

Spatio-temporal partitioning facilitates mesocarnivore sympatry in the Stara Planina
Mountains, Bulgaria

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Abstract

The top trophic level in many terrestrial food webs is typically occupied by mammalian carnivores (Order Carnivora) that broadly affect and shape ecosystems through trophic cascades. Their inter-specific interactions can further complicate effects on community dynamics as a consequence of intra-guild competition. The capacity for competitive mammalian carnivores to segregate their hunting and activity regimes is in major part a function of their similarity, in terms of body-size and dietary niche; termed the ‘niche variation hypothesis’. In this study, we used camera-trapping to investigate intra-guild interactions and spatio-temporal partitioning among five mesocarnivores, the golden jackal (*Canis aureus*), European badger (*Meles meles*), red fox (*Vulpes vulpes*),

European wildcat (*Felis sylvestris*) and stone marten (*Martes foina*), in the Stara Planina Mts, Bulgaria. We amassed a total of 444 images of golden jackals, 236 images of European badgers, 200 images of red foxes, 171 images of stone martens, and 145 images of European wildcats, from 6612 camera-days across fifteen camera-trapping stations. With respect to body size, the three smaller species (fox, wildcat and marten) were separated temporally from the two larger competitors (jackal and badger) through both the warm and cold season. The more similar the trophic niche (i.e., primarily rodentivorous) between two species, the greater the spatio-temporal separation within the pair; however, this adapted to seasonal dietary shifts. In conclusion, spatial and temporal (fine-scale and seasonal) niche partitioning reduced encounter probabilities and competition and was important for sympatric coexistence among this regional mesocarnivore guild.

1. Introduction

Predators at higher trophic levels (i.e., third or fourth level consumers) broadly affect and shape ecosystems through trophic cascades (Ritchie and Johnson, 2009; Ripple et al., 2014). Inter-specific interactions among sympatric predators can further complicate

effects on prey dynamics and expand on the range of prey exploited (Polis et al., 1989) as a consequence of intra-guild competition (Ritchie and Johnson, 2009). For example, the extirpation of apex predators (the highest level consumer in a food web who is never predated) can cause meso-predator (the intermediated-level consumer who predares smaller animals at lower-level, in turn who could be predated by apex predators) releases, altering their abundance and activity regimes, as observed in both aquatic and terrestrial ecosystems (Ritchie and Johnson, 2009; Ripple et al., 2014). Insights into these effects can be crucial to understanding and predicting changes in community composition and developing conservation strategies (Newsome and Ripple, 2015).

The top trophic level in many terrestrial food webs is typically occupied by a mammalian carnivore species (Order Carnivora) (although apex species have been extirpated in many regions; Atkins et al., 2019), involving the suppression of intra-guild competitors (Ripple et al., 2014; Sivy et al., 2017). For example, regionally in North America, wolves (*Canis lupus*) can suppress coyote (*C. latrans*) populations, which in turn suppress fox (*Vulpes* spp. and *Urocyon* sp.) populations (Levi and Wilmer, 2012; Newsome and Ripple, 2015), ultimately altering the diversity of prey being exploited (Crooks and Soule, 1999; Miller et al., 2012). Intra-guild suppression can involve direct aggression and killing (Palomares and Caro, 1999; Linnell and Strand, 2000; Donadio

and Buskirk, 2006), or, in situations where the competition has reached equilibrium, there will be trophic, spatial or temporal partitioning between competing predators (Carvalho and Gomes, 2004; Hayward and Slotow, 2009; Vanak et al., 2013; Karanth et al., 2017).

Such differentiation in resource use patterns among sympatric carnivores is fundamental to their coexistence. The capacity for competitive mammalian carnivores to segregate their hunting and activity regimes is in major part a function of their similarity, in terms of size and dietary niche (Palomares and Caro, 1999; Donadio and Buskirk, 2006); termed the '*niche variation hypothesis*' (Van Valen and Grant, 1970; Soule and Stewart, 1970; Bolnick et al., 2007). For example, introduced eutherian mammals compete with their native marsupial counterparts in Australia (Glen and Dickman, 2008). Nevertheless, substantial trophic niche overlap still occurs between many sympatric carnivores, either seasonally, or through the entire year, depending on the extent to which the availability of prey exploited varies (Linnell and Strand, 2000; Lanszki et al., 2006).

