

Niche segregation between two medium-sized carnivores in a hilly area of Hungary

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The Eurasian badger (*Meles meles*) and the red fox (*Vulpes vulpes*) are the two most widespread medium-sized carnivores in Hungary. We hypothesise that niche segregation between these species may be observed in the selection of burrow sites. Burrow-site selection was investigated by evaluating habitat preferences for three habitat categories (forest covered, open and mixed). Differences between overall habitat selection by the two species within the study areas were not significant, but the area ratios of habitat categories within the immediate surroundings (400 m) of burrows were significantly different. Around the red fox burrows, the ratios of mixed habitats and small-mammal hole densities were significantly higher ($p < 0.001$ and $p = 0.007$, respectively) than around those of the Eurasian badger. This led us to conclude that the red fox, due to its diet, may select sites rich in small mammals, which is manifested in the preference and use of mixed habitats.

Introduction

The impacts of carnivore species on ecosystems have been described by several studies (Crooks & Soulé 1999, Glen *et al.* 2007). Since activity, feeding habits, habitat selection, predator–prey and predator–predator relations of these species determine food web structures (Crooks & Soulé 1999, Glen *et al.* 2007), the investigation and understanding of predator–predator and predator–prey relations are essential in determining well-grounded conservation measures and treatments (Glen *et al.* 2007, Csányi 2007, Ripple & Beschta 2012). There are different types of interactions among carnivore species. In some cases, larger carnivores regulate the number of smaller carnivores in direct and indirect ways (top-down)

(Crooks & Soulé 1999, Miller *et al.* 2001, Glen *et al.* 2007). This regulation may manifest itself by exclusion from the territory (Arjo & Pletscher 2004, Helldin & Danielsson 2007), by forcing dietary shifting, by changes in daily activity, or simply by treating smaller carnivores as prey (Palomares *et al.* 1995, Palomares & Caro 1999, Glen *et al.* 2007, Kowalczyk *et al.* 2009, Kowalczyk & Zalewski 2011). These relations apply to carnivores at the same trophic level. Between carnivore species of the same size, indirect niche segregation occurs instead of competition by direct interactions. Species living in the same habitats, having similar body sizes and diets, may diverge in their spatial (Fedriani *et al.* 1999, Holmala & Kauhala 2009) and temporal (Fedriani *et al.* 1999, Biró *et al.* 2004, Glen *et al.* 2007)

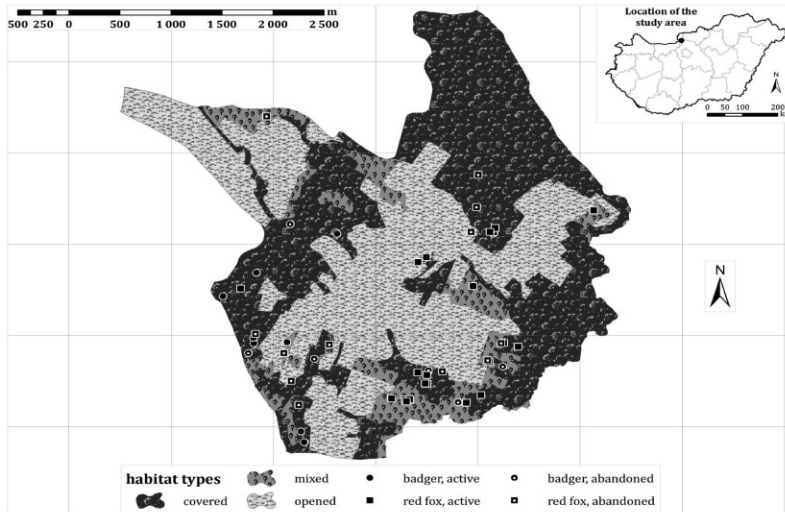


Fig. 1. Study area and burrow locations in northern Hungary.

