Terrestrial Ecology and Behaviour
Research Article

ACTA ZOOLOGICA BULGARICA
Acta zool. bulg., 68 (3), 2016: 375-390

Niche Partitioning among the Red Fox *Vulpes vulpes* (L.), Stone Marten *Martes foina* (Erxleben) and Pine Marten *Martes martes* (L.) in Two Mountains in Bulgaria

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Abstract: The trophic, spatial and temporal characteristics of the ecological niches of the red fox *Vulpes vulpes* (L.), stone marten *Martes foina* (Erxleben) and pine marten *Martes martes* (L.) were analysed based on collected scat samples and camera trap data from Vitosha and Pirin Mts, South-western Bulgaria. The trophic niches overlapped to a great extent in spring (93-97%) while the least level of overlap was observed in autumn (38-53%). We did not find clear niche partitioning by forest type and visibility nor patterns in the spatial strategies of the three species. These results suggested that their habitat preferences were similar. When fruits were abundant (in summer and autumn) and the studied species fed mainly on plant matter, we found higher tolerance to each other in terms of habitat selection and preferred altitudes. The food and space competition was likely alleviated by temporal avoidance between the species, as there were clear hourly shifts in their activity patterns.

Key words: *Vulpes vulpes*, *Martes martes*, *Martes foina*, niche partitioning, diet, camera traps

Introduction

The ranges of the red fox *Vulpes vulpes* (L.), stone marten *Martes foina* (Erxleben) and pine marten *Martes martes* (L.) (Carnivora) are overlapping to a great extent in Europe, which is a prerequisite for overlapping their spatial and trophic ecological niches (citation).

The red fox dietary preferences have been extensively documented worldwide, with numerous papers on its diet throughout Europe (citations). These studies demonstrate that its diet is versatile and includes over 350 animals and dozens of plant species, with murid rodents being their main food source. The diet of the red fox in Bulgaria has been well studied in lowlands (Petkov 1929; Dumanov 1939; Ruskov 1953; Atanasov 1958; Tsonkov 1961; Peshev 1963; Grigorov 1987). There is a limited number of studies from mountain habitats (Kiurkchiev 2005, 2008; Vasileva 2005) focusing on the Rhodopi and Osogovo Mts. The habitat requirements of the red fox are also well documented (Cavallini & Lovari 1991; Lucherini *et al.* 1995; Weber & Meia 1996) and the species is characterised as generalist occupying various habitats.

Studies on the diet of the stone marten and pine marten are from areas where they live in sympatry and therefore these examinations often face the problem of faeces identification. The excrements of the stone marten and pine marten cannot be differentiated morphologically from one another. Therefore, in many cases the food preferences of these two species are considered at the generic level (as *Martes* spp.). Many studies in Europe (see below) show that the diet of martens is diverse and includes vertebrates, invertebrates and plants. Data from Bulgaria are limited and concern mainly the stone marten (Vasileva *et al.* 2005; Georgiev & Raichev 2009; Kirkova *et*

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al. 2011; Georgiev 2013; Hisano *et al.* 2013). To our knowledge, there are no publications on the diet of pine marten from Bulgaria.

Several studies aimed to determine the degree of overlap between the trophic (Baltrūnaitė 2001; Padial *et al.* 2002; Vasileva 2005; Lanszki *et al.* 2007; Prigioni *et al.* 2008; Skalski & Wierzbowska 2008; Vlachos *et al.* 2010) and spatial (Rosellini *et al.* 2008; Zabala *et al.* 2009; Lombardini *et al.* 2015) aspects of the ecological niches of the three species. Our study is the first to consider the three species together and aims to contribute to understanding of how the red fox, stone marten and pine martens coexist and share the limited resources.

Materials and Methods

Study area

The study was carried out in two mountains in Bulgaria, Vitosha and Pirin (Fig. 1). Vitosha (declared as Nature Park) has mean altitude of 1500 m, reaching 2290 m. The climate is temperate-continental (Michev *et al.* 1980). Four vegetation belts can be recognised in this mountain (Hubenov 1990): 1. mixed oak (*Quercus* spp.)–hornbeam (*Carpinus betulus* L.) forests (altitude 1100-1400 m); 2. beech (*Fagus sylvatica* L.) forests (1400-1840 m); 3. coniferous forests (1700-2050 m); 4. subalpine belt (above forests) consisting of mountain pine (*Pinus mugo* Turra), common juniper (*Juniperus communis* L.), European blueberry (*Vaccinium myrtillus* L.), lingonberry (*Vaccinium vitis-idaea* L.) and bog bilberry (*Vaccinium uliginosum* L.) (Zaharieva 1941). Vitosha Nature Park is in proximity to the capital city of Bulgaria and faces significant human disturbance to its wildlife. There are numerous settlements bordering to the park as well as a large number of hiking trails through the mountain. Pirin National Park occupies most of the second highest mountain in Bulgaria, with a mean altitude of 1033 m and the highest peak 2914 m. The mountain is divided into two parts in terms of climate: the northern slopes, with temperate-continental climate, and southern slopes, with strong Mediterranean influence (Tishkov 1982). Six vegetation belts can be distinguished in Pirin (Velchev *et al.* 1986): 1. xerotermic oak forests (below altitude of 700 m); 2. mesophilic and xeromesophilic oak and hornbeam forests (900-1000 m) 3. beech forests (900-1500 m); 4. coniferous forests (1500-2200 m); 5. subalpine zone (2200-2500 m); 6. alpine zone covered with dwarf willow *(Salix herbacea* L.), alpine sedge (*Carex curvula* All.), *Sesleria comosa* Velen. and other specific plant species. Pirin is generally less accessible than Vitosha due to its rugged slopes. Tourism is also a factor in this mountain but not to the same extent as in Vitosha.

Data collection and analyses

Scat analyses

The scats of the two species of *Martes* cannot be distinguished morphologically (without DNA analysis) and therefore we pooled the data as *Martes* spp. Marten scats are typically dark, long, heart shaped or slightly curled, whereas fox scats tend to be larger in size, shorter and thicker. However, bias could be introduced, since some marten scats could be misidentified as fox scats (Baines *et al.* 2013). To reduce this bias, we included in the analyses only scats that could be clearly distinguished as belonging to red fox or to martens. The excrements were collected opportunistically during field studies in 2010-2014. Samples were taken in plastic bags, with a label containing the species name, GPS location, date and the name of the collector. Scat samples were collected at altitudes of 850-1650 m from Vitosha, while in Pirin the study area covered the whole forest belt (1000-2250 m). A total of 185 fox excrements and 186 marten excrements from Vitosha and 164 fox and 160 marten excrements from Pirin were collected and analysed. For the analyses of excrements, the classical procedure of Kruuk & Parish (1981) was followed. Scat samples were washed in 500-1000 ml of water through a sieve (mesh size < 2 mm). Smaller particles were identified using a stereomicroscope whereas macroscopic components were sorted into groups, i.e. bones, fir, feathers, scales, claws, teeth, plant matter (pyrenes, leaves, seeds), stones, artificial materials, etc. Sample content was then divided into food types: plants, invertebrates, amphibians, reptiles, birds, mammals and garbage (with anthropogenic origin). The objects were then precisely identified by experts in botany, herpetology, ornithology, entomology and theriology, down to the species level when possible. The relative frequency (Fr%) of food types in each sample (Lockie 1959) was calculated as percentage of each food type from the total number of samples. Trophic niche breadth was calculated using the Levins measure (B_A) and overlap between the trophic niches was calculated using Morisita's index of similarity (C) (Levins 1968; Morisita 1959). The same analyses were performed for the seasonal data as follows: spring (March 16 – June 15), summer (June 16 – September 15), autumn (September 16 – December 15) and winter (December 16 – March 15).

