.F. Arnold) plantations, with natural beech forests (*Fagus sylvestris* L.) at higher elevations. On the basis of a faunal analysis using mammalian inventory records (Popov 2007), two zoogeographic zones in the study region are suggested: the western-central mountainous subdistrict and the southern lowland subdistrict.

Material and Methods

Camera-trapping

The focal species of the present study are six medium-sized (body mass < 15 kg) carnivores (golden jackal *Canis aureus* Linnaeus, 1758, European badger *Meles meles* Linnaeus, 1758, red fox *Vulpes vulpes* Linnaeus, 1758, European wildcat *Felis sylvestris* Schreber, 1777, pine marten *Martes martes* Linnaeus, 1758; and stone marten *Martes foina* Erxleben, 1777) and two large-sized carnivores (grey wolf *Canis lupus* Linnaeus, 1758 and brown bear *Ursus arctos* Linnaeus, 1758). We also included domestic dogs (*C. lupus familiaris* Linnaeus, 1758) and cats (*Felis catus* Linnaeus, 1758), which are typically free-roaming in human-modified landscapes (Vanak & Gompper 2010, Krauze-Gryz et al. 2012, Gil-Sanchez et al. 2015). The Eurasian lynx (*Lynx lynx* Linnaeus, 1758) has been extirpated and is not currently found in this region (Popov 2007). Smaller mustelids, such as weasels and polecats (genus *Mustela* and *Vormela*), were excluded because our camera-trapping method would not adequately detect these small species and underestimated their abundance (Glen et al. 2013, Meek et al. 2014; for the details of camera-trapping, see below). Pine and stone martens both live in the high-altitude zone (> 1,000 m a.s.l.) in the Central Stara Planina (Popov 2007, Raichev 2018). It was difficult to distinguish the two marten species from camera-trapping data, which typically consist of black and white images (Tsunoda et al. 2020). Therefore we treated the two martens as a single category, *Martes* sp., in this study.

We recorded the spatial occurrence and periods of activity of the focal carnivores in four camera-trapping campaigns between 2015 and 2020. In the first campaign, we conducted camera-trapping from May 2015 to August 2016 in the Upper Thracian Plain and low-elevational zones of the Sredona Gora Mountains (Table 1). In this area, a total of eight cameras were located in forest or shrub patches in agricultural lowlands in the Upper Thracian Plain (< 300 m a.s.l.) and oak forests in foothills of the Sredona Gora Mountains (300-400 m a.s.l.). In the second and third campaigns, we conducted the surveys from July 2016 to September 2017 on the southern slopes and from September 2018 to November 2019 on the northern slopes of the Central Stara Planina Mountains, respectively (Table 1). A total of 15 cameras were located in oak/beech forests at different elevational levels (500-650 m, 650-800 m, 800-1,000 m, 1,000-1,200 m and > 1,200 m a.s.l.) in each campaign. In the fourth campaign, we conducted surveys from June 2019 to March 2020 in the River Arda valley (150-500 m a.s.l.) in the Eastern Rhodopes (Table 1). A total of 11 cameras were located in forest or shrubs in the studied area. Camera-trapping stations were located along animal trails and, therefore, were nonuniformly spaced owing to steep terrain in mountainous sites or highly fragmented forest patches in human-dominated landscapes. Each camera was mounted on a tree approximately 1.0-1.5 m above the ground, without bait or scent lures, and was placed at an angle to take pictures of medium- and large-sized animals. We used three models of passive infrared cameras (Keep Guard Cam KG690NV, Keepway Industrial Inc.; Ltl Acorn 6310-3G, Zhuhai Ltl Acorn Electronics Inc.; SG560K-14mHC, BMC Inc.), with trigger speeds ranging from 0.8 to 1.2 s. The cameras were programmed to take three pictures in a capture event with a 5 min delay. Batteries were changed and memory cards were replaced at intervals of two weeks to three months. In order to check on thefts or damage by humans, we inspected cameras located in agricultural lowlands more frequently than those in mountainous areas. We identified all animal images to species level if possible and recorded the time and date of the capture. We excluded unclear photos from statistical analyses. When we found consecutive images of the same species within 30 min at a station, we treated them as a single capture event.

