

FEEDING HABITS OF SYMPATRIC MUSTELIDS IN AN AGRICULTURAL AREA OF HUNGARY

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The feeding ecology of the badger (*Meles meles*) and its interspecific trophic relationship with the sympatric marten (*Martes foina* and *M. martes*) were investigated in a temperate climate agricultural area of southwestern Hungary. On the basis of food remains found in scats (over four years, badger $n = 166$, marten $n = 545$), both predators consumed the most abundant and accessible foods according to the season. No significant differences were found between predators concerning the consumption of small mammals as primary foods (mean; badger 59.3% and marten 48.0%) and other food types, except birds. Regarding plants as secondary foods, badgers consumed mainly maize, while martens ate predominately fruits. Both mustelids preferred open-field living common vole and avoided forest-living bank vole; both consumed primarily small (< 50 g) (97% vs 94%), open-field living (78% vs. 55%) and terrestrial (98% vs 86%) prey species, but marten preyed more on arboreal animals. Diets were diverse, but the trophic niche, especially of the badger, was very narrow. The mean food overlap between predators was high (67.1%). Considering that the chosen primary or secondary food resources are unlimited in central European agricultural areas, it is not possible to prove food resource partitioning between mustelids. Interspecific differences in feeding habits are rather the consequences of individual patterns than niche segregation.

Key words: *Meles meles*, *Martes*, prey preference, trophic niche overlap, food partitioning

INTRODUCTION

The Eurasian badger (*Meles meles*), the stone marten (*Martes foina*) and the pine marten (*Martes martes*) are widely distributed mustelids in Europe, occurring in a great diversity of habitats (MITCHELL-JONES *et al.* 1999). In Hungary these can co-exist in agricultural areas with forest patches (HELTAI 2010). Among the mustelids we studied, the badger is the largest with a massive, strong body (with short and extremely strong limbs), typically fossorial and terrestrial (KRUUK 1989, NEAL & CHEESEMAN 1996), while stone marten and pine marten, similar in size, both have slender, elongated bodies and are agile and well adapted for arboreal pursuit (CLEVENGER 1994).

The carnivores studied can alter their food preferences depending on the type of area and on the particular season. They are trophic generalists, because they use a wide variety of food resources. The diet of the badger mainly consists of earth-

worm, insect, vertebrate and plant resources at or below ground level. Local feeding specialisation has also been reported (KRUUK 1989, ROPER & LÜPS 1995, NEAL & CHEESEMAN 1996, GOSZCZYNSKI *et al.* 2000). Among the similarly wide range of foods the martens consume, terrestrial and arboreal prey species and fruits can also be found (review: CLEVINGER 1994, ZALEWSKI 2004). Although overlapping diets are known from studies (CLEVINGER 1994), the scats of the habitat-generalist stone marten and those of the mainly forest-living pine marten cannot be distinguished in absence of molecular genetics (PILOT *et al.* 2007) or radio-telemetry (GENOVESI *et al.* 1996). This is the reason why in several studies (GOSZCZYNSKI 1986, PEDRINI *et al.* 1995, PRIGIONI *et al.* 2008), and in the present study, where both martens occurred on the area, the taxon *Martes* was used instead. Although feeding studies, especially those focusing on interspecific interactions, are important (HAYWARD & KERLEY 2008), we still know little about the trophic relationships between sympatric mustelids living in the Pannonian biogeographical region (LANSZKI *et al.* 1999).

In order to have a better understanding of the trophic relations between the badger and the marten in a temperate climate agricultural area in southwestern Hungary, we compared data from different seasons and different years on the diet composition and trophic niche overlap between the species studied.