The roles of terrestrial carnivores in structuring ecological communities has been well-documented across the European Continent (e.g., Palomares et al., 1996; Jedrzejewska and Jedrzejewski, 1998; Lanszki et al., 1999, 2006; Motterroso et al.,

2014). Previous research has demonstrated that larger species, as the grey wolf and Eurasian and Iberian lynx (*Lynx lynx* and *L. pardinus*), function as an apex carnivore within their guilds, constraining the ranges, abundance and/or resource usage of smaller sympatric competitor species (Palomares et al., 1996; Pasanen-Montensen et al., 2013; Newsome et al., 2017). In regions where these larger carnivores have been regionally extirpated, due to historical human persecution, meso-carnivores (e.g., red fox, *Vulpes vulpes* and European badger, *Meles meles*) predominate the predator guild (Lindstrom et al., 1995; Barrull et al., 2014), and compete with each other (Macdonald et al., 2004). In the Balkan Peninsula, however, the carnivore community involves higher endemism and rarity than elsewhere in Europe, as specified by the golden jackal (*C. aureus*; Baquero and Telleria, 2001) as well as steppe polecat (*Mustela eversmannii*) and marbled polecat (*Vormela peregusna*; Popov 2007). Here, we investigate the eco-behavioural knowledge gap on carnivore sympatry in the Balkan Mountains, involving two canids, the golden jackal and red fox; two mustelids, the European badger and stone marten (*Martes foina*); and one felid, European wildcat (*Felis sylvestris*) (Table 1). Our aim was to investigate spatial and temporal partitioning, or overlap, between these species. Specifically, we address the effects of body size and trophic niche similarity (Palomares and Caro, 1999; Donadio and Buskirk, 2006). We tested three main hypotheses: *H1*,

whether smaller-sized species (with typical body weight <10 kg; i.e., red fox, wildcat and stone marten) exhibited spatial and/or temporal avoidance/separation from larger competitors (>10 kg; i.e., golden jackal and European badger) to avoid agonistic encounters (*sensu* Palomares and Caro, 1999; Donadio and Buskirk, 2006); *H2*, whether these smaller species exhibited a stronger spatial and/or temporal separation from the predominantly carnivorous golden jackal than from the more generalist badger due to more substantial trophic overlap in diet preferences (informed by Raichev, 2002; Hisano et al., 2014; Macdonald et al., 2004; Tsunoda et al., 2017, 2019); and *H3*, whether the four predominantly carnivorous species (i.e., other than the omnivorous badger) exhibited stronger spatio-temporal partitions in the cold season compared with the warm one, due to restricted resource availabilities and, thus, higher levels of competition for rodent prey in the winter. To do this we looked at data on the spatial and temporal location of these carnivores that were collected using camera traps deployed across the study area.

2. Materials and Methods

2.1. Study site

The study area (ca. 15 km²; 42°36–42N, 25°25–46E) was located along the southern slope of the Central Stara Planina Mountains, between an elevation of 500 m to 1400 m above sea level (a.s.l.) (Fig. 1). Average monthly temperature during the study period averaged ca. 19.4 °C in the warm season (May–Oct.) and ca. 3.5 °C in the cold season (Nov.–Apr.) (taken at Shipka town, 650 m a.s.l.; World Weather Online, <https://www.worldweatheronline.com/> accessed 20 March 2019). The area was almost entirely covered with secondary oak forests (*Quercus* sp.) up to 1,000 m a.s.l., and primarily with beech forests (*Fagus sylvatica*) at higher elevations. Other land cover, e.g., grasslands, a monument building (named the “Buzludzha Monument”), settlements (including some tourist hotels) and agricultural lands, comprised < 5% of the area. Our investigation was focused on the microhabitat, or patch use scale, similar to comparable studies (e.g., Fedriani et al., 2000; Shamoon et al., 2017, 2018); nevertheless our site was large enough to include the core areas of several individual golden jackals (ca. 3.5 km²; Rotem et al., 2011), which had the largest average home range size among the species investigated.

2.2. Targeted species

The targeted mesocarnivores occurred in various habitats from agroforests to montane forests, ranging broadly through Bulgaria, except in the alpine regions (Popov, 2007). Although their trophic niches are substantially separated (Table 1), their staple foods were seasonally overlapped, potentially being resource competitions specifically for rodents or fruits, evidenced from our previous observation in the study area; for example, golden jackals, red foxes and stone martens shared rodents and fruits in warmer season (Tsunoda et al., 2019), while the smaller species (i.e., foxes, wildcats and martens) relied more on rodents in winter (Raichev, 2002; Hisano et al., 2014; Tsunoda et al., 2017; Table 1). Other potential competitors, e.g., wolves, domestic dogs (*C. l. familiaris*) and cats (*Felis catus*), were less common in this study area (see Table S1 in Supplementary Material) and Eurasian lynx was regionally extinct (Popov and Sedefchev, 2003), thus, excluded from the target species.