habitat use, or in the role that common prey species play in the predator's life history (Kauhala *et al.* 1998, Lanszki *et al.* 1999, Lanszki *et al.* 2006). We know little about these interactions in the case of such commonly widespread species as the Eurasian badger (*Meles meles*) or the red fox (*Vulpes vulpes*). According to some data (Kowalczyk *et al.* 2000, Macdonald *et al.* 2004, Kowalczyk *et al.* 2008), the Eurasian badger is seen to be a better competitor. Several studies (Kauhala 1994, Goszczyński 1999) have shown that partial winter hibernation and monogamous upbringing of cubs are reproductive assets for the raccoon dog (*Nyctereutes procyonoides*) against the red fox. Based on this finding, it is logical to assume that larger, similarly behaving animals, such as the Eurasian badger (Kruuk 1989, Neal & Cheeseman 1996, Heltai 2010), are better competitors than the red fox. Nonetheless, in most European countries, including Hungary, both the Eurasian badger and the red fox are common and abundant (Mitchell-Jones *et al.* 1999, Heltai *et al.* 2001, Kranz *et al.* 2008, Macdonald & Reynolds 2008, Heltai 2010). The occurrence of the two species highly overlaps (Heltai 2010), they dig similar burrows (Fedriani *et al.* 1999, Kowalczyk *et al.* 2008), and can even use each other's burrow (Kowalczyk *et al.* 2008, Heltai 2010). Thus, the badger and the fox coexist while using similar sources, and we predict that this may be due to niche segregation between these two species.

According to our hypothesis, these species select different burrow sites with different vegetation, habitat structure and diversity. Our hypothesis was tested in a Hungarian deciduous, mid-mountainous forest where both species are commonly found and have always coexisted (Heltai 2010).

Material and methods

Study area

The study area is located in northern Hungary, on the southern slopes of the Börzsöny Mountains among the villages Szob, Márianosztra and Kóspallag. Its area is 1256.7 ha; bordered by roads to the north, west and east, and by a stream at the southern edge (Fig. 1). The highest point of the area is 335 m a.s.l., whilst the lowest lies at 140 m a.s.l. Deciduous forest covers 54.8% (688.2 ha) of the area, where the Turkey oak (*Quercus cerris*) and the sessile oak (*Quercus petraea*) dominate, but common hornbeam (*Carpinus betulus*) and Scots pine (*Pinus sylvestris*) stands are also present. The common privet (*Ligustrum vulgare*), common hawthorn (*Crataegus monogyna*) and common dogwood (*Cornus sanguinea*) primarily form the shrub strata. Smaller parts of the area may be classified into two categories: 33.4% is in agricultural use (420.1 ha) and 11.8% lies within a shrubby-

grassy (148.4 ha), natural-like area. Almost half of the agricultural lands are meadows (209.5 ha), and crop production (common wheat *Triticum aestivum*, barley *Hordeum vulgare*, rapeseed *Brassica napus*, sunflower *Helianthus annuus* and corn *Zea mays*) takes place in 210.6 ha.

The climate is mountainous temperate with a mean annual rainfall of 700 mm. Eighty to 90 days per year have more than 1 mm of precipitation. The mean annual temperature is 9.0–9.5 °C. The mean temperature in January is –2 °C, while in June it is 16 °C. The temperature remains below 0 °C for 120–140 days per year. Snow cover is present for 100–150 days per year. The annual number of sunny hours can reach 1850.

Sampling methods

We carried out a complete count of burrows on 18, 19, 20 and 25 February 2011 and on 17, 23, 27 and 30 January and on the 2 February 2012. Altogether, 53 burrows (Eurasian badger $n = 20$, red fox $n = 33$) were found and recorded using GPS. The following data were recorded in each case: use (active or abandoned), species, number of entrances/exits, footprints, faeces, latrine, odour, prey remains and vegetation. Burrows with identifiable species-specific footprints, and at least one other indirect index were considered “active”. Burrows not fulfilling this criterion were recorded as “abandoned”. Fieldwork was carried out in the winter because it was easier to find all the burrows when the vegetation had died back. The state of burrows (whether it was active or abandoned) was rechecked on 3 and 4 August 2011, and during the small-mammal hole density estimation in 2012. Surveys carried out on different dates did not show significant differences [Fisher’s exact test, two-sided: $p = 1.000$ (2011), $p = 1.000$ (2012); Fisher 1922] in burrow occupancy.