MATERIALS AND METHODS

Study area and predator populations

The study area is located in the Pannonian biogeographical region of southwestern Hungary (Ormánság region, between Kétújfalu, Potony and Lakócsa, 45°56'N, 17°41'E; 103–123 m a.s.l.). In the study area, which is a mosaic of agriculture and small woodlands, there are four main habitat types. During the study from December 2000 to November 2004, the area of abandoned fields (*Erigeron* spp.) decreased from 56.1% to 14.4%, while the distribution of plough-lands (cereals and soy) increased from 10.9% to 48.7%. The coverage of mixed oak-elm-ash forests (*Quercus*, *Ulmus*, *Fraxinus* spp.) and shrubby areas and banks (mainly *Salix alba* and *Prunus spinosa*) experienced only a small change (22.9% to 29.5%, and 10.2% to 7.4% respectively). Duration of snow cover was 4, 21, 48 and 16 days per year, and the mean snow depths were 6, 70, 84, 18 mm per winter. During the study period, 2003 was an extreme year with a particularly cold and long winter, a hot summer and little rainfall.

Maximum small mammal densities (86–254 individuals per ha) were measured in autumn (October) and minimum densities (2–39 individuals per ha) at the end of winter (February) by capture-mark-recapture technique. Small mammal density data are related to actual coverage of four main habitat-types (more details: LANSZKI & HELTAI 2010). During the study period, besides the badger and the marten, populations of two canids, namely the golden jackal (0.25 family groups/km², acoustic survey) and the red fox (2.8 individual/km², den survey on transects) were considerable (LANSZKI *et al.* 2006). The calculated mean (\pm SE) relative abundance of badger scats was 0.20 \pm 0.051

on the basis of collected scats per km route, and mean badger sett density was 0.33 ± 0.090 inhabited sett per km² (den survey on transect, authors unpubl. data). The calculated mean relative abundance of marten scats was 0.62 ± 0.089 scats/km route.

Scat collection and diet analysis

The diet composition of the badger and the marten was studied by analysis of scats collected monthly from December 2000 to November 2004. Scat samples were collected on a standard route (12.8 km in 2001, 21.3 km in 2002 and 22.7 km in 2003 and 2004) within an area of 650 ha. Badger scats were collected from latrines along the route found the closest to two badger setts. Samples were frozen at -20°C for three months prior to analysis. Scats of sympatric stone marten and pine marten were impossible to distinguish in the field macroscopically (size, shape, odour, track), therefore samples of these two species were drawn together to the taxon marten (or *Martes* sp.).

A total of 166 badger scats (seasonal mean \pm SE, $n = 10 \pm 0.6$) and 545 marten scats (seasonal mean, $n = 34 \pm 3.9$) were analyzed by means of a standard procedure (JĘDRZEJEWSKA & JĘDRZEJEWSKI 1998, GOSZCZYŃSKI *et al.* 2000). The presence of earthworms in the badger scats was determined by microscope identification of chaetae, and the biomass of earthworms was calculated following KRUK and PARISH (1981) and JĘDRZEJEWSKA and JĘDRZEJEWSKI (1998). Scats were soaked in water, then washed through a sieve (0.5 mm mesh) and dried. All food remains were separated and identified under the microscope with the aid of keys from TEERINK (1991), MÄRZ (1972), BROWN *et al.* (1993), and our own vertebrate, invertebrate and plant reference collections. Frequency of occurrence generally emphasizes the importance of small prey in the diets of predators (e.g., beetles frequently eaten by badgers, although only in small quantities; LANSZKI 2004), and the estimation of actual biomass consumed provides a more realistic measurement of the nutritive value of a food, emphasizing the importance of larger prey. Therefore, diet composition of the predators was expressed by percentage of fresh weight (biomass) consumed, but number of consumed items (N) are also demonstrated (Table 1). In order to estimate the fresh weight of food ingested (REYNOLDS & AEBISCHER 1991), all dry food remains were weighed and weight data were multiplied by an appropriate conversion factor (insectivores and small rodents $\times 23$, medium sized mammals $\times 50$, wild boar and domestic ungulates $\times 118$, deer $\times 15$, birds $\times 35$, reptiles and amphibians $\times 41.3$ for badger and $\times 18$ for marten, fish $\times 25$, molluscs $\times 7$ for badger, insects $\times 5$, fruit and seed $\times 14$ and other plant material $\times 4$ for badger and $\times 14$ for marten; factors summarized by JĘDRZEJEWSKA & JĘDRZEJEWSKI 1998). The consumed prey species were classified (LANSZKI *et al.* 2006, 2007) firstly on the basis of their weight (< 15 g, $15-50$ g, $51-100$ g, $101-300$ g and > 300 g). Secondly, they were classified on the basis of their typical habitat associations – lack of radio-tracking reflects the location of where the prey species were actually found in relation to the predators. Classes were, 1 – open field species (e.g. *Microtus* voles, steppe mouse *Mus spicilegus*, harvest mouse *Micromys minutus*), 2 – forest species or species living in dense shrubbery (e.g., bank vole *Myodes glareolus*, dormouse species Gliridae), and 3 – habitat generalist species which may live both in open fields and in forests (e.g. *Apodemus* mice, European brown hare *Lepus europaeus*, wild ungulates and most invertebrates). A third classification was based on the characteristic zonation such as: 1 – terrestrial (and mainly terrestrial but sometimes arboreal), 2 – arboreal (and mainly arboreal but sometimes terrestrial) and 3 – aquatic (or water-related).