2.3. Camera trapping

Camera trapping was conducted continuously between 6 July 2016 to 6 October 2017. We used KeepGuard Cam KG-690NV, passive infrared cameras (Keepway Industrial

Inc.) with a trigger speed of 0.8 s, programmed to take three photos with a five min delay. We set three cameras at least 200 m apart at five different elevational zones, <650 m, 650–800 m, 800–1000 m, 1000–1200 m, and 1200–1400 m a.s.l., comprising a total of 15 camera trapping stations. Cameras were deployed at intersections of animal trails to maximize the probability of animal detections (Meek et al., 2014; Cusack et al., 2015; Apps and McNutt, 2018a); noting that placement was also dictated by precipitous slopes elsewhere. We mounted cameras on trees 1.0–1.2 m above ground level, at an appropriate distance (between ca. 5–15 m) from the trail and angled to take pictures of the whole body of medium- and large-sized animals (see examples in Fig. S1 in Supplementary Material) (Apps and McNutt, 2018a and b). We used no baits or lures. Batteries were changed and memory cards replaced at an interval of one to three months – at no time were batteries depleted or cards full. Therefore no detections could have been missed. All animal images were subsequently identified to species and logged against the date and time (24:00 hour unit) of capture. Consecutive images of the same species within 30 min at a station were treated as a single detection event, logged against the initial time. We used only data for stone marten below 1000 m a.s.l. (Raichev, 2018), to avoid potential confusion (due to poor subject framing in camera trap images at night; Apps and McNutt, 2018a) with pine martens (*M. martes*) that live only at

higher elevations in the Balkan Mountains (Popov and Sedefchev, 2003).

2.4. Statistical analyses

Distances between cameras are important when evaluating the spatial patterns of animal species occurrences (Meek et al., 2014); when cameras are set close together within a small area, positive spatial autocorrelation can arise due to repeated observations of the species, affecting assessment of faunal composition (Meek et al., 2014). To assess for positive spatial autocorrelation, by season, we used Mantel's correlogram (Legendre and Legendre, 1998; Borcard and Legendre, 2012). Correlation indices were calculated using 10000 randomizing simulations based on the number of captures of each carnivore species per day per camera and the longitudinal/latitudinal positions of cameras. This was done using R ver. 3.5.1 (R Core Team, 2018) and the 'vegan' package 2.5-2 (Oksanen et al., 2019) for R.

To assess seasonal spatial overlap between each of the 10 carnivore-pairs (see Fig. S2 in Supplementary Material), we calculated Pianka's index (α ; Pianka, 1973), where α can range from 0 (no overlap) to 1. We performed separate analyses for the warm (May–Oct.) and cold (Nov.–Apr.) seasons. We also conducted a null-model test

using a ‘scrambled-zeros’ randomization algorithm with 1000 data randomizations (Winemiller and Pianka, 1990). From this, significant spatial overlap arises when the observed value is $> 95\%$ of the simulated value, at $P < 0.05$. These analyses were performed using the ‘EcoSimR’ package (Gotelli et al., 2015) in R.

Daily activity was estimated using Kernel density interference (Ridout and Linkie, 2009) for the time (i.e., 0:00–23:59) the animal image was captured, transformed to circular data (i.e., $0-2\pi$). We pooled these data from all camera-trapping stations for each species and undertook separate analyses for the warm and cold seasons. To determine inter-specific overlaps in daily activity, we then estimated the coefficient of temporal overlap (D) for each species-pair separately for the warm and cold seasons, which ranged from 0 (no overlap) to 1 (complete overlap) (Ridout and Linkie, 2009). For carnivore species datasets containing fewer than 50 samples we used D_1 ; for species datasets containing >50 samples we used D_4 , in accordance with the criteria given by Meredith and Ridout (2017). To assess the reliability of these estimated D statistics and estimate 95% confidence intervals (CI), we performed a smoothed bootstrap test with 10,000 bootstrap samples. We assessed statistical significances in interspecific differences of daily activity patterns using the Watson’s two-sample test (Pewsey et al., 2013). For these analyses, we used ‘overlap’ (Meredith and Ridout, 2017) and ‘circular’

(Agostinelli and Lund, 2017) packages for R.