Although we aimed to locate the camera-trapping stations at least 500 m apart, some cameras were located less than 500 m from each other (by straight-line distance) because of steep slopes, winding roads, or zigzag footpaths or trails in the studied sites of the Central Stara Planina and the Eastern Rhodopes (e.g. Tsunoda et al. 2020). We also relocated cameras to prevent theft when we found images of humans passing, specifically in the study site of the Upper Thracian Plain (Tsunoda et al. 2018). In those cases, we summed data from cameras located < 500 m apart to reduce the effects of spatial autocorrelation by spatially biased camera-trapping (Meek et al. 2014). Following this procedure, we obtained data from a total of 42 camera-trapping stations (Table 1).

Acquisition of data on geo-environmental parameters

We recorded and obtained coordinates and altitudinal data for each camera-trapping station using a portable GPS device (eTrex20, Garmin Inc.). For landscape features, we estimated the relative cover area (%) of forest, shrubland-grassland, cropland-pasture, and artificial constructions (e.g. houses and buildings) within a surrounding buffer zone of 500 m radius (0.785 km^2 area) from each camera-trapping station. To estimate the relative land cover area, we used land cover data from open-sourced CORINE Land Cover (CLC) 2012 (Copernicus Land Monitoring Service, https://land.copernicus.eu/ pan-european/corine-land-cover) and QGIS ver. 3.10 (QGIS Development Team, http://qgis.org/). We also estimated ruggedness within the 500 m-radius buffer of each camera-trapping station using open-sourced data of digital elevation model (DEM) with a 25 m resolution (EU-DEM v1.1; Copernicus Land Monitoring Service, https://land.copernicus.eu/ imagery-in-situ/eu-dem) and QGIS. When two or more camera-trapping stations were located within a 500 m buffer radius (the criterion for removing the effects of spatial autocorrelation), we estimated the average values for altitude and land cover area. We checked whether our camera stations were located inside protected areas (i.e. national or nature parks) using open-sourced data of Natura 2000 sites (European Environmental Agency; https://www.eea. europa.eu/data-and-maps).

Statistical analysis

We analysed spatial distribution patterns of the carnivore species using a non-metric multidimensional scaling (NMDS) method with Bray-Curtis matrix. For standardization of sampling efforts, we calculated the number of observations per camera-day for each camera-trapping station for the nine focal carnivores as variables for the NMDS analysis. To assess factors associated with carnivore distribution patterns, we then fitted eight covariates for altitude, ruggedness, land cover (the relative proportion of forest, shrubland-grassland, cropland-pasture, or artificial construction coverage), camera locations inside/outside protected areas, and direct human activities (observations per camera-day of humans and domestic animals such as cows, horses and goats) (Mori et al. 2020) as vectors onto the NMDS ordination plot. Prior to the analyses, we checked multicollinearity among numerical parameters of the vectors (i.e. other than "camera locations inside/ outside of protected areas" as nominal scale) using Spearman's correlation and variance inflation factor

Table 1. Overview of camera-trapping campaigns in the present study.

Project ID	Study area (size)	Sampling duration	Elevational range of camera stations	Station number	Camera number	Camera-days
1	Upper Thracian Plain and Sredona Gora Mountains (112.5 km^2)	May 2015-August 2016	201-361 m	10	8	431
2	Southern slope, Central Stara Planina Mountains (14.9 km^2)	Jul 2016-September 2017	581-1,250 m	10	15	6612
3	Northern slope, Central Stara Planina Mountains (65.5 km^2)	September 2018-November 2019	554-1,470 m	14	15	5238
4	Valley of Eastern Rhodope Mountains (84.6 km^2)	Jun 2019-March 2020	171-499 m	8	11	1,707

Table 2. Sum of images captured (per 100 camera-trapping days) and total number of observed stations (proportions per total 42 stations) by camera-trapping of the focal carnivore species studied in central Bulgaria.

Family	Common name	Latin name	Sum of images captured (/100 camera-trapping days)	No. of observed stations (% of 42 stations)
Ursidae	Brown bear	*Ursus arctos*	13 (0.09)	7 (16.7)
Canidae	Grey wolf	*Canis lupus*	8 (0.06)	2 (4.8)
	Domestic dog	*Canis lupus famirialis*	60 (0.43)	15 (35.7)
	Golden jackal	*Canis aureus*	847 (6.05)	30 (71.4)
	Red fox	*Vulpes vulpes*	576 (4.12)	34 (81.0)
Mustelidae	European badger	*Meles meles*	1,108 (7.92)	36 (85.7)
	Pine and stone martens	*Martes martes, Martes foina*	425 (3.04)	34 (81.0)
Felidae	European wildcat	*Felis silvestris*	271 (1.94)	32 (76.2)
	Domestic cat	*Felis catus*	56 (0.40)	8 (19.0)

(VIF). These analyses were performed using R 4.1.3 (R Core Team 2022) and the "vegan" package (Oksanen et al. 2020) for R.