Apodemus spp. in the study area included the yellow-necked mouse (*A. flavicollis*), the common field mouse (*A. sylvaticus*) and the striped field mouse (*A. agrarius*), while *Microtus* spp. included the common vole (*Microtus arvalis*, 99% of the *Microtus* species), the field vole (*Microtus agrestis*) and the European pine vole (*Microtus subterraneus*). The various species were grouped at

the genus level, because it was not always possible to identify the individual species on the basis of the hairs or teeth found in the scats.

Statistical analysis

The following ten food taxa were used in the calculations related to the comparative analysis of scat composition and trophic niche for predator species (LANSZKI *et al.* 2006): 1 – small-sized mammals (insectivores and rodents), 2 – brown hare, 3 – cervidae carcasses, 4 – wild boar (*Sus scrofa*) carcasses, 5 – pheasant (*Phasianus colchicus*), 6 – other birds, 7 – reptiles, amphibians and fish together, 8 – invertebrates, 9 – domestic animal carcasses and 10 – fruits, seeds and other plant matter.

With the carnivores two-way analysis of variance (MANOVA, GLM procedure, LSD post-hoc test) – with season and year as fix factors, and with year or season as covariant – was applied for the evaluation of the consumption of fresh biomass of the ten main food taxa (logarithmic %B data). The first and second years of the study period were drawn together in this calculation. The Pearson correlation (r_p) test was used to examine the relationship between small mammal availability (biomass, kg/km²) and proportion of consumed biomass (%B) of small mammals; to examine the relationship between small mammal availability (average for each year) and coverage (%) of four main habitat types for each year; and to examine the relationship between consumption of main food types (%B of small mammals, plants) and coverage of main habitat types. Small mammal survey started only in autumn of 2001. The missing small mammal biomass average value for this year was calculated on the basis of those three years (2002–2004) when small mammal surveys were performed in all seasons (by the ratio of annual average and autumn data, i.e. mean 48.4%).

The consumption of the ten food taxa on the basis of the estimated percentage biomass values during 16 seasons was compared between the two mustelids using paired samples t-test.

Trophic niche breadth was calculated in accordance with Levins (KREBS 1989): $B = 1/\sum p_i^2$, where p_i = the relative biomass consumed of the i th taxon; and standardized across food taxa: $B_A = (B-1)/(n-1)$, rating from 0 to 1.