In accord with previous studies (Monterroso et al., 2014; Torretta et al., 2016), we defined spatial (α) and temporal (D) overlap indices with ≤ 50 th percentile as “low”, between 50th < and ≤ 75 th percentile as “moderate”, and 75th < percentile as “high”.

3. Results

We amassed a total of 2886 animal images from 6612 camera-days across 15 stations. Animal (including non-target species) detections (images per day per camera) ranged from 0.11 to 1.18 (mean \pm SD: 0.43 ± 0.29). We observed a total of 17 mammal species, including the five carnivores targeted (see details Table S1 in Supplementary Material). We found no positive spatial autocorrelation in these data for each season (Fig. S3 in Supplementary Material), indicating that proximity between cameras did not affect spatial similarities in detected species compositions.

3.1. Inter-specific spatial partitioning

The two larger species, golden jackals and European badgers, were observed mainly at

lower elevations (<1000 m), while smaller species (red foxes, European wildcats and stone martens) were commonly observed across all elevations (Fig. 2).

With respect to *H1*, in the warm season, we observed mostly low and moderate spatial overlaps (Pianka's indices $\alpha < 0.75$) between the two larger and three smaller carnivores (Table 2), with an exception in badger–marten pair ($\alpha = 0.76$). In contrast, pairs of similar body-sized species (i.e., jackal–badger, or among smaller species) showed relatively high overlaps ($\alpha = 0.75$ – 0.92), with statistical significance for three pairs ($P < 0.05$; Table 2). In the cold season, however, we observed low spatial overlaps between badgers and the three smaller species ($\alpha = 0.34$ – 0.39), whereas jackals exhibited moderate to high spatial overlaps with the smaller species ($\alpha = 0.55$ – 0.90), with statistical significance for jackal–wildcat and jackal–marten pairs ($P = 0.01$; Table 2). Among pairs of similar sized species in the cold season, we observed moderate or high spatial overlaps for all three smaller species pairings ($\alpha = 0.50$ – 0.91 ; with statistical significance for the wildcat–marten pair, $P < 0.01$), while the lowest overlap was for jackal–badger ($\alpha = 0.27$; Table 2).

With respect to *H2*, in the warm season, spatial overlap indices between golden jackals and the three smaller species ($\alpha = 0.19$ – 0.66) were lower than those between European badgers and these small species ($\alpha = 0.49$ – 0.76). In the cold season, however,

badgers showed lower overlap indices values ($\alpha = 0.34\text{--}0.39$, $P = 0.12\text{--}0.45$) than did jackals ($\alpha = 0.55\text{--}0.90$, $P = 0.01\text{--}0.21$; Table 2).

With respect to *H3*, we observed significantly higher spatial overlaps in the cold season between golden jackals and the smaller species, as well as for the wildcat–marten pair ($\alpha = 0.91$, $P < 0.01$), than in the warm season (Table 2). In contrast, spatial overlaps during the cold season were lower for fox–wildcat ($\alpha = 0.70$) and fox–marten pairs ($\alpha = 0.78$; Table 2) than in the warm season.

3.2. Inter-specific temporal partitioning

The largest species, the golden jackal, exhibited bimodal crepuscular activity peaks, while the other four species were mainly active at night (Fig. 3).

With respect to *H1*, golden jackals exhibited highly significant ($P < 0.001$) temporal segregations from all three smaller carnivores in both the warm ($D = 0.55\text{--}0.65$) and cold ($D = 0.50\text{--}0.73$) seasons (Table 3 and Fig. 3). Similarly, we also observed significant temporal segregation between European badgers and the three smaller carnivores in both the warm ($D = 0.74\text{--}0.83$, $P < 0.01$) and cold seasons ($D = 0.71$, $P < 0.05$); the exception being the badger–marten pair in the cold season ($D = 0.86$,

n.s.). In the warm season, all three smaller species showed high temporal overlap indices ($D = 0.84\text{--}0.88$), with non-significant temporal segregations, whereas their temporal overlap indices were lower in the cold season ($D = 0.68\text{--}0.79$).