Camera traps

Thirty camera traps (Ltl Acorn 5210) were set up in Vitosha (June 2013 to November 2014) and 24 cam-

era traps (SG DTC-565V and KG 680V) were set up in Pirin (April–November 2014). The two mountains were divided into zones and the camera traps were set according to a predetermined grid (Kilshaw & Macdonald 2011), with a cell width of 600 m in Vitosha and 1000 m in Pirin (Fig. 2). Camera traps were left in the field for 22-35 days in one zone before being moved to the next. The devices were mounted on animal trails in suitable habitats (predominantly forests) for detecting middle-sized and large mammals.

Camera traps were set to record three photos and a videoclip, printing the time, date, temperature and moon phase on each photo. A standard form was completed for each camera trap station, containing information on the zone number, GPS coordinates, camera trap serial number, team members, habitat description, dominant tree species, forest type (deciduous, coniferous or mixed), forest visibility (open, with visibility > 10 m or closed, with visibility < 10 m), height of the camera trap position and altitude of the location.

The camera trap photos and videoclips were imported and analysed using CameraBase 1.6. (Tobler 2013) translated in Bulgarian and complemented to adapt the needs of local research (Zlatanova 2014, unpublished). We considered photos of prolonged stay of the same individual at a camera trap station as one independent event (hereafter registration) unless it was clear that two or more different individuals were captured. This was done to avoid overestimation of the species in a certain location or time period due to the activity of a single individual spending a relatively long period of time in front of the camera. The two martens are often difficult to differentiate in camera trap photos (especially nocturnal) and when identification was impossible the species was noted as *Martes* sp. The total number of registrations for the red fox was 733 and 103, for the stone marten – 333 and 27, for the pine marten – 21 and 43, and for *Martes* sp.–160 and 30 registrations for Vitosha and Pirin Mountains, respectively. The camera trap data were analysed as the percentages of registrations of the focal species in different forest types, forest visibility classes, altitudinal classes (divided in 200 m intervals as follows: 801-1000 m, 1001-1200 m, 1201-1400 m, 1401-1600 m, 1601-1800 m, 1801-2000 m), general activity patterns (diurnal, nocturnal and crepuscular), and activity patterns by hour of the day. Differences in the habitat use (different altitudes) and activity patterns were tested for significance using the χ^2 test in Excel following McDonald (2014). Samples of small size (less than 0.5) were excluded from the analyses. The relative preference for different habitat types (type and visibility of the forest) was calculated as Ivlev's Selectivity Index (D), partially modified by Jacobs (1974). This approach was chosen because statistical methods (such as the

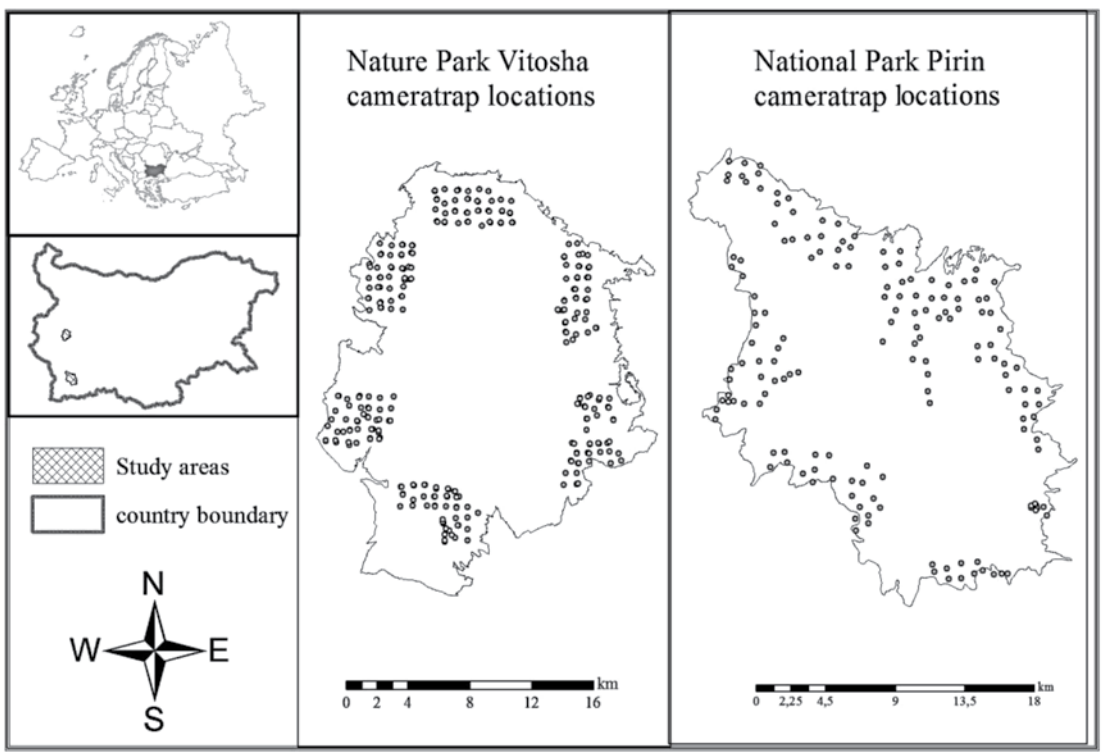


Fig.1. Locations of camera traps in Vitosha Nature Park and Pirin National Park

G-test of goodness-of-fit) would underestimate the absence or avoidance of certain habitats due to small sample sizes (e.g. in Pirin deciduous forests are present but the pine marten actively avoids them). Analyses were also performed for the three seasons separately (spring, summer and autumn).

Results and Discussion

Species diets

Vulpes vulpes*:* In both study areas (Pirin and Vitosha), the red fox diet consisted of rodents, plant matter such as wild plums (*Prunus cerasifera*), raspberry and blackberry (*Rubus* sp.), blueberries (*Vaccinium* spp.), *Juniperus* sp. fruits, dog rose (*Rosa canina*), etc.; insects (Coleoptera) as well as remains of hare (*Lepus europaeus*), wild boar (*Sus scrofa*) and various birds. Prevoius data for Bulgaria covered mostly lowlands where the main food sources were domestic fowl and hares (Ruskov 1953; Tsonkov 1961; Peshev 1963) followed by rodents. The few studies in mountain areas found that rodents prevailed in the diet of the fox in Osogovo Mt. (Vasileva *et al.* 2005) and Western Rhodopi Mts. (Kyurkchiev 2008).

In Vitosha, the most important food source were rodents (Fr% = 31.1) followed by insects and dog rose fruits (Fr% = 15.9 and Fr% = 12.4, respectively). Similarly, in Pirin rodents prevailed (Fr% = 36.7) while blackberries, dog rose fruits and other plant matter (Fr% = 7) were less frequent. Insects (Fr% = 6.1), *Juniperus* fruits and, seeds of *Pinus peuce* (only in Pirin, Fr% = 5.2) were less important. Additionally, exclusively in Pirin, foxes fed on insectivores, amphibians and mulberry (*Morus* sp.).

Our results are consistent with data obtained in Finland (Lampio 1952), England (Lever 1957), Germany (Prost et al. 1975; Greutz 1978), Sweden (Englund 1965), Northern Ireland (Fairley 1970), Holland (van Haaften 1970), Poland (Goszsynski 1974; Pielowski 1976; Jędrzjewska & Jędrzjewski 2001), Switzerland (Fuch 1973), Scotland (Hewson & Leitch 1983) and Denmark (Jensen & Sequeira 1978), demonstrating that rodents, insects and fruits are the main food sources for the fox.