In order to calculate habitat preferences based on the location of active burrows of the two species, the study area was classified into different vegetation groups. Basic land cover data were obtained from the Corine Land Cover (CLC) database (scale 1:100 000), which were modified with the ArcGIS 9.3 software and veri-

fied using forestry maps and fieldwork. Three habitat categories (covered, open and mixed) were established. The covered category consists exclusively of stands with a closed canopy. Areas in agricultural use, meadows and fallows were considered as open habitats. Shrubby areas and young forest stands were grouped into the mixed category. Distribution per habitat type of the two carnivores’ burrows was investigated using Fisher’s exact test. Habitat preferences were evaluated using Ivlev’s selectivity index and Bonferroni’s Z-test (Strauss 1979, Byers *et al.* 1984), using Microsoft Excel 2010 and GraphPad InStat softwares. Habitats of the entire designated study area were considered when testing for habitat preference.

We obtained detailed data on the generic soil type structure of forest stands in the sample area from the forestry units. Since the soil data contained information only on forested areas, we excluded burrows that were not located within the range of these stands. However, this did not lead to major changes in sample size; only one fox-burrow had to be excluded. Three soil-type categories were established: brown forest soils, leptosols and grassland soils. Distribution per soil type of the two carnivores’ burrows was investigated using Fisher’s exact test.

The second question our study focused on was the ratios of habitat categories in the immediate surroundings of burrows. Buffer areas with a radius of 1200 m, 800 m and 400 m were delineated around each burrow. This resulted in three different buffer areas (452.2 ha, 201.0 ha and 50.2 ha, respectively). These areas correspond to home range sizes of the two species measured in continental climates (Weber & Meia 1996, Tuytens *et al.* 2000, Kowalczyk *et al.* 2003, Kowalczyk *et al.* 2006). Within these buffer areas, habitat categorization was based on the modified CLC layer. The same three categories were used as in the habitat preference study (covered, open and mixed). Ratios of habitat categories around burrows of the Eurasian badger and the red fox were compared in Microsoft Excel 2010 by a two-sample *t*-test and the Welch test (Ruxton 2006).

Diversity of the vegetation mosaic within buffer areas was calculated using Simpson’s and Shannon’s diversity indices (Heip & Engels

1974) and calculated using Ken Buja's Diversity Calculator. The basic difference between these diversity indices is that Shannon's diversity index takes small-sized habitat patches into account with larger weight, since Simpson's diversity index is more sensitive for dominant habitats (Heip & Engels 1974). The data were compared in Microsoft Excel 2010 using a two-sample *t*-test and the Welch test (Ruxton 2006).

Small-mammal hole densities were measured on 25 and 26 February and 2, 3 and 4 March 2012. Holes were recorded in four directions (north, east, south, west) from the large burrows (with at least three entrances/exits) in two parallel, 2-m-wide, and 400-m-long transects. The distance between the two parallel transects was 5 m. Only holes fulfilling the criteria of Váczi and Altbäcker (2005) (i.e. diameter does not exceed 4 cm, angle between the soil surface and the hole direction is less than 30°, and holes are joined to other holes by trace net within 0.5–1 m²) were taken into consideration. The following small mammal species occur in the study area: bi-coloured white-toothed shrew (*Crocidura leucodon*), lesser white-toothed shrew (*Crocidura suaveolens*), common shrew (*Sorex araneus*), pygmy shrew (*Sorex minutus*), Miller's water shrew (*Neomys anomalus*), water shrew (*Neomys fodiens*), common vole (*Microtus arvalis*), European pine vole (*Microtus subterraneus*), water vole (*Arvicola amphibius*), bank vole (*Myodes glareolus*), striped field mouse (*Apodemus agrarius*), yellow-necked mouse (*Apodemus flavicollis*), harvest mouse (*Micromys minutus*), eastern house mouse (*Mus musculus*) and steppe mouse (*Mus spicilegus*) (Bihari *et al.* 2007, Hicker *et al.* 2010). The data were analyzed in Microsoft Excel 2010 using the Welch test (Ruxton 2006). The relationships of small-mammal hole density to habitat categories and to

diversity indices was investigated using a simple linear regression, where hole density was the response variable. These calculations were done using the GraphPad InStat software.