Trophic niche overlap was calculated by means of the Renkonen index: $P_{jk} = [\sum n(\text{minimum } p_{ij}, p_{ik})]100$, where P_{jk} = percentage overlap between species j and species k ; p_{ij} and p_{ik} = the proportion of resource i represented within the total resources used by species j and species k ; n = the total number of resource taxa (KREBS 1989). The food niche breadths and overlap were compared with MANOVA (GLM procedure), using standardized trophic niche breadth and trophic overlap values as dependent variables, season (4) and year (4), and predator species (only for niche breadth), as fixed factors.

MANOVA was applied to compare mustelids in consumption of fresh biomass of prey (logarithmic %B data) on the basis of the prey weights, zonation or habitat types as dependent variables, carnivore species as fixed factors, seasons and weight or zonation or habitat type categories as covariates.

Ivlev's index (E_i) of preference on the basis of yearly changes of habitat types was applied as follows: $E_i = (r_i - n_i)/(r_i + n_i)$, where r_i = percentage biomass of a given (i th) item in the diet and n_i = percentage of biomass of a given (i th) item in the environment (KREBS 1989). Electivity varies from –1.0 to +1.0, where –1.0 indicates avoidance, and +1.0 indicate a preferred prey. The preference indices from 13 seasons were compared with paired samples t-test between the two predators and with one-way analysis of variance (ANOVA, LSD post hoc test) among the food taxa. The SPSS 10.0 for Windows (1999) statistical package was used for the data processing.

RESULTS

Diet of mustelids, and interspecific differences in diets

The two main types of food, small mammals and plants, showed alternating dominance in the diet of the badger (Fig. 1a). The *Microtus* spp. was the most important food taxon, represented predominantly (> 90%) by the common vole. Badgers consumed food of other animal origin very rarely, or only in rather small amounts. As for plants in the diet, maize proved to be the most important plant resource all year long (Table 1). During the second half of our study (2003–2004), following the extraordinarily cold and long winter of 2002/2003, consumption of small mammals decreased noticeably, though not significantly (MANOVA, $F_1 = 3.93$, $P = 0.069$), whereas the consumption of birds (excluding pheasant, $F_1 = 7.98$, $P < 0.05$) and plant materials ($F_1 = 6.01$, $P < 0.05$) showed a significant increase, as compared to the first two years of our investigations (2001–2002). Seasonal difference was not significant in the case of any type of food resource (MANOVA, $F_3 = 0.20$ – 3.27 , $P = 0.063$ – 0.897).

Small mammals and plants were the dominant elements in the diet of the marten as well (Fig. 1b). In the second half of the study period consumption of small mammals decreased significantly (MANOVA, $F_1 = 21.51$, $P < 0.001$), while that of plants increased ($F_1 = 5.11$, $P < 0.05$), as compared to the first two years. Among the great variety of small mammal prey, the common vole proved to be the dominant species (Table 1). Brown hare was eaten all year long with the exception

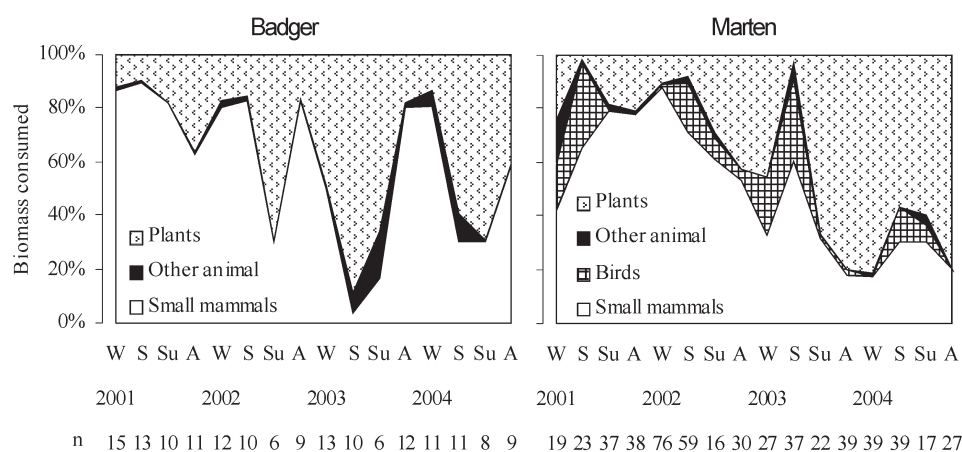


Fig. 1. Seasonal diet composition changes of the badger (*Meles meles*) and the marten (*Martes* sp.) in the Ormánság region (SW Hungary). W = winter, S = spring, Su = summer, A = autumn, (n) = number of individual scats analysed