We estimated diel activities of focal species using Kernel density interference (Ridout & Linkie 2009) for the time of day (0:00-23:59) that the animal images were captured, and transformed into circular data (0-2π). In this analysis, we pooled the data from all camera-trapping stations. For this analysis, we used the "overlap" package (Meredith & Ridout 2021) for R.

Results

We obtained a total of 3,364 images of the nine focal carnivores from 13,988 camera-trapping days across 42 stations between 2015 and 2020. The species most frequently detected was the European badger, with

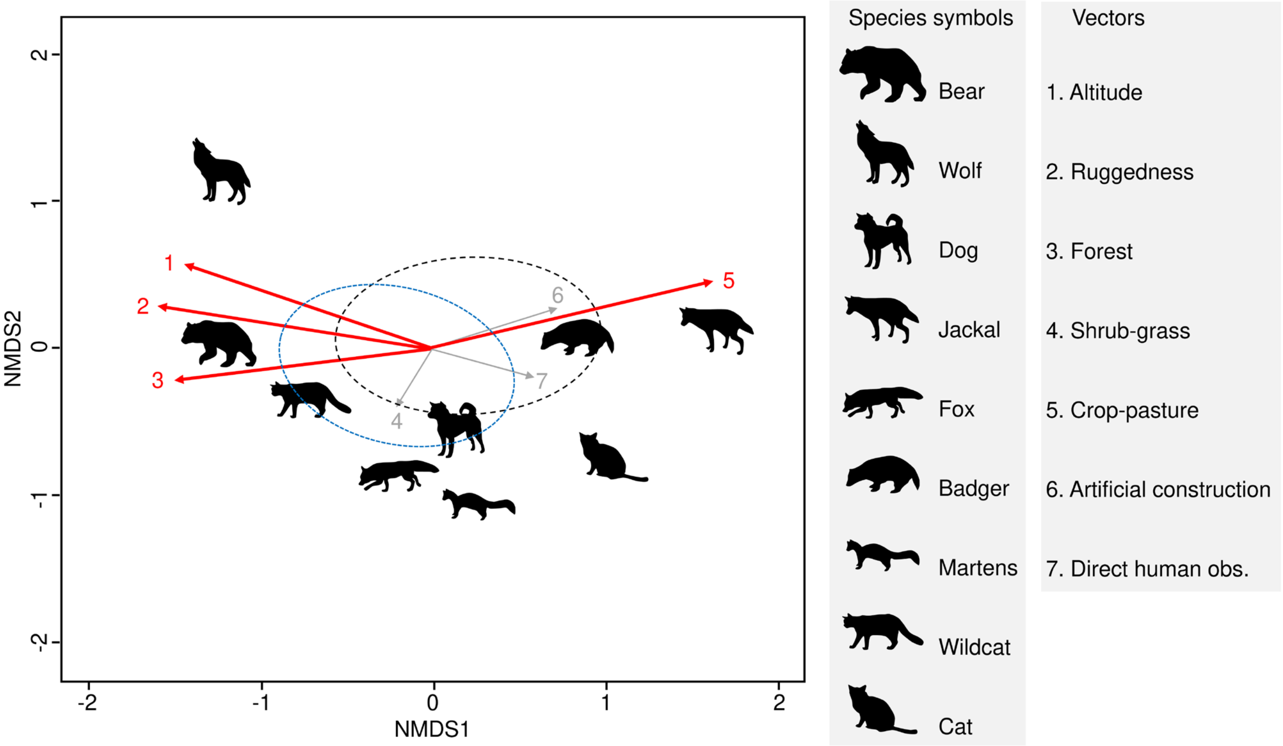

Fig. 2. Ordination plots of non-metric multidimensional scaling (NMDS) on carnivore species composition observed by camera-trapping in central Bulgaria (stress value = 0.153), fitted with environmental and anthropogenic vectors (indicated by arrows and ellipses) of camera-trapping stations. Red arrows represent vectors with statistical significance ($P < 0.001$), and grey arrows represent nonsignificant vectors ($P > 0.05$). Blue-dotted and black-dashed ellipses represent inside and outside protected areas, respectively.