Results

Only active burrows of the Eurasian badger and the red fox were taken into consideration in the habitat preference calculations. There was no habitat selection based on generic soil types either for the Eurasian badger (Fisher's exact test, two-sided: $p = 1.000$) or for the red fox (Fisher's exact test, two-sided: $p = 0.175$).

Taking vegetation instead of soil type into consideration, a different picture emerges. The two species had the same number of burrows in covered habitats. In mixed habitats, red fox burrows were present in higher numbers, and neither European badger nor red fox burrows were found in open habitats (Table 1).

Both the Eurasian badger (Fisher's exact test, two-sided: $p = 0.002$) and the red fox (Fisher's exact test, two-sided: $p < 0.001$) seemed to use habitat categories to different degrees, which is to be expected given the different proportions of habitat categories in the study area. Habitat preferences calculated for the entire area, based on active burrows, showed that the Eurasian badger preferred covered habitats (0.31) and avoided open (−1.00) and mixed (−0.13) habitats. The red fox preferred covered (0.16) and mixed (0.54) habitats and avoided open habitats (−1.00). The Bonferroni Z-test revealed that the Eurasian badger's preference for covered and avoidance of open habitats are significant (Bonferroni Z-test [3] = 2.407, $p < 0.05$, $n = 13$); however in the case of the red fox only the avoidance of open habitats

Table 1. Size and proportion of habitat categories and the number (*n*) and percentage of active burrows per habitat category.

Habitat types	Size (ha)	Proportion (%)	Active burrows			
			Badger (<i>n</i>)	Badger (%)	Red fox (<i>n</i>)	Red fox (%)
Covered	610.6	48.6	12	92.3	12	66.7
Opened	521.8	41.5	0	0	0	0
Mixed	124.3	9.9	1	7.7	6	33.3
Total	1256.7	100	13	100	18	100

seemed to be significant (Bonferroni Z-test [3] = 2.407, $p < 0.05$, $n = 18$) (Fig. 2). No differences were found between the two carnivores' overall habitat selection within the study area (Fisher's exact test, two-sided: $p = 0.191$).

Within the 1200-m buffers, differences were found between the two species. Around the red fox burrows, the ratio of mixed habitat category was significantly higher than for burrows of the other species (Table 2). Taking into account the active burrows only, we found that the ratios of open habitat category in the case of the Eurasian badger, and of mixed habitat category in the case of the red fox, are significantly higher. When only large active burrows (with at least three entrances/exits) were studied, the only significant difference was found in the mixed habitat category (Table 2).

Within the 800-m buffer areas, the ratio of the mixed habitat category seemed to be significantly higher around red fox burrows than around those of Eurasian badgers. Similar results were found when only the surroundings of active burrows were compared: the ratio of the mixed habitat category was significantly higher around red fox burrows, but the ratios of covered and open habitat categories within the 800-m buffer areas did not differ between the two species. The same applies to the results calculated only with large active burrows (Table 2).

The ratios calculated in the 400-m buffer zones for each burrow demonstrate that the mixed habitat category was significantly higher around red fox burrows, while the ratios of covered and open habitat categories were not significantly different (Table 2). Similarly, in the case of active red fox burrows, only the ratio of the mixed habitat category was statistically higher. Focusing only on large active burrows, the same result was obtained (Table 2).

Differences between the two species in terms of vegetation diversity (Simpson's index) for the buffer area of 1200 m for all burrows were not significant; however, significant differences were found when only the active burrows and the large active burrows were used in the calculations (Table 3). Within the 800-m buffer area, a slight difference was apparent: Simpson's diversity was higher in areas surrounding the red fox burrows than in those around the burrows

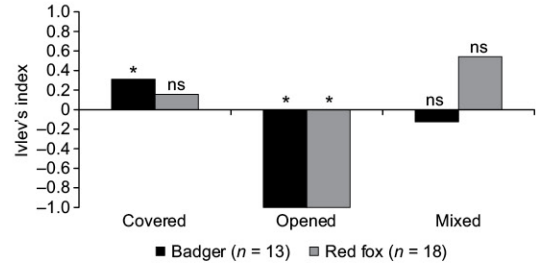


Fig. 2. Habitat selection of the Eurasian badger and the red fox based on Ivlév's electivity index and Bonferroni's Z-test. * = $p < 0.05$, ns = $p > 0.05$

of Eurasian badgers, especially for large active burrows (Table 3). Within the smallest (400 m) buffer area, Simpson's diversity index was not statistically different between the two species (Table 3), except when only the large active burrows were analysed.