Consistent with *H2*, we observed more significant temporal segregations between golden jackals and all three smaller species, in both seasons ($D = 0.50\text{--}0.73$), than with European badgers ($D = 0.71\text{--}0.86$), except for the badger–fox pair in the cold season ($D = 0.73$ for jackal and $D = 0.71$ for badger, respectively; Table 3).

With respect to *H3*, temporal overlaps between golden jackals and the three smaller carnivores were not substantially different between the warm and cold seasons (Table 3). In contrast, temporal overlaps among the three smaller species were lower in the warm ($D = 0.84\text{--}0.88$) than in the cold season ($D = 0.68\text{--}0.79$), with significant segregations for fox–marten ($P < 0.01$) and wildcat–marten ($P < 0.001$) pairs (Table 3).

4. Discussion

In relation to hypothesis *H1*, that body-size might influence the extent of mutual spatio-temporal avoidances between sympatric carnivores, we found significant temporal separations in most pairings involving the two larger-sized (i.e., golden jackal

and European badger) and three smaller-sized species (i.e., red fox, European wildcat and stone marten) in both seasons (Table 3). Although large and small species were predominantly active at night (with the exception of golden jackals), asynchrony in their activity peaks (Fig. 3) evidenced temporal partitioning (Monterroso et al., 2014). In mammalian carnivore guilds, smaller (or subordinate) species typically partition their time in active from larger competitors, maybe owing to avoid their encounters (Palomares and Caro, 1999; Fedriani et al., 2000; Hayward and Slotow, 2009; Schuette et al., 2013), particularly, when their trophic and/or spatial niches overlap (Barrull et al., 2014; Toretta et al., 2016). Spatial and trophic overlaps among the carnivores we studied were evident, or partly-evident, in both seasons (Tables 1 and 2), consistent with previous dietary research in this same study area (Raichev, 2002; Hisano et al., 2014; Tsunoda et al., 2017, 2019).

Our hypothesis *H2*, that smaller species might exhibit a stronger spatial and/or temporal separation from the predominantly carnivorous golden jackal than from the more omnivorous European badger, due to more substantial trophic overlap in diet preferences (Raichev, 2002; Hisano et al., 2014; Tsunoda et al., 2017, 2019), was supported by our observations evidencing a more substantial and significant temporal separation between the three smaller species and golden jackals than with European

307 badgers (Table 3). Spatial partitioning, however, varied with season: smaller species
308 separated spatially from golden jackals only in the warm season; in the cold season,
309 they separated more substantially from European badgers than from jackals (Table 2).
310 This is consistent with our previous research that found that jackals and two of the
311 smaller species (red foxes and stone martens) exhibited higher dietary overlaps in the
312 warm season when all three species ate fruits and rodent prey (Hisano et al., 2016;
313 Tsunoda et al., 2019; no data was available on European wildcats in this season in our
314 area, but see Lozano et al., 2006), whereas in the cold season they exhibited less trophic
315 overlap and more partitioning: the smaller species mostly consumed rodents while
316 jackals consumed wild ungulates (Raichev 2002; Raichev et al. 2013; Hisano et al.,
317 2014; Tsunda et al., 2017; also see Table 1). Generally, dietary overlaps between
318 sympatric species increase the probability of interference interactions (i.e., killing,
319 aggression and harassment by larger species) at resource patches (Macdonald et al.,
320 2004; Donadio and Buskirk, 2006; Scheinin et al., 2006; Wikenros et al., 2014)
321 resulting in fine-spatial scale segregations and displacements (Kitchen et al., 1999;
322 Shamoon et al., 2017). Two explanations could explain the pattern of separations with
323 European badgers in the cold season: Firstly, badgers predominantly eat earthworms
324 (Goszczynski et al., 2000) lessening their competition with the smaller rodentivorous

carnivores in the cold season, while golden jackals consumed ungulates (particularly roe deer, *Capreolus capreolus*, and wild boar, *Sus scrofa*) in this season (through both predation and scavenging: Raichev et al., 2013; Tsunoda et al., 2017), causing differentiation in their foraging patch selection. Secondly, European badgers tend to be less active in the cold season (Kowalczyk et al., 2003; Noonan et al., 2014), and were detected significantly less often by our cameras than in the warm season (mean images per day per camera = 1.59 in the cold season vs 5.12 in the warm season; $P = 0.01$ by Wilcoxon test; see also Fig. 2); indeed, we detected no badgers at all from 9th Dec 2016 to 6th Feb 2017. In contrast, there was no statistically significant variation in detection rates with season for any of the other species (Table S2 in Supplementary Material).