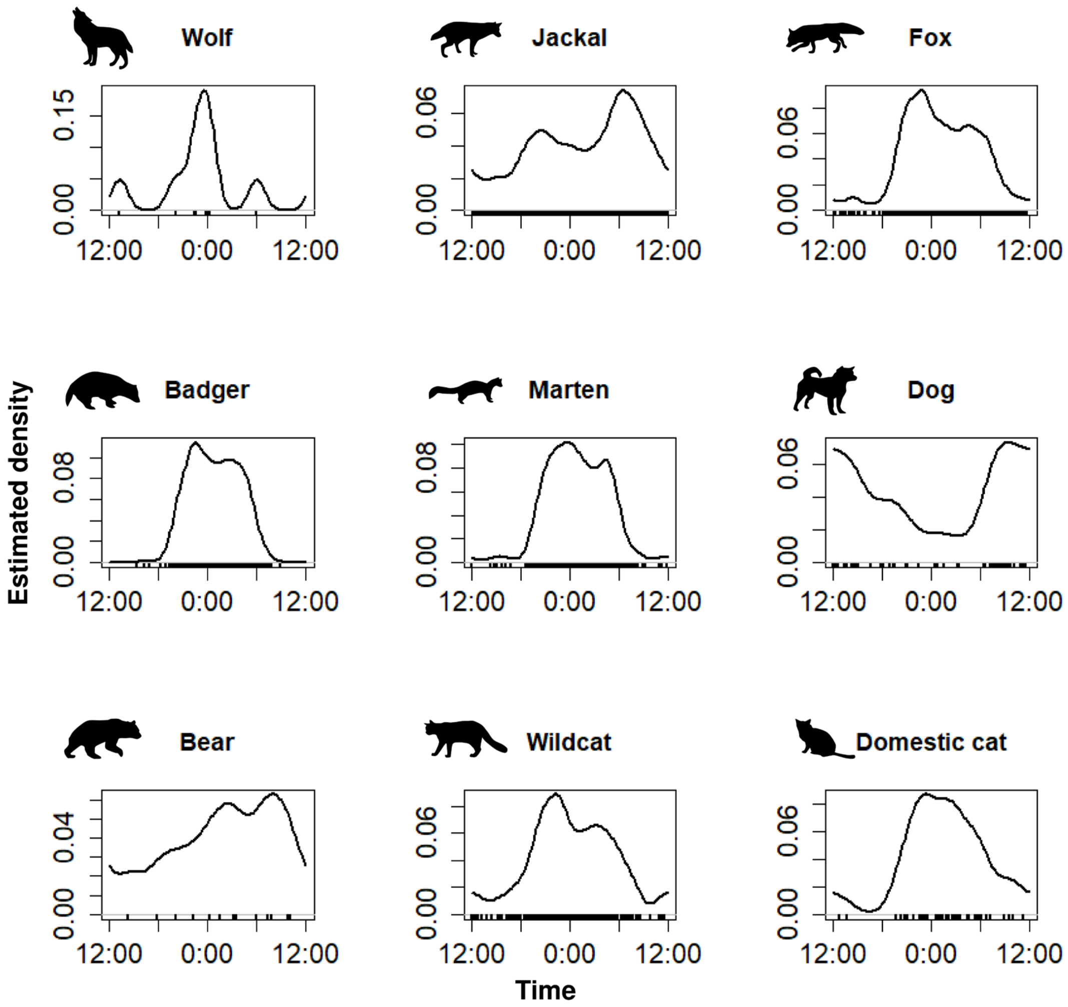

Fig. 3. Diel activity patterns (estimated using Kernel's density) of nine carnivore species observed by camera-trapping in central Bulgaria. The centre of the x-axis represents midnight. Vertical bars represent time (minutes) when the animals were observed.

1,108 independent events, and the least frequently detected was the wolf, with eight independent events (Table 2).