Table 1. Seasonal number and biomass of food types in scats of the badger (*Meles meles*) and the marten (*Martes sp.*) in the Ormánság region (SW Hungary). Data collected between Dec. 2000–Nov. 2004. Abbreviation: W = winter, S = spring, Su = summer, A = autumn, N = no. food items consumed, %B = % of biomass of each food item consumed, means from 16 seasons, + = biomass under 0.05%. Empty cells mean that the given taxon was not detected.

Food taxon	Badger						<i>Martes sp.</i>											
	W	S	Su	A	Mean	W	S	Su	A	Mean								
	N	%B	N	%B	N	N	%B	N	%B	N	N	%B	N	%B				
Bank vole (<i>Myodes glareolus</i>)	2	6.2	2	2.9	1	+	2	7.5	4.4	21	8.7	11	6.0	7	5.3	8	3.1	5.9
<i>Microtus</i> spp.	36	55.4	28	52.1	19	43.5	27	46.1	50.4	73	31.9	48	22.5	54	40.7	65	29.0	30.2
<i>Apodemus</i> spp.	9	7.0			2	2.0	4	15.9	6.0	24	7.6	32	16.6	12	7.5	25	6.7	9.6
Other rodents (Rodentia)	1	3.6			2	+	2	4.6	2.2	4	0.6	10	3.5	3	0.6	5	1.1	1.5
Shrews (Soricidae)			1	0.1			2	1.2	0.3	3	0.3	8	5.8	6	3.7			2.1
Mustelids (Mustelidae)					1	+												
Brown hare (<i>Lepus europaeus</i>)												6	1.6	2	0.6	1	+	0.5
Wild boar (<i>Sus scrofa</i>)			1	+			2	0.1	+	4	2.0	2	0.4	1	0.1	1	0.2	0.8
Cervids (Cervidae)			1	0.2	1	0.1		0.1	0.1	3	0.2			1	0.2			0.1
Passerines (Passeriformes spp.)	3	0.1	3	+	2	+	3	0.1	+	20	4.1	66	22.2	19	3.0	5	0.8	6.8
Other birds										3	1.8	8	1.2	1	+	2	1.0	1.5
Reptiles, amphibians and fish	3	+	5	2.7			3	+	0.8			8	1.2	1	+			0.3
Domestic cat and dog										1	0.2			1	0.6			0.2
Domestic ungulate carcasses					1	4.5	2	0.7	0.9	1	0.1							+
Beetles (Coleoptera)	23	+	47	0.1	18	+	11	+	+	7	+	86	0.8	40	0.4	18	+	0.3
Earthworms (Lumbricidae)	21	2.2	14	1.9	2	0.1	6	0.2	1.3									
Other invertebrates	2	+	3	+	3	+	1	+	+	2	+	5	0.2	18	0.8	4	+	0.2
Blackthorn (<i>Prunus spinosa</i>)	4	0.8					2	0.5	0.4	33	28.5	15	7.1	8	6.8	67	41.9	23.4
Pear (<i>Pyrus</i> spp.)					6	13.6	4	6.6	3.8	2	0.4			19	10.0	22	7.7	4.0
Rose-hips (<i>Rosa canina</i>)					11	14.6	1	+	2.6	3	+	4	0.6	44	18.9	4	2.4	4.0
Other fruits					20	21.6	34	16.4	26.2	5	0.1	2	0.1			13	0.2	0.1
Maize (<i>Zea mays</i>)	50	24.7	38	37.8	20	1.8	1	+	0.1	5	0.1	2	0.0	4	+	3	0.2	0.2
Other seeds	2	+	7	0.3	4	+	3	+	0.1	6	0.1	4	0.4	5	0.3	6	+	0.2
Grasses																		
Number of scats	51		44		30		41			161		158		110		134		