Shannon's diversity was higher both within 1200- and 800-m buffers surrounding the red fox burrows when all burrows, active burrows, or large active burrows were considered (Table 3). Focusing only on the 400-m buffer area of each burrow, Shannon's diversity of the burrows' surroundings was not significantly different between the red fox and the Eurasian badger. For active burrows, still no significant differences were found, but for large active red fox burrows, this diversity index was significantly higher (Table 3).

We showed that small mammal hole densities were statistically higher (Welch-test: $t_w = 3.975$, $df = 6$, $p = 0.007$, $n = 16$) next to red fox burrows (mean \pm SD) (201.12 ± 81.23 holes ha^{-1}) than next to Eurasian badger burrows (74.22 ± 26.21 holes ha^{-1}) (Fig. 3). The density of small mammal holes was not statistically dependent on the ratio of the covered habitat category, but in the case of open vegetation, a significant relationship was found that explained almost a quarter of the variance in small mammal hole density. In the mixed habitat category, a significant relationship was found that explained 90% of the variance in small mammal hole density (Table 4). Significant effects were also found in relation to Simpson's and Shannon's diversity indices, where these predictors explained 28% and 37% of the variance in small mammal hole density, respectively (Table 4).

Table 2. Comparison of habitat category ratios (mean \pm SD, %) for different buffer sizes and burrow categories. t = Students test, t_w = Welch test.

Buffer	Habitat types	All burrows			Active burrows			Active large burrows		
		Badger (n = 20)	Red fox (n = 33)	t/t_w	Badger (n = 13)	Red fox (n = 18)	t/t_w	Badger (n = 9)	Red fox (n = 7)	t/t_w
1200	Covered	43.6 \pm 6.6	45.0 \pm 8.4	$p = 0.514$	43.6 \pm 5.2	44.0 \pm 9.7	$p = 0.871$	43.7 \pm 5.8	43.3 \pm 7.0	$p = 0.905$
	Opened	47.3 \pm 9.7	41.6 \pm 10.8	$p = 0.056$	49.6 \pm 5.6	41.8 \pm 12.1	$p = 0.023$	49.0 \pm 5.9	40.9 \pm 10.9	$p = 0.080$
	Mixed	9.1 \pm 5.7	13.4 \pm 6.8	$p = 0.020$	6.8 \pm 3.5	14.2 \pm 6.8	$p < 0.001$	7.3 \pm 4.2	15.8 \pm 6.7	$p = 0.007$
800	Covered	45.5 \pm 13.7	41.0 \pm 13.2	$p = 0.246$	47.5 \pm 12.9	39.4 \pm 14.5	$p = 0.117$	47.4 \pm 15.1	37.2 \pm 7.6	$p = 0.124$
	Opened	45.4 \pm 14.3	43.3 \pm 14.9	$p = 0.618$	47.1 \pm 11.6	42.8 \pm 17.1	$p = 0.437$	47.9 \pm 13.3	41.9 \pm 14.2	$p = 0.403$
	Mixed	9.2 \pm 8.7	15.7 \pm 10.6	$p = 0.023$	5.4 \pm 2.3	17.8 \pm 10.6	$p < 0.001$	4.7 \pm 2.4	20.9 \pm 9.5	$p = 0.004$
400	Covered	50.7 \pm 18.5	42.7 \pm 18.7	$p = 0.133$	53.8 \pm 19.7	41.9 \pm 16.9	$p = 0.081$	53.3 \pm 23.9	35.1 \pm 9.7	$p = 0.062$
	Opened	40.8 \pm 19.9	35.8 \pm 19.4	$p = 0.371$	41.5 \pm 19.0	31.3 \pm 21.7	$p = 0.185$	42.6 \pm 22.5	28.7 \pm 16.4	$p = 0.190$
	Mixed	8.5 \pm 10.4	21.5 \pm 18.5	$p = 0.001$	4.7 \pm 4.7	26.8 \pm 20.7	$p < 0.001$	4.1 \pm 4.7	36.2 \pm 17.7	$p = 0.003$

Table 3. Comparison of diversity values (mean \pm SD) for different buffer sizes and burrow categories. t = Students test, t_w = Welch test.