We observed a clear difference in food diversity and food consumption frequency by the red fox in different seasons and between mountains (Fig. 2). The seasonal differences were a direct consequence of the availability of particular food types. In spring, mammals (mainly rodents) formed almost half of the relative frequency of the food intake (44.2% for Pirin and 44.4% for Vitosha). In Vitosha, invertebrates (Coleoptera) and plants were of secondary importance, while in Pirin only plant matter (dog rose) was in second place of importance for the diet of the fox. Birds were also occasionally consumed in both mountains. The rodents' dominance in the fox diet during spring has been reported also by Baltrūnaite (2001) for Lithuania, Hartová-Nentvichová *et al.* (2010) for the Czech Republic, Pandolfi & Bonacoscia (1991) for Central Italy. Yet the red fox may show adaptability to local differences feeding in spring mainly on ungulate carrion in Bialowieza (Jędrzejewski & Jędrzejewska 1992), invertebrates in Greece (Vlachos *et al.* 2010) or worms, fruits and garbage in Jura Mountain (Ferrari 1995).

In Vitosha, the importance of mammals as food for the fox was decreasing in summer and they were replaced by fruits (wild plums, blackberries and blueberries *Vaccinium* sp.) and insects, while in Pirin the importance of rodents and fruits remained high, maybe owing to the higher altitude and the presence of mainly coniferous forests. Invertebrates (insects) were of low significance in Pirin in all seasons. Our results are similar to the result for Central and Southern Europe, especially for other mountain areas in Europe (Brangi 1995; Baltrūnaite 2001; Prigioni *et al.* 2008; Vlachos *et al.* 2010), except in Norway and Sweden (citation).

In autumn fruits were again prevailing in the diet of the red fox in both areas (Fr% = 46.3 for Pirin and 42% for Vitosha, respectively). The diversity and Fr% were similar to that in the summer, but the species of fruits were typical of each season. Similar results were reported for other European countries. In winter, the fox diet was relatively poor, especially in Pirin where only mammals and plants were consumed. While the plants (dog rose and juniper fruits) and mammals were equally important for the species in Pirin (Fr% = 50), in Vitosha mammals were more important (Fr% = 57.7% versus 34.6% for plants). Presence of deer, wild boar and domestic animals carrion in the fox diet was also typical for the winter due to their higher mortality. The hare presence in the fox diet also increased in winter. The increased presence of mammals in the fox diet in winter is congruent with the results from Central Europe, while in more southern countries like Italy and Greece the invertebrates and fruits prevail (Brangi 1995, Prigioni *et al.* 2008, Vlachos *et al.* 2010).

In spring, summer and autumn, in both mountains, foxes sometimes ingest garbage such as plastic, nylon and even glass, which probably contained anthropogenic food remains.

***Martes* spp**.: In both mountains, the most important food source for the two marten species were plants, with Fr% = 59.35% for Pirin and 48.4% for Vitosha. They were followed by rodents and inver-

tebrates (mainly coleopterans and grasshoppers). Although the two martens may show great variability in their food preferences, our results are consistent with those from many countries both in lowlands and in mountains (Tester 1986; Marchesi 1989; Brangi 1995; Lanszki *et al.* 1999; Pandolfi *et al.* 2008; Vlachos *et al.* 2010). Yet our results differ substantially from the data coming from the European part of Russia and Central Europe where rodents, birds and insects are much more frequently consumed (Donaurov *et al.* 1938; Aspisov 1973; Grakov 1981; Storch *et al.* 1990; Pulliainen & Olinmäki 1996; Baltrūnaitė 2001; Russell & Storch 2003). This could be owing to the fact that these regions are inhabited mainly by pine martens (which is reported to ingest more animal food than the stone marten), whereas in our study areas (particularly Vitosha) the stone marten is more abundant. Yet, studies from South-eastern Romania (Romanowski & Lesinski 1991) show that birds and mammals may be dominant in the stone marten diet too, while fruits, insects, reptiles and amphibians form less than 10% of its diet. This might be a local adaptation to the adundant birds and small mammals in the region.

In spring, the diet of *Martes* spp. in Pirin consisted of plant matter (Fr% = 41.7), mammals (37.5%) and invertebrates (15.3%). Only in this study area and for this season, the amphibians were of importance, too (Fr% = 4.2%). In Vitosha, mammals were of the greatest importance in spring (Fr% = 39.3) followed by plants (34.5%) and invertebrates (20.2%). Similar results for the importance of plants for the spring diet of *Martes* spp. from Bulgaria were also obtained by Georgiev (2013) for the lowland areas around the towns of Plovdiv and Stara Zagora (Thracian Lowland). The findings of Vasileva *et al.* (2005) for martens' diet in spring in Osogovo Mt. were similar to ours for Vitosha; these aythors reported that the diet was dominated by rodents (Fr% = 37.5%), followed by plants (30.4%) and insects (14.3%). An increased consumption of insects was reported also for the Italian Alps (Prigioni *et al.* 2008) and Central Greece (Vlachos *et al.* 2010) where invertebrates were the main food source in spring, followed by mammals.

During summer in both mountains plant matter (mainly fruits, such as strawberries, blackberries, blueberries and wild plums) had the highest relative abundance. In Pirin, it was twice as big (Fr% = 64.3) as in Vitosha (32%). Invertebrates were second in terms of relative abundance in Pirin (coleopteran and orthopterans), while mammals (rodents) prevailed in Vitosha. Such a preference for fruits is also reported for the pine marten for Spain (Clevenger 1993) and the Italian Alps (Brangi 1995); for the stone marten for Spain (Delibes 1978; Such & Calabuig 2002; Lópes-Martin 2003) and Northern Italy (Bertolino & Dore 1995); and for *Martes* spp. for the Italian Alps (Prigioni *et al.* 2008) and for Central Greece (Vlachos *et al.* 2010).

In autumn and winter, the plant matter (mainly fruits) consumption remained still high for both mountains. For Pirin, in autumn the share of plant matter was even higher than in summer (Fr% =79.4). This is in agreement with the data from other regions in Europe: Eastern Lithuania (Baltrūnaitė 2001), Central Poland (Goszczyński 1986), Northern Italy and the Italian Alps (Brangi 1995; Prigioni *et al.* 2008), Central Italy (Serafini & Lovari 1993) and Central Greece (Vlachos *et al.* 2010). In lowlands of Bulgaria, fruits (*Vitis vinifera*, *Rosa* spp., *Rubus* spp.) were also prevailing in the stone marten diet (Georgiev 2013). Only with few exceptions (Romanowski & Lesiński 1991 for Romania), mammals and birds dominated autumn and winter diet of martens.

While the plant consumption in Pirin in summer and winter was almost the same (64.3% and 65.4%, respectively), fruit and other plant matter consumption in Vitosha increased in winter (Fr% = 57.4) compared to summer (32%). In winter, the diet of martens was relatively poor, consisting only of mammals, plants and birds, with an increase of mammal consumption for both mountains in order to compensate the complete lack of invertebrates during this season. Birds were also ingested more often.

Our findings on the winter diet of martens are similar to studies from other parts of Europe: fruits are the main food item in the Italian Alps (Prigioni *et al.* 2008), Central Italy (Serafini & Lovari 1993) and Central Greece (Vlachos *et al.* 2010). Only in more southern parts where snow covers is absent or scarce (like is Greece), the rodents are replaced by insects.

Trophic niches

We found a substantial overlap in the diets of the red fox and the two marten species in each of the two mountains. This overlap was also clearly valid and strong for the different seasons (Fig. 2), especially for the summer and autumn.

The analyses of the trophic niche breadth (standardised Levins index, $\mathbf{B_A}$) and degree of overlap (Morisita's index of similarity, **C**) for the focal species by season and mountains are shown in Table 1. The general niche breadth was found to be relatively narrow, especially for the fox and *Martes* spp.