of winter in a low proportion according to biomass calculations. With regard to birds as food resources, we could detect remains of the sparrow (*Passer* spp., in autumn), nuthatch (*Sitta europaea*, in winter and in spring) unidentifiable passeriformes, starling (*Sturnus vulgaris*, in spring), pheasant (in summer), medium-sized birds and eggs. In spring, the diet of martens included lizards, frogs and fishes, and in autumn fish; they ate from carcasses of domestic dogs (in winter) and domestic cats (in summer), and even sheeps wool was found in their scats in winter. Rarely, and in small amounts, remains were found of roe deer in summer, red deer and fallow deer in winter, wild boar all year long and young wild boar in spring. Among the invertebrates, carabid beetles occurred most frequently (in summer), but relevant consumption of honey bees, sometimes together with parts of the bees' nest and bees' wax – probably from the predation of bee hives – could also be found. Plant food was mainly composed of the seasonally available fruits growing wild (Table 1). Seasonal difference proved significant only in the case of plants (MANOVA, $F_3 = 4.88$, $P < 0.05$) and invertebrates consumed in small proportions ($F_3 = 11.77$, $P < 0.001$), while as for the more dominant types of animal food this difference was not supported statistically ($F_3 = 0.61$ – 2.60 , $P = 0.105$ – 0.622).

No coherent relation (badger: $r_p = 0.26$, $P = 0.383$, marten: $r_p = 0.15$, $P = 0.623$) was found between the small mammal consumption (%B values) of predators and biomass of small mammal availability (Fig. 2). The biomass of small mammal availability showed close negative relation with coverage of plough-lands ($r_p = -0.978$, $P < 0.05$) and conversely, close positive relation with coverage of abandoned fields ($r_p = 0.957$, $P < 0.05$); while this relation was not supported statistically in cases of forests and shrubby areas ($P = 0.257$ – 0.355). The

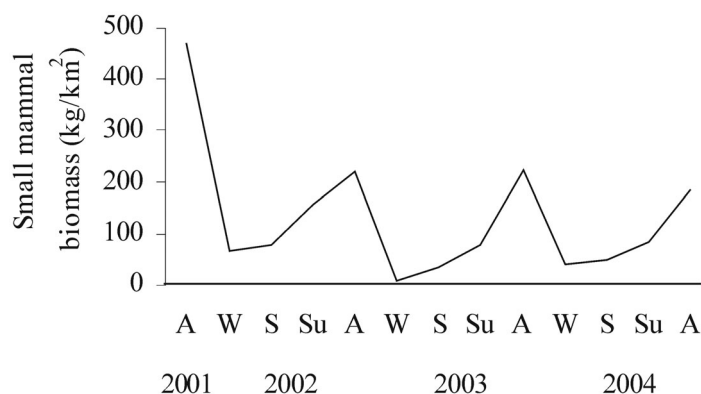


Fig. 2. Changes in biomass of small mammals in the Ormánság region (SW Hungary). Biomass of small mammals was calculated from summarized capture data (from individual weights and MNA) in each season (more details: LANSZKI & HELTAI 2010)

marten consumed less small mammals with increasing forest coverage ($r_p = -0.987$, $P < 0.05$), and positive relation was found between the plant consumption and the forest or bank coverage ($r_p = 0.994$, $P < 0.001$ and $r_p = 0.960$, $P < 0.05$, respectively). Similar relationships were not found in case of the badger.