Buffer	Diversity index	All burrows			Active burrows			Active large burrows		
		Badger (n = 20)	Red fox (n = 33)	t/t_w	Badger (n = 13)	Red fox (n = 18)	t/t_w	Badger (n = 9)	Red fox (n = 7)	t/t_w
1200	Simpson	0.562 \pm 0.035	0.585 \pm 0.046	$p = 0.059$	0.553 \pm 0.030	0.586 \pm 0.052	$p = 0.035$	0.557 \pm 0.035	0.602 \pm 0.042	$p = 0.031$
	Shannon	0.906 \pm 0.072	0.961 \pm 0.087	$p = 0.022$	0.882 \pm 0.060	0.965 \pm 0.091	$p = 0.007$	0.890 \pm 0.070	0.991 \pm 0.077	$p = 0.016$
	Simpson	0.535 \pm 0.061	0.572 \pm 0.079	$p = 0.079$	0.521 \pm 0.053	0.574 \pm 0.091	$p = 0.053$	0.508 \pm 0.057	0.612 \pm 0.058	$p = 0.002$
800	Shannon	0.862 \pm 0.105	0.938 \pm 0.140	$p = 0.041$	0.829 \pm 0.085	0.952 \pm 0.148	$p = 0.007$	0.804 \pm 0.090	1.009 \pm 0.101	$p < 0.001$
	Simpson	0.489 \pm 0.136	0.541 \pm 0.134	$p = 0.183$	0.465 \pm 0.150	0.543 \pm 0.124	$p = 0.123$	0.435 \pm 0.173	0.605 \pm 0.055	$p = 0.021$
	Shannon	0.784 \pm 0.218	0.875 \pm 0.228	$p = 0.158$	0.734 \pm 0.231	0.883 \pm 0.214	$p = 0.074$	0.688 \pm 0.261	0.980 \pm 0.137	$p = 0.018$

Discussion

Based on the locations of the two carnivores' active burrows, the distribution of burrows among habitat categories, both for the Eurasian badger and the red fox, was significantly different from the distribution that would have been expected based on habitat supply in the study area. This suggests that both species are actively selecting burrow sites based on some kind of habitat characteristic (i.e. vegetation or soil type, hydrological conditions, feeding resources, etc.) (Neal & Cheeseman 1996). Habitat preference calculated for the three habitat categories used in this study shows preference for the covered habitat category, and avoidance of the open and mixed habitat categories in the case of the Eurasian badger (Fig. 2). The red fox seemed to prefer covered and mixed habitats and completely avoided open habitat categories. These results are in line with those of the previous studies conducted in similar habitats (Neal & Cheeseman 1996, Heltai 2010, Heltai *et al.* 2011). Comparing the data of the habitats of active burrow locations we found no significant differences between the two species. However, differences became obvious after we delineated buffer zones around the burrows, considering the home range sizes of the two species (Weber & Meia 1996, Tuytens *et al.* 2000, Kowalczyk *et al.* 2003, Kowalczyk *et al.* 2006) and studying the ratios of habitat categories within these buffers (Table 2). Analyses of the buffer zones showed that vegetation near the burrows regulates the selection of the burrow site (Table 2). In case of the red fox, a two dimensional tendency

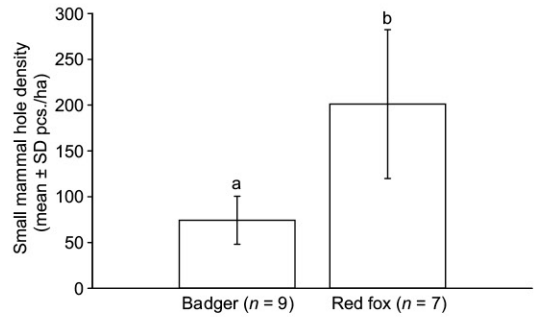


Fig. 3. Small mammal hole densities next to large burrows of the Eurasian badger and the red fox.

was found: the proportion of the mixed habitat category increased from the largest to the smallest buffer zones ($1200 < 800 < 400$ m), and from abandoned to active and large-active burrows (Table 2). We conclude that covered habitats for the Eurasian badger and mixed habitats for the red fox are of considerable importance (Table 2) when it comes to locating burrows (Neal & Cheeseman 1996, Heltai 2010, Heltai *et al.* 2011).