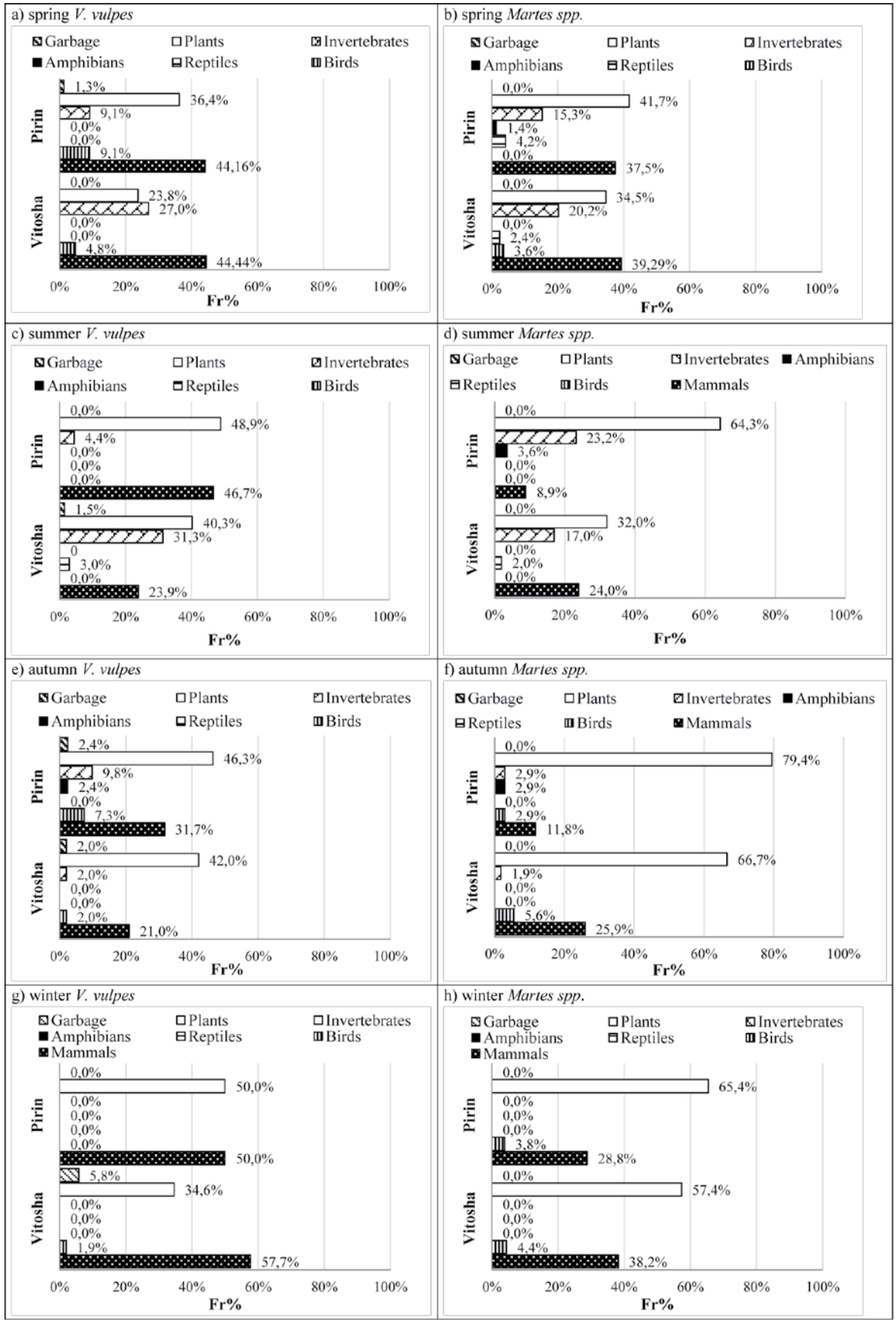


Fig. 2. Relative frequency (Fr%) during different seasons (a-h) of the main diet components for *V. vulpes* and *Martes* spp. in the two study areas

from Vitosha, while it was broader for the martens from Pirin. This was due to the fact that although the species may use numerous types of food, they prefer a limited number of food sources, which are with high significance in their diet. Thus, although *Martes* spp. and *V. vulpes* are extremely abundant and adaptable food opportunists capable of taking a wide spectrum of food (Amores 1975), in our study areas they were mostly facultative specialists preferring limited food types.

The trophic niche breadth was narrowest in spring in both mountains. The degree of overlap between the red fox and the martens was the highest (0.97) during this season in Vitosha. This was due to the fact that, for both *V.vulpes* and *Martes* spp., about 70% of the diet consisted of only three types of food, thus the overlap was expectedly high. Such substantial spring overlap is also found in other areas in Europe: in Hungary by Lanszki *et al.* (2007), in Spain by Padial *et al.* (2002), in Southern Poland by Skalski & Wierzbowska (2008). The niche overlap was still high in summer in Vitosha, while it was lowest (with the widest niche breadth) in autumn, again in Vitosha when plant matter was abundant and the largest amount of plants was ingested by studied species. Pirin is covered mainly by coniferous forests (92.36% of its territory) and in autumn the niche breadth was narrow. The overlap was relatively less pronounced in winter in both mountains.

Spatial niches

Spatial niche analyses were made based on the camera trap data. The comparison of the forest type selectivity index in the two study areas (Fig. 3 a and b) showed that while in Pirin *M. foina* preferred strongly scattered trees and shrubs (0.90) and rarely visited deciduous forests, *M. martes* preferred coniferous forests and strongly avoided areas with scattered trees and shrubs. The fox showed a slight preference for coniferous forests and complete avoidance of scattered trees and shrubs. In Vitosha, all three species exhibited clear preference for coniferous forests (more pronounced for the stone marten than for the pine marten). There was no forest type where the fox was completely dominant. In all forest types, the three species clearly avoided scattered trees and shrubs.

Forest visibility is a relative but an important factor for avoiding predators and competitors. It is habitat dependant and may vary in different areas. In our study (Fig. 3 c and d), the fox showed a strong selection for border areas between open and closed forests (0.99) in Pirin and avoided them in Vitosha. Although some studies (Brainerd & Rolstad 2002) showed that the pine marten strongly avoided clear cuts and openings, in our study we found a positive selection for open forest by pine martens in Vitosha. Such positive selection for open forests was found also for the fox. Open forests might be a place for competition for food resources or even intraguild predation (Lindström *et al.* 1995). The stone marten showed a positive selection to closed forest in both mountains, while in Pirin such selection was observed for the fox and the pine marten, too.

The results of this partitioning by forest type and visibility did not show clear patterns regarding the spatial strategies of the three species to avoid competition. Moreover, the presence of unidentified martens (*Martes* sp.) was contributing additionally to the unclear picture. As the spatial niche partition is a dynamic process, it likely depends on a combination of factors (i.e., type of forest and visibility as well as other intrinsic adaptations as temporal displacement of the activity).

There was, however, a distinct seasonal pattern of preferences and avoidance of some forest types in both mountains (Table 2). Mixed (deciduous and coniferous) forests were avoided by the three species in spring, as well as the deciduous forests by the two marten species. In summer, the pine marten had a persistent positive selection for mixed forests in both mountains, while deciduous forests were avoided by the species during the three seasons in both mountains. In autumn, the pine marten and the fox had a positive selection for mixed forests, while the stone marten selected for all three type of forests in Vitosha. Mixed forests were preferred by all

Table 1. Trophic niche breadth (as standardised Levins index–B_A) and overlap (as Morisita's index of similarity–C) for the studied species by season and mountains

	Vitosha			**Pirin**		
	B_A		**C**	B_A		**C**
	Vulpes vulpes	***Martes* spp.**		***Vulpes vulpes***	***Martes* spp.**	
Spring	0.35	0.34	0.97	0.38	0.41	0.93
Summer	0.40	0.40	0.88	0.44	0.76	0.56
Autumn	0.46	0.51	0.38	0.60	0.40	0.53
Winter	0.44	0.34	0.44	0.66	0.48	0.42