With respect to hypothesis *H3*, that the extent of spatial and/or temporal separations among trophic competitive (i.e., rodent-preferring) species may be stronger in the cold season than in the warm one, our observations supported this hypothesis for spatial and/or temporal separation among all three smaller species pairs (Tables 2 and 3). Specifically, stone martens, the smallest species, separated temporally from both larger red foxes and European wildcats. This temporal partitioning by stone martens might be to avoid larger competitors as per *H1*, and is in accord with other studies (Lindstrom et al., 1995; Palomares and Caro, 1999; Wikenros et al., 2014). In contrast, red foxes and

European wildcats partitioned each other species spatially. Given the similarities in their diet and activity regime (Tables 1 and 3), this was perhaps due mutual avoidance, or divergent hunting and foraging behaviors (Murray et al., 1995; Kok and Nel, 2004).

We had expected smaller species to segregate spatially from larger competitor, golden jackals (as per *H1* and *H2*), especially with restricted food availability in the cold season. This was not the case, inconsistent with *H3*; actually their spatial and temporal overlap indices with jackals were greater in the cold than in the warm season (Tables 2 and 3). From our previous research, in the cold season, golden jackals in our study area prey on wild ungulates, or scavenge carcasses, rather than predating on rodents (Raichev et al., 2013). This likely explains these dietary niche separation patterns between golden jackals and the smaller species (Raichev, 2002; Hisano et al., 2014; Tsunoda et al., 2017; Table 1), enabling spatial overlaps, according with hypothesis *H2* (see above).

5. Conclusion

By reducing encounter probabilities (Palomares and Caro, 1999; Linnell and Strand, 2000; Hayward and Slotow, 2009), niche partitioning through spatial and temporal (fine

scale and seasonal) was important for sympatric coexistence within this Bulgarian carnivore community. The regional importance of understanding intra-guild competition among carnivores in this region of Bulgaria is heightened by recent colonization by the golden jackal (Markov, 2012), which can displace all other native carnivores, aside from the rare gray wolf (Zlatanova and Popova, 2013; Newsome et al., 2017).

Given the ever increasing problems of anthropogenic impacts on natural systems (e.g., landscape modification, habitat fragmentations and hunting/persecution pressure; Fischer and Lindenmayer, 2007; Packer et al., 2009), the carefully balanced partitioning of sympatric carnivore guild structures are in jeopardy of destabilization, risking cascade effects across ecological communities (Wang et al., 2015; Sivy et al., 2017; Shamoon et al., 2018; Smith et al., 2018; Cunningham et al., 2019). We thus advocate for more research to better understand intra-guild partitioning in order to prepare informed community conservation strategies and species management plans.

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Figure captions:

Fig. 1. Study area and locations of camera-trapping sites in a forest area in the Central Stara Planina Mts, Bulgaria

Fig. 2. Photos per day per camera (mean with standard deviations) for larger- (a and b) and smaller-sized (c and d) mesocarnivores in the warm and cold season at five elevational zones, in the Central Stara Planina Mts, Bulgaria

Fig. 3. Comparisons of daily activity patterns (estimated using Kernel's density) for five mesocarnivores in the warm (left) and cold season (right), in the Central Stara Planina Mts, Bulgaria. Horizontal bar represents nighttime (black) and daytime (white), while vertical dotted lines represent timing of sunrise or sunset. Shaded areas in both ends are duplicated plots.

614 Table 1. Comparisons of trophic niches and body size differences among the mesocarnivores studied.

Common name	Major food sources	% rodents in diets*	Trophic overlap**			Mean body mass (kg)	Arcsine square-rooted body size difference***			
			Jackal	Fox	Wildcat		Jackal	Badger	Fox	Wildcat
Golden jackal	Rodents, ungulates, fruits	14.6	-	-	-	11.0	-	-	-	-
European badger	Earthworm, fruits	No data	-	-	-	10.8	7.8	-	-	-
Red fox	Rodents, fruits, insects	41.3	0.68	-	-	5.7	44.0	43.4	-	-
European wildcat	Rodents	66.7	0.43	0.95	-	4.7	49.2	48.7	24.8	-
Stone marten	Fruits, rodents, insects	50.0	0.56	0.91	0.92	1.4	69.1	68.9	60.3	57.0

615 * Data from stomach content analyses in the studied area: for more details see Raichev (2002), Hisano et al. (2014), Tsunoda et al. (2017)

616 ** Data from Raichev (2002)

617 *** This index was proposed by Donadio and Buskirk (2006)

618

619 Table 2. Pianka's overlap indices (α) on spatial activities between each carnivore pair in a forest area in the Central Stara Planina Mts,
620 Bulgaria.