Although there were relatively high correlations ($r > |0.7|$) among some parameters (e.g. altitude-ruggedness and forests-croplands/pastures), the low VIF values (< 2.5) indicated little multicollinearity (Table S1). With regard to spatial distribution patterns, the NMDS ordination plot indicated that the compositions of the focal carnivore guilds were different along the NMDS axis 1 (with stress value = 0.153), which was significantly associated with altitudinal gradients, ruggedness, forest cover and cropland-pasture surrounding the camera-trapping stations ($P < 0.001$; Fig. 2 and Table 3). Three of the focal species; grey wolf, brown bear, and European wildcat, were mainly distributed in forested mountains, while the golden jackal, European badger, and domestic cat were distributed in agricultural lowland habitats (Fig. 2 and Fig. S1). The remaining three carnivores (domestic dog, red fox, and martens) were mainly distributed in sites with intermediate levels of altitude, ruggedness and forest/agricultural coverage (Fig. 2). Moreover, camera locations inside/outside of protected areas showed marginal significance (P = 0.075; Table 3), indicating both wildcat and domestic dog were more frequently observed at camera stations inside protected areas (Fig. 2).

With regard to diel activity, six of the focal carnivores (grey wolf, red fox, European badger, martens, European wildcat, and domestic cat) had mostly nocturnal patterns (Fig. 3). The remaining three species had different patterns of diel activity. The brown bear was cathemeral, the golden jackal was crepuscular, and the domestic dog was diurnal (Fig. 3).

Discussion

The present study showed low detection rates for the two largest species, the grey wolf and brown bear, by camera-trapping survey. This outcome was

Table 3. Results of non-metric multidimensional scaling (NMDS) scores (axes 1 and 2) on carnivore guilds fitting with geological, landscape and anthropogenic variables.

Variable	NMDS 1	NMDS 2	R^2	*P*
Altitude (m)	−0.925	0.380	0.353	< 0.001
Ruggedness	−0.985	0.175	0.379	< 0.001
Forest coverage (%)	−0.991	−0.133	0.331	< 0.001
Shrub-grassland coverage (%)	−0.481	−0.877	0.0263	0.602
Cropland-pasture coverage (%)	0.962	0.274	0.418	< 0.001
Artificial construct coverage (%)	0.931	0.364	0.084	0.179
Direct anthropogenic activities*	0.942	−0.338	0.057	0.318
Inside/outside of protected area**	-	-	0.063	0.075
(Inside of protected area)	−0.214	−0.108	-	-
(Outside of protected area)	0.195	0.098	-	-

* Observations of humans and domestic ungulates (cows, horses and goats) per camera-trapping days. ** Nominal scale.

similar to the result from a previous study conducted in the Osogovo Mountains on the Bulgarian-North Macedonian border (Zlatanova & Popova 2018). Low detectability of these large carnivores was typically owing to their large home-range sizes and low occurrence rates at a given trapping station (Chutipong et al. 2014). Baits or lures at camera-trapping stations potentially improve the detectability of large carnivores (Satterfield et al. 2017) with potential to alter their behavioural responses (Meek et al. 2014). For this reason, we decided not to use baits or lures in the present study. Although our sample sizes were small for these two species, we reported them in this study because there was little information on the spatial distributions and daily activity in central Bulgaria.

Our findings indicated that the spatial distribution of the focal carnivore guilds varied with changes in altitudinal gradient, ruggedness and landscape features. The results of NMDS indicated that the two largest species, the grey wolf and brown bear, might be associated with forest, high altitudes and ruggedness, consistent with previous reports from other study sites in Bulgaria (Zlatanova & Popova 2013, Gavrilov et al. 2015). These species are typically intolerant of anthropogenic landscape modifications, such as urbanization, intensive farming, and habitat fragmentation (Cimatti et al. 2021). In contrast to the large carnivores, the golden jackal and European badger were mainly distributed in the less-wooded agricultural-lowlands. Jackals prefer human-modified landscapes with fewer forested areas and avoid mountainous habitats (Šálek et al. 2014b, Spassov & Acosta-Pankov 2019). The presence of wolves may also be a major driver constraining the distribution of the jackal in high-altitude areas (Krofel et al. 2017, Spassov & Acosta-Pankov 2019), as was demonstrated in our NMDS ordination plot (Fig. 2). Badgers were also found mainly in agricultural lowlands, but in more-wooded sites than those in jackals (Fig. 2). Badgers often use pasture to forage for their staple food, earthworms (Kruuk et al. 1979), and select open-wood pastures for their sett (Virgos & Casanovas 1999). Smaller mesocarnivores (foxes, wildcats, and martens) were mainly found at higher altitudes and in more forested habitats than jackals and badgers, although these species can also adapt to human-altered landscapes (Šálek et al. 2014a). Local-scale competitive avoidance of large predators is a key driver of the spatial structures of mesocarnivore guilds (Monterroso et al. 2020). Our previous observations demonstrated spatiotemporal separation between jackals and the smaller carnivores due to avoidance of direct confrontation at small scales (Tsunoda et al. 2018, 2020). Although based on a marginally not-significant result, we showed that wildcats tended to occur inside protected areas (Fig. 2 and Table 3). This species has been listed as protected under Bulgarian national law since 2007 and conservation actions to maintain their habitats have been implemented in nature parks and reserves, including the Central Balkans National Park and the Eastern Rhodopes (Spassov et al. 2011).