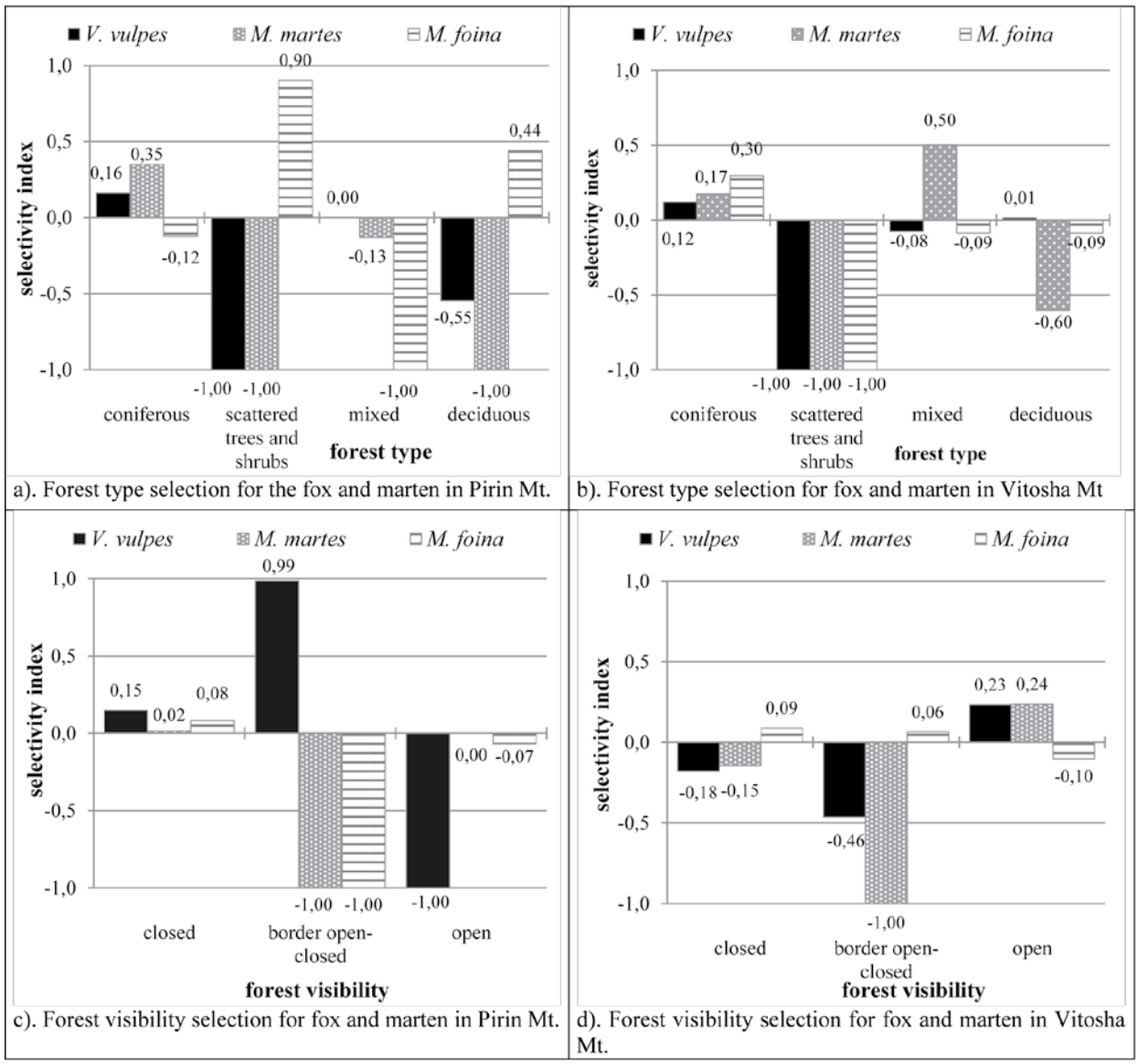


Fig. 3. Forest type and visibility selectivity index comparison for the fox and martens species in the two study areas. Values above 0 are showing positive selection of the habitat, values below 0 are showing level of avoidance

species in Vitosha in autumn because they provided the diversity of plants ingested predominantly by the three species. Nevertheless, this dod not contribute to an increasing overlap of the food niche, which suggests that not the spatial avoidance but another mechanism has been responsible for the competition alleviation.

The camera trap data were also tested for spatial shifts on the altitude gradient for these sympatric species. The percentage of registrations of the focal species at different altitudinal classes pooled for all seasons in Vitosha and Pirin are presented in Table 3.

Based on the pooled data for all seasons in Vitosha, the red fox and the stone marten were most frequently registered at altitudes 1001-1400 m, whereas the pine marten inhabited sites of slightly higher altitude (1201-1600 m). This is in accordance with the results from a study in Sardinia, Italy (Lombardini *et al.* 2015). Inhabiting the same altitude might lead to a high overlap between the food and spatial niches of the red fox and the stone marten. The pine marten also had an altitudinal overlap with the other two species, but is known to prefer primary, undisturbed forests (Kurki *et al.* 1998; Goszczyński *et al.* 2007; Fusillo *et al.* 2009; Caryl *et al.* 2012). This may be the reason why it avoided the area 1000-1200 m in Vitosha, an attitudinal belt with intensive human presence and activities. In Pirin, the red fox was registered mostly at 1401-1800 m. The pine marten was registered in areas at 1401-1600 m and 1801-2000 m, while the stone marten was mostly present in lower areas (1001-1400 m). This could be due to competitive exclusion (the stone marten

Table 2. Selectivity index for the forest type use during the three studied seasons for the red fox and the two martens in Vitosha and Pirin Mts.
Values above 0, are showing positive selection of the habitat, values below 0 are showing level of avoidance

		Pirin Mt.				Vitosha Mt.			
		V. vulpes	*M. martes*	*M. foina*	*Martes* sp.	*V. vulpes*	*M. martes*	*M. foina*	*Martes* sp.
forest type-spring	coniferous	**0.50**	***1.00***	***1.00***	***1.00***	-0.07	-1.00	-1.00	***0.79***
	mixed	-0.50	-1.00	-1.00	-1.00	-0.52	-1.00	-1.00	-1.00
	deciduous	-1.00	-1.00	-1.00	-1.00	**0.40**	-1.00	-1.00	**0.79**
forest type-summer	coniferous	-0.22	-0.35	-0.69	-0.29	-0.88	-1.00	-0.07	**0.35**
	mixed	-0.15	**0.35**	-0.98	-1.00	-0.49	**0.71**	**0.52**	-1.00
	deciduous	***1.00***	-1.00	-0.95	-0.97	**0.64**	-0.57	***0.87***	**0.94**
forest type-autumn	coniferous	-0.73	-0.76	-0.38	-0.78	**0.27**	**0.54**	**0.15**	**0.35**
	mixed	**0.73**	***0.76***	-0.96	-0.93	**0.27**	**0.60**	**0.68**	**0.85**
	deciduous	-1.00	-1.00	-1.00	-0.97	-0.36	-0.83	***0.76***	**0.35**

Table 3. χ^2-test of the differences between the distributions of the studied species in different altitudinal classes of the both mountains

a). Vitosha Mt.
(samples between 1601 m. a.s.l. and 1800 m. a.s.l. were too small to be analyzed and are excluded)

	χ^2	d.f.	P
M.martes vs. M. sp.	7.155	3	0.067
M. foina vs. M. sp.	0.206	3	0.977
M. martes vs. M. foina	7.169	3	0.067
V. vulpes vs. M. martes	10.547	1	**<0.05***
V. vulpes vs. M. foina	7.95	3	**<0.05**
V. vulpes vs. M. sp.	9.906	3	**<0.05**

* only samples between 1201-1400 m. a.s.l. and 1401-1600 m. a.s.l. were big enough to be included)

b). Pirin Mt.
Due to small sample sizes not all altitudinal classes are included in the analyses (noted with asterisks)