Carnivores		Warm season				Cold season			
Larger sp.	Smaller sp.	$\alpha_{\text{obs.}}$	$\alpha_{\text{sim.}}$	95% <i>CI</i> of $\alpha_{\text{sim.}}$	P^*	$\alpha_{\text{obs.}}$	$\alpha_{\text{sim.}}$	95% <i>CI</i> of $\alpha_{\text{sim.}}$	P^*
<i>C. aureus</i>	<i>M. meles</i>	0.92	0.20	(0.03 – 0.90)	< 0.001	0.27	0.34	(0.10 – 0.73)	0.47
	<i>V. vulpes</i>	0.19	0.26	(0.07 – 0.59)	0.48	0.55	0.42	(0.15 – 0.70)	0.21
	<i>F. silvestris</i>	0.36	0.22	(0.04 – 0.82)	0.08	0.74	0.37	(0.10 – 0.70)	0.01
	<i>M. foina</i>	0.66	0.29	(0.04 – 0.73)	0.10	0.90	0.52	(0.24 – 0.84)	0.01
<i>M. meles</i>	<i>V. vulpes</i>	0.49	0.48	(0.29 – 0.76)	0.39	0.34	0.48	(0.25 – 0.75)	0.17
	<i>F. silvestris</i>	0.55	0.41	(0.22 – 0.90)	0.09	0.39	0.43	(0.21 – 0.77)	0.45
	<i>M. foina</i>	0.76	0.48	(0.24 – 0.84)	0.12	0.36	0.55	(0.28 – 0.86)	0.12
<i>V. vulpes</i>	<i>F. silvestris</i>	0.75	0.53	(0.36 – 0.77)	0.04	0.50	0.55	(0.33 – 0.79)	0.35
	<i>M. foina</i>	0.78	0.58	(0.32 – 0.87)	0.09	0.70	0.59	(0.32 – 0.85)	0.24
<i>F. silvestris</i>	<i>M. foina</i>	0.89	0.47	(0.21 – 0.85)	0.01	0.91	0.62	(0.38 – 0.87)	< 0.01

621 * Null-model test ($\alpha < 0.05$)

622 Table 3. Overlap indices of daily activity patterns (estimated using Kernel's density; *D*) between each carnivore pair in a forest area in
623 the Central Stara Planina Mts, Bulgaria.

Carnivore pair		Warm season			Cold season		
Larger sp.	Smaller sp.	<i>D</i>	95% <i>CI</i>	<i>P</i> *	<i>D</i>	95% <i>CI</i>	<i>P</i> *
<i>C. aureus</i>	<i>M. meles</i>	0.39	(0.34 – 0.46)	< 0.001	0.48	(0.39 – 0.57)	< 0.001
	<i>V. vulpes</i>	0.65	(0.57 – 0.73)	< 0.001	0.73	(0.61 – 0.84)	< 0.001
	<i>F. silvestris</i>	0.61	(0.53 – 0.71)	< 0.001	0.62	(0.51 – 0.73)	< 0.001
	<i>M. foinea</i>	0.55	(0.47 – 0.62)	< 0.001	0.50	(0.40 – 0.59)	< 0.001
<i>M. meles</i>	<i>V. vulpes</i>	0.74	(0.66 – 0.80)	< 0.001	0.71	(0.59 – 0.83)	< 0.05
	<i>F. silvestris</i>	0.77	(0.69 – 0.85)	< 0.01	0.71	(0.58 – 0.83)	< 0.05
	<i>M. foinea</i>	0.83	(0.75 – 0.90)	< 0.01	0.86	(0.72 – 0.96)	n.s.
<i>V. vulpes</i>	<i>F. silvestris</i>	0.88	(0.80 – 0.95)	n.s.	0.79	(0.65 – 0.91)	n.s.
	<i>M. foinea</i>	0.84	(0.77 – 0.92)	n.s.	0.73	(0.61 – 0.85)	< 0.01
<i>F. silvestris</i>	<i>M. foinea</i>	0.86	(0.78 – 0.94)	n.s.	0.68	(0.53 – 0.81)	< 0.001

624 * Watson's two sample test; n.s., non-significance