Badgers, as compared to martens, consumed significantly less birds (excluding pheasant, paired samples t-test, $t_{15} = 4.14$, $P < 0.001$). No statistically or biologically significant differences ($t_{15} = 0.06-1.34$, $P = 0.200-0.950$) were found between the badger and the marten in the consumption of other main food types.

Trophic niche breadth and overlap

On the basis of the calculation of the ten main food categories, the standardized trophic niche breadth of both predators was very narrow, but the badger had a narrower mean value than the marten (paired samples t-test, mean \pm SE, badger: $B_A = 0.07 \pm 0.01$ and marten: $B_A = 0.11 \pm 0.02$, $t_{15} = 2.15$, $P < 0.05$). Badger and marten diets contained 38 and 49 different prey taxa (meaning taxonomic species or higher classification), as well as 11 plant taxa. The mean trophic niche overlap between the badger and the marten was high (mean \pm SE, 67.1 \pm 6.13%). A value lower than 30% was found only after a long winter in spring of 2003 (8.8%). The standardized trophic niche breadth values did not vary significantly between years (MANOVA, badger: $F_3 = 1.26$, $P = 0.336$ and marten: $F_3 = 0.15$, $P = 0.925$) and seasons (badger: $F_3 = 0.30$, $P = 0.827$ and marten: $F_3 = 0.70$, $P = 0.571$), and neither did trophic niche overlap between years (MANOVA, $F_3 = 0.68$, $P = 0.580$) and seasons ($F_3 = 0.64$, $P = 0.603$).

Prey choice

Small-sized prey (15–50 g) was the most important food of the predators (badger: 92.5%, marten: 89.7%). Consumption of very small-sized (< 15 g) and relatively large (> 300 g) prey species was low. The main effect of carnivore species was not significant in calculating percentage of consumed biomass data (MANOVA, LSD post-hoc test, $F_1 = 0.913$, $P = 0.346$). Animal food of both mustelids mainly belonged to the group of terrestrial animals (badger: 98.8%, marten: 86.1%), however martens consumed more arboreal food (12.9%; $F_1 = 4.786$, $P < 0.05$). Aquatic prey species were eaten in low ratios in the agricultural study area (1.2% and 0.9%, respectively). Animals living in open fields were the most important food of both carnivores (badger: 77.8%, marten: 55.2%), but both consumed habitat generalist species in relatively large amounts (badger: 16.4%, marten:

Table 2. Mean (\pm SE) small mammal preferences of the badger (*Meles meles*) and the marten (*Martes* sp.) in SW Hungary. Differences among consumption of each prey taxa (within predator) marked with different letters (^{a,b,c}) are significant (ANOVA, LSD test).

Prey taxon	Ivlev's preference index (E_i)	
	Badger	Marten
<i>Microtus</i> spp.	+0.56 \pm 0.091 ^a	+0.45 \pm 0.115 ^a
<i>Myodes glareolus</i>	-0.57 \pm 0.194 ^{bc}	-0.44 \pm 0.158 ^b
<i>Apodemus</i> spp.	-0.74 \pm 0.112 ^{bc}	-0.35 \pm 0.056 ^b
<i>Mus spicilegus</i>	-0.20 \pm 0.379 ^b	-0.02 \pm 0.308 ^{ab}
<i>Micromys minutus</i>	-0.01 \pm 0.995 ^{abc}	-0.20 \pm 0.000 ^{ab}
<i>Sorex</i> and <i>Crocidura</i> spp.	-0.83 \pm 0.129 ^c	-0.35 \pm 0.220 ^b
P	0.001	0.01

33.3%). The main effect of carnivore species was not significant regarding consumed biomass of prey from different habitat types ($F_1 = 0.543$, $P = 0.283$).