	χ^2	d.f.	P
M.martes vs. *M.* sp.	0.103	1	0.749*
M. foina vs. *M.* sp.	10.205	2	**<0.05****
M. martes vs. *M. foina*	16.542	2	**<0.05****
V. vulpes vs. *M. martes*	7.54	2	**<0.05*****
V. vulpes vs. *M. foina*	3.976	1	**<0.05******
V. vulpes vs. *M.* sp.	0.007	1	0.935*

* 1201-1400 m. a.s.l. and 1601-1800 m. a.s.l.
** 1201-1400 m. a.s.l., 1401-1600 m. a.s.l., 1601-1800 m. a.s.l.
*** 1201-1400 m. a.s.l., 1601-1800 m. a.s.l., 1801-2000 m. a.s.l.
****1201-1400 m. a.s.l. and 1401-1600 m. a.s.l.

being the smallest and the submissive species of all three; Rosellini at al. 2008) or better adaptability of the stone marten to human presence and the occurrence of stray dogs. Alternative explanation could be the evolutionary differences between the two marten species: the pine marten, being a more northern species, is adapted to more humid environment provided by the higher altitudes, whereas the stone marten, being a southern species, is adapted to lower xerophilous habitats.

The percentage of registrations of the three species at different altitudinal classes in spring in Vitosha and Pirin are presented in Fig. 4 a and b.

In spring the red fox and the stone marten were mostly present at altitudes of 801-1400 m in Vitosha, although they have lower overlap at sites at 1001-1200 m, possibly indicating the dominance of the red fox in its most preferred areas (Prigioni *et al.* 2008; Carvalho & Gomes 2004). Areas at 801-1000 m and 1201-1400 m were inhabited by all three species simultaneously in spring. This might be owing to scarce food resources and the related expansion of their foraging territories, which caused a greater overlap. In Pirin, there was a clear pattern of avoidance between the red fox (registered mostly at 1801-2000 m) and the stone marten (with 0 registrations in this altitudinal class), likely an evidence of competitive exclusion. There was an overlap between the altitudinal distribution of the stone and pine martens.

The percentage of registrations of the three species at different altitudinal classes during the summer in Vitosha and Pirin are presented at Fig. 5.

In summer all three species were registered in Vitosha mostly at 1001-1400 m. Food resources are

abundant during this season which alleviates the effects of trophic competition without the need of competitive exclusion (Barrull *et al.* 2013). In Pirin, during the summer there was a high overlap between the altitudinal distribution of the pine marten and the red fox (both most frequently registered at 1601-1800 m), whereas the stone marten was most abundant in the belt at 1401-1600 m. Areas with elevation of 1001-1200 m were of secondary importance for all three species, where they coexisted with relatively high abundance. The martens in Pirin had higher trophic niche breadth compared to the red fox, and the degree of overlap between the food niches was low. The competition here is alleviated by differential use of food resources (Barrull *et al.* 2013) and partial displacement of the stone marten.

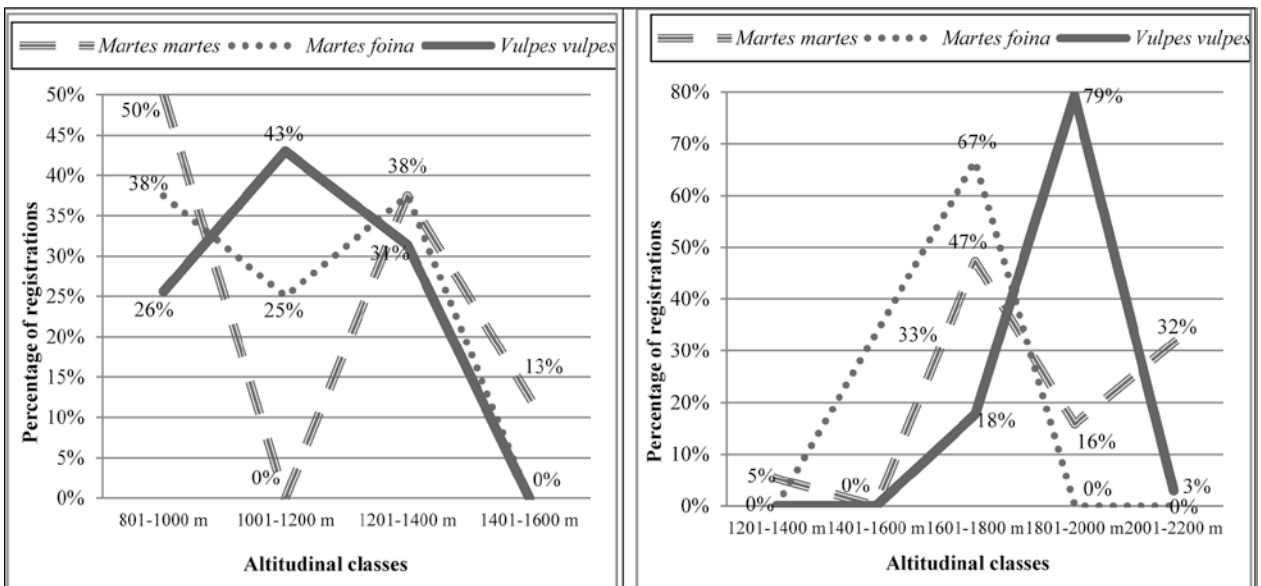
The percentage of registrations of the focal species at different altitudinal classes in autumn in Vitosha and Pirin are presented at Fig. 6 (a and b). In Vitosha, during the autumn there was high overlap between the altitudinal distribution of the red fox and the stone marten, alleviated by the low food niche overlap. The same is valid for the pine marten and the fox at 1601-1800 m in Pirin.

Behavioral mechanisms alleviating competition

Apart from seasonal shifts of habitat use and altitude displacement, there was a clear activity pattern of species avoidance. The χ^2-test of the differences in circadian activity did not show a significant difference in the overall activity between the species (Table 4). However, there was such a difference within the different seasons and hourly activity.

The circadian activity of the red fox and the two martens are summarised in Fig. 7 (a-f). The red fox was predominantly nocturnal in all seasons in both mountains with around 30% of the registrations recorded during the day and about 5% crepuscular activity. Being highly adaptable and the dominant of the three studied species, the red fox does not need to adjust its daily activity in order to avoid competition (Rosellini *at al.* 2008). The pine marten was predominantly diurnal in Vitosha during the spring and summer (it was not registered during autumn), whereas it had arrhythmic activity during all seasons in Pirin. In spring, the stone marten from both mountains was active mostly during the night. In the summer and autumn in Vitosha Mountain the stone marten had arrhythmic activity (indicated by similar number of registrations during the day and night). Possible explanation could be owing to switching partially to plant food which is generally abundant in these seasons and can be accessed during the daytime, thus avoiding the stronger competitors temporally. In Pirin the stone marten was more active during the night during all seasons and avoided direct competition by spatial displacement.