Overall, the following phenomenon was observed: the smaller the buffer zone, the lower the diversity of vegetation in all burrow categories. The reason for this may lie in the spatial resolution of the habitat data. This trend, however, disappears in the case of active and large red fox burrows, which may underline the importance of mixed and more diverse habitats for this species.

The density of small mammal holes was significantly higher next to the active red fox burrows than next to the active Eurasian badger burrows (Fig. 3). In addition, variance in small-

Table 4. Linear regression for the relationship between small mammal hole density and habitat types and diversity indices.

	ANOVA				Linear regression	
	F	df	p	n	r ²	y
Habitat types						
Covered	3.145	1,14	> 0.05	16	–	–
Opened	4.721	1,14	< 0.05	16	0.252	$-2.0651x + 205.19$
Mixed	136.1	1,14	< 0.001	16	0.907	$4.0037x + 57.152$
Diversity indices						
Simpson	5.615	1,14	< 0.05	16	0.287	$289x - 17.484$
Shannon	8.360	1,14	< 0.025	16	0.374	$202.02x - 35.042$

mammal hole density was explained by the ratio of the mixed habitat category within the 400-m zone surrounding the burrows (Table 4).

Based on our results, we conclude that besides investigating overall habitat preference, it is important to obtain information on fine-scale habitat use. This can reveal small but important differences, which would not be recordable at the scale of the study area, that enable these two medium-sized carnivores to coexist with increasing abundances. Furthermore, our study underlines that burrows are important for both species (Kruuk 1989, Neal & Cheeseman 1996, Heltai 2010), and that large burrows are of primary importance for these species, since in this burrow category differences were always significant.

The observation of the different habitat structures associated with Eurasian badger and red fox burrows is consistent with the fact that their main prey species are different (Neal & Cheeseman 1996, Lanszki *et al.* 1999). Even though small mammals are important prey resources for both species (Canova & Rosa 1993, Lanszki *et al.* 1999), results of several studies have shown that invertebrates and plants are the primary food source for the Eurasian badger (Canova & Rosa 1993, Lucherini & Crema 1995, Neal & Cheeseman 1996, Lanszki *et al.* 1999, Lanszki 2004), while the red fox's diet consists primarily of small mammals (Canova & Rosa 1993, Lanszki *et al.* 1999, Baltrunaite 2002, Lanszki *et al.* 2007). The mixed habitat category showed significant differences between the two species in all cases, and the key role of this vegetation type was also stressed by the two-dimensional trend for the red fox. Results of the linear regression indicate that the red fox finds its primary food resource in the mixed habitat category (Fig. 4), which may be explained by the ecological edge effect (Smith *et al.* 1997). For the Eurasian badger, invertebrates and plants of the covered and open habitats may provide a sufficient diet (Kruuk 1989, Canova & Rosa 1993, Neal & Cheeseman 1996).

Shannon's diversity index (in terms of vegetation diversity) supports our hypothesis described above. Its values show significant differences in multiple categories between the two species (Table 3). This can be explained by the

fact that this index emphasizes the influence exerted on the diversity of small-sized habitat patches — in our study, mixed habitats (Heip & Engels 1974).

We suggest that burrows, especially large ones, and the spatial distribution of the main prey resources play an important role in the niche segregation of these medium-sized carnivore species. They select habitats with different vegetation structures as burrow sites, but this selection is not based solely on the vegetation but follows the habitat preference of their prey species.

Our method, based on buffer areas and using small mammal hole densities, provides a fairly quick and simple way of showing niche segregation of these two carnivore species. Nevertheless, the validity and applicability of the method should be tested in different areas and habitats.

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