The two domestic species, the dog and the cat, had different spatial distributions. Dogs were found at higher altitudes and in more forested habitats than cats in the present study, although free-roaming animals typically were found closer to settlement cores than wild species (Vanak & Gompper 2010, Krauze-Gryz et al. 2012). There were two possible reasons for the distribution patterns of the dog. First, feral and stray dogs are culled by hunters in Bulgaria (Raichev et al. 2013), limiting their densities in rural areas. Second, because of methodological limitations on identification of the animal images, the dogs observed by our camera-trapping may have included hunting dogs, which occur in forested areas. Dogs were also found inside protected areas (with a marginal statistic-significance; Table 3). Our camera stations were located in buffer zones of protected areas (i.e. non-strict reserves) and their fringes, including pasture, agricultural fields, small hamlets as well as hunting areas.

With regard to diel activities, six of our focal carnivores were mainly nocturnal. Generally, diel activity patterns in carnivores are synchronized with those of their sympatric prey (Monterroso et al. 2014). For example, wolves predominantly prey on red deer and wild boar (Zlatanova et al. 2014), and the smaller mesocarnivores (foxes, wildcats, domestic cats, and martens) prey on rodents (Hisano et al. 2013, Tsunoda et al. 2017, 2019). All of these prey animals (i.e. ungulates and rodents) are typically nocturnal (e.g. Monterroso et al. 2014, Mori et al. 2020). Badgers are also nocturnal (Barrull et al. 2014, Tsunoda et al. 2020), seeking and foraging on earthworms during the night (Kowalczyk et al. 2003). The remaining three species are typically omnivorous, predominantly consuming vegetable matter such as fruits and acorns (bear) (Bojarska & Selva 2012) or anthropogenic food resources, such as human food waste (dogs and jackals) (Vanak & Gompper 2009, Raichev et al. 2013).

Moreover, nocturnal activity in mesocarnivores (fox, wildcat, martens, and domestic cat) may be facilitated by temporal niche separation from sympatric competitive dogs and jackals, thereby reducing direct confrontations (Scheinin et al. 2006, Vanak et al. 2009). Temporal partitioning between competitive mesocarnivores plays a key role in successful sympatry in many carnivore guilds (Monterroso et al. 2013, Barrull et al. 2014, Carricondo-Sanchez et al. 2019, Tsunoda et al. 2020).

Conclusions

In agreement with our hypothesis, the present study demonstrated distributional patterns and diel activities in carnivore guilds that might be associated with landscape features and intraguild interactions. We found that modifications of the landscape by humans (e.g. forest fragmentation and agricultural land use), rather than direct human presence, may affect spatial distributions in carnivore guilds. Our findings also indicated that potential interspecific competition (interference or confrontation) might result in partition of their spatial distribution and temporal activities. Our results showed that intense human activity in lowland areas might constrain the distribution of wolves and bears, resulting in a broader distribution of the golden jackal in the local mesocarnivore guild. We conclude that spatial and temporal partitioning may be key to successful sympatry among trophic competitive mesocarnivores (Monterroso et al. 2020, Tsunoda et al. 2020).

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Author Contributions

H. Tsunoda conceptualized, designed, analysed and wrote the first draft; H. Tsunoda, S. Peeva, and E. Raichev revised the second draft; all authors conducted data collection by camera-trapping and confirmed the first and revised drafts.

Data Availability Statement

The datasets that support the findings of this study are available from the corresponding author on reasonable request.

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Supplementary online material

Table S1. Spearman's correlations (bottom left corner) and variance inflation factor (VIF, upper right corner) among seven numerical variables used in non-metric multidimensional scaling (NMDS) analysis.

Fig. S1. NMDS ordination plot of four variables with statistical significances ($P < 0.001$).

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