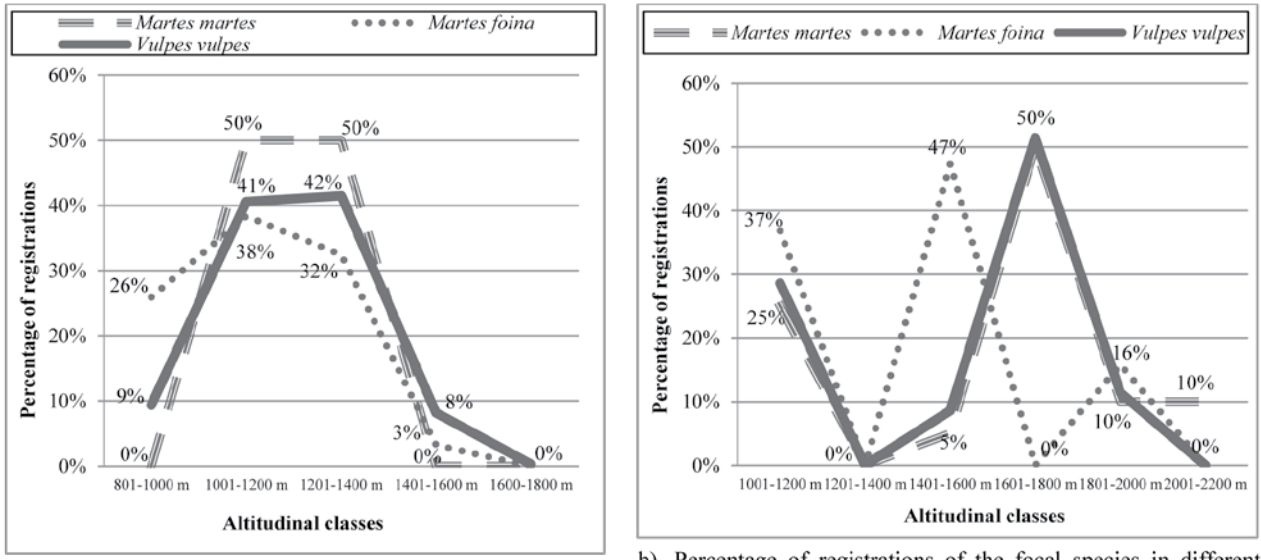
The hourly activity of the red fox and the martens in different seasons in Vitosha and Pirin is presented in Fig. 8 (a-h). In Vitosha, throughout the year the activity of the focal species peaked during the night or crepuscular hours while diurnal activity



a) Percentage of registrations of the focal species in different altitudinal classes in Vitosha during the spring

b). Percentage of registrations of the focal species in different altitudinal classes in Pirin during the spring

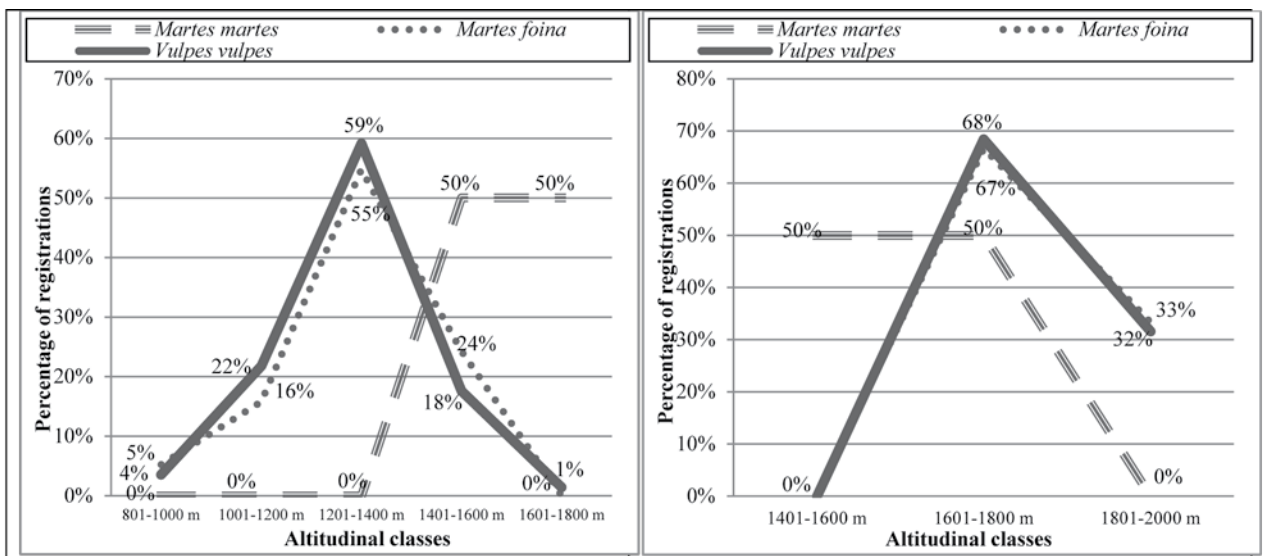
Fig. 4. Percentage of registrations of the focal species in different altitudinal classes in both mountains during the spring



a). Percentage of registrations of the focal species in different altitudinal classes in Vitosha during the summer

b). Percentage of registrations of the focal species in different altitudinal classes in Pirin during the summer

Fig. 5. Percentage of registrations of the focal species in different altitudinal classes in both mountains during the summer



a). Percentage of registrations of the focal species in different altitudinal classes in Vitosha during the autumn

b). Percentage of registrations of the focal species in different altitudinal classes in Pirin during the autumn

Fig. 6. Percentage of registrations of the focal species in different altitudinal classes in both mountains during the autumn

was much lower. These results are similar to those of Akbaba & Ayas (2012) obtained for Turkey, Barrull *et al.* (2013) for Spain, Monterosso *et al.* (2014) in Portugal and Spain and Bischof *et al.* (2014) in Pakistan. Such rhythms of activity can be explained with significant human disturbance, typical of this urbanised mountain, frequently visited by tourists, gatherers and hunters. The general trend of temporal avoidance between the martens and the fox had an offset between the activity peaks of approximately one or two hours during all seasons. In most cases, the martens were active earlier in the morning and later in the night, as compared to the activity peaks of the red fox. In Pirin, during the day we had higher number of registrations of the focal species, which could be attributed to the more isolated and inaccessible nature of the mountain with its limited human presence and disturbance. The peaks of activity of the fox and the martens in Pirin also had an offset (1-4 hours), which again points to temporal avoidance as an important mechanism for coexistence between these species.

Table. 4. χ^2-test of the differences in the overall circadian activity of the studied species in both mountains (crepuscular activity was excluded due to small sample size)

a) Vitosha Mt.

	χ^2	d.f.	P
M.martes vs. *M.* sp.	30.778	1	**<0.05**
M. foina vs. *M.* sp.	4.78	1	**<0.05**
M. martes vs. *M. foina*	12.567	1	**<0.05**
V. vulpes vs. *M. martes*	5.42	1	**<0.05**
V. vulpes vs. *M. foina*	7.566	1	**<0.05**
V. vulpes vs. *M.* sp.	38.238	1	**<0.05**

b). Pirin Mt.

	χ^2	d.f.	P
M.martes vs. *M.* sp.	12.71	1	**<0.05**
M. foina vs. *M.* sp.	-*	1	**<0.05**
M. martes vs. *M. foina*	16.162	1	**<0.05**
V. vulpes vs. *M. martes*	4.227	1	**<0.05**
V. vulpes vs. *M. foina*	8.769	1	**<0.05**
V. vulpes vs. *M.* sp.	6.051	1	**<0.05**

*sample size too small to be analyzed

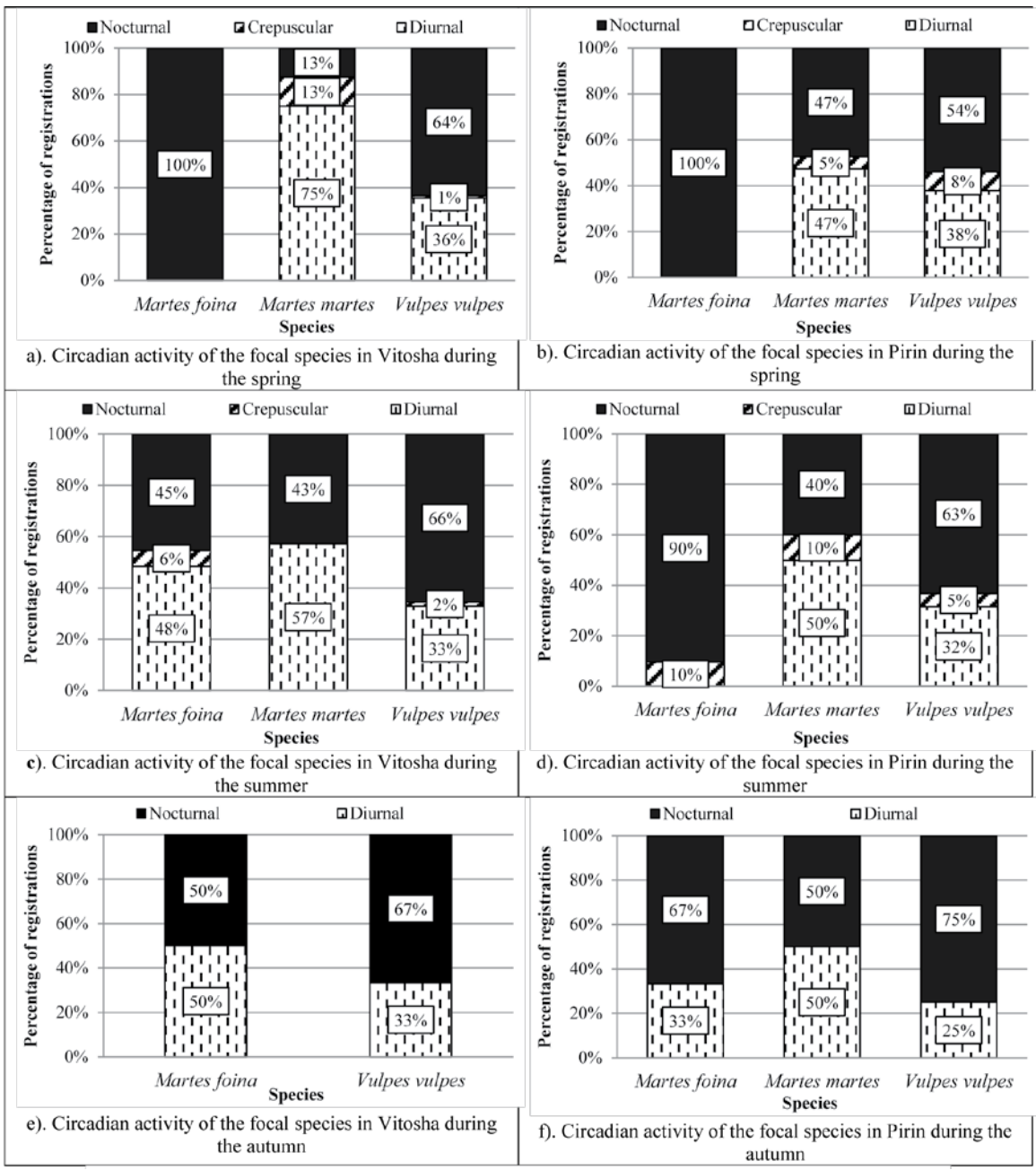


Fig. 7. Circadian activity seasonality of the red fox and the two martens in Vitosha and Pirin

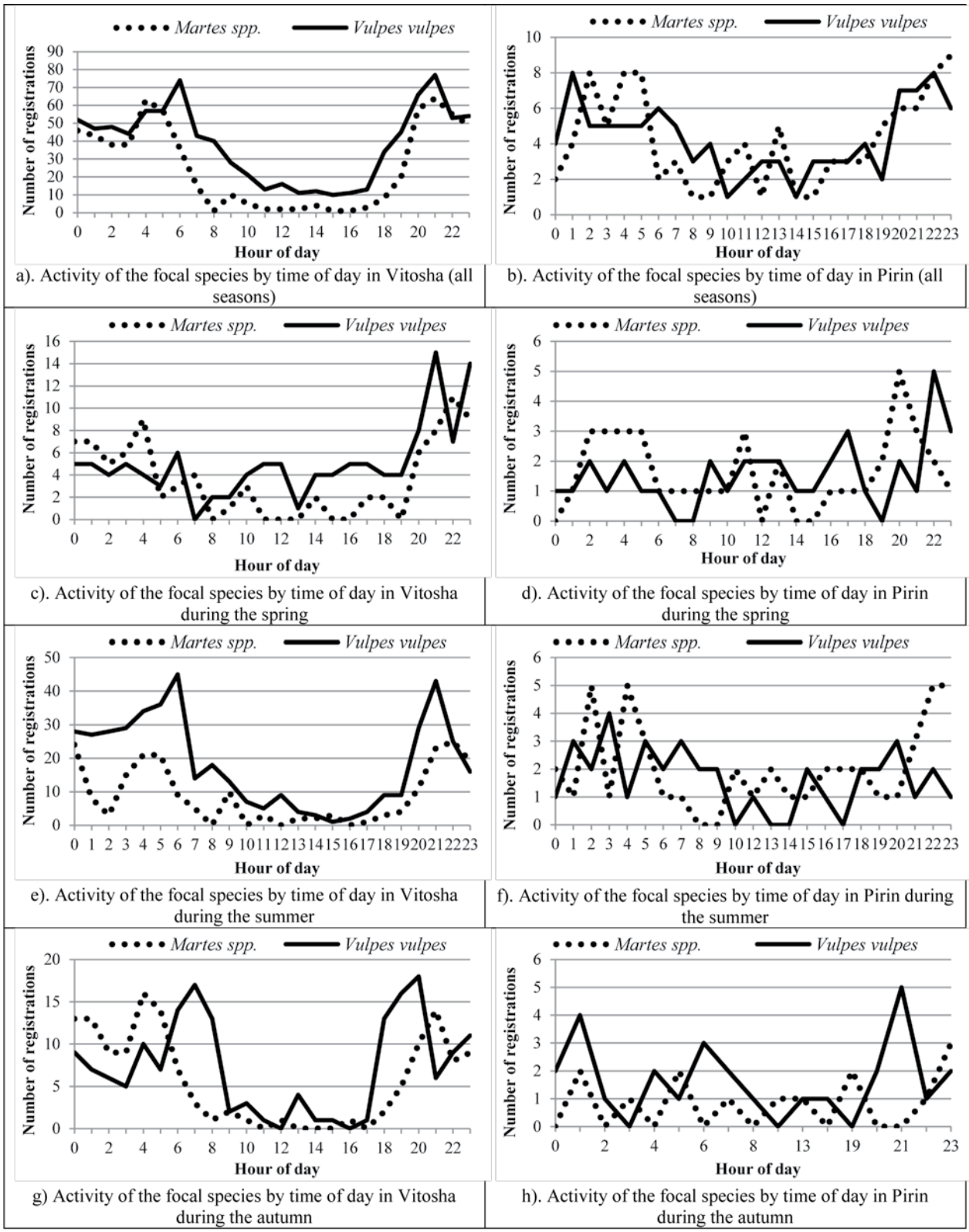


Fig. 8. Hourly activity of the focal species for Vitosha and Pirin by season. Hourly activity samples for the martens were too small and thus were pooled as *Martes* spp

Conclusions

The red fox *V. vulpes* and the two marten species (*M. martes* and *M. foina*) are widely distributed and abundant in mountain areas in Bulgaria; however, their interspecific relationships and competition have not been extensively studied. The mechanisms for avoiding competition or even intraguild predation were a combination of factors, which show seasonal and temporal shifts in the habitat use and, thus, in food resource utilisation. These mechanisms are very robust and provide the species with the appropriate adaptation tools for successful coexistence with all three species being able to maintain high abundance. Further studies are needed in order to reveal the intrinsic links between the food and spatial niches of these successful sympatric species.

Acknowledgements: We express our sincere gratitude to the staff of Vitosha Nature Park and Pirin National Park for providing the camera traps. We appreciate the commitment and enthusiasm of everyone involved in the fieldwork. We thank the anonymous reviewers for their constructive comments, which helped us improve the manuscript.

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Received: 08.05.2015
Accepted: 12.08.2016