Badgers significantly preferred (ANOVA, $F_5 = 9.539$, $P < 0.0001$) the open-field living *Microtus* voles, and no clear preference (near zero value) was found in the case of *Micromys minutus*. They also preferred less (or avoided) the forest-living *Myodes glareolus* and the habitat generalist *Apodemus* mice and shrews (Table 2). Martens also preferred significantly the *Microtus* voles, and no clear preference was found in the case of *Mus spicilegus* and *Micromys minutus*. They also preferred less (or avoided) species such as the *Myodes glareolus*, *Apodemus* mice and shrews (ANOVA, $F_5 = 3.341$, $P < 0.01$, Table 2). With the exception of *Apodemus* mice (paired samples t-test, $t_{12} = 2.81$, $P < 0.05$), no significant difference was found between predators in preference of rodents ($P = 0.121$ – 0.688) or shrews ($P = 0.120$).

DISCUSSION

The diet composition of the badger and the marten did not show characteristic interspecific differences. Both mustelids fed upon two alternately dominant types of food, namely small mammals and plants. This, especially in the case of badgers differed remarkably from European trends as well as from earlier Hungarian experiences. In northern latitudes the most important foods for badgers are earthworms and vertebrates (e.g. KRUK & PARISH 1981, NEAL & CHEESEMAN 1996), in lower latitudes, in farmland areas earthworms and plants become primary or secondary foods (e.g. LÜPS *et al.* 1987, WEBER & AUBRY 1994, GOSZCZYNSKI *et al.* 2000), while in southern areas plants and insects (e.g. CIAMPALINI

& LOVARI 1995, DE MARINIS & ASPREA 2004, PRIGIONI *et al.* 2008), and rarely mammals (FEDRIANI *et al.* 1998) are the main foods. No latitude and seasonal dependent consumption of birds was found by HOUNSOME and DELAHAY (2005). In Hungary, in pond systems surrounded by forest (LANSZKI 2004) the main foods of badgers were earthworms (in winter) and amphibians (from spring to autumn), while in farmland mosaic habitats (LANSZKI *et al.* 1999) besides primary insects and earthworms (in spring and summer) or plants (in autumn, mainly maize), small mammals were consumed only as secondary foods. The badger, with its strong canines, is one of the most massively built carnivores, and it can out compete the fox (KOWALCZYK *et al.* 2008), and probably its opportunistic food searching strategy (KRUUK 1989, NEAL & CHEESEMAN 1996) is the only reason why it consumes less small mammals in most habitats than in the present study. Primary foods of stone martens living in agricultural areas consisted mainly of plants, especially fruits (RASMUSSEN & MADSEN 1985, LODÉ 1994, GENOVESI *et al.* 1996, RÖDEL & STUBBE 2006). In an agricultural area in Hungary, the main food of stone martens was small mammals (especially common vole) in winter and spring, while it was plants (especially fruits) in summer and autumn (LANSZKI 2003) similar to the present study in the case of *Martes* sp. Carnivores in European ecosystems are considered to be important dispersal vectors for fleshly fruited plants (HERRERA 1989, SCHAUMANN & HEINKEN 2002). On the basis of reviews by CLEVINGER (1994) and ZALEWSKI (2004), consumption of small mammals in pine marten diets increases from the Mediterranean to northern regions, and reaches a peak in the temperate woodlands, while plants and insects are more frequently eaten by pine martens in southern Europe. Medium-sized mammals and large birds are consumed more often in higher latitudes, as the food niche of pine martens is generally wider in northern than in southern areas. In a flatland forest in Hungary, primary foods of pine martens consisted of small mammals (principally the bank vole), and fruits in summer (LANSZKI *et al.* 2007). In contrast to this, in the present study common vole was the main prey of the *Martes* sp.

Although the badger had a narrower trophic niche than the marten, both predators consumed a great variety of foods, as is typical of the generalist species, and very narrow trophic niche values showed high specialization (KRUUK 1989, NEAL & CHEESEMAN 1996, CLEVINGER 1994) to the seasonally most abundant and accessible foods.

Besides the measured high trophic niche overlap between the badger and the marten for their co-existence they are supposed (SCHOENER 1974) to partition food resources. Contrary to (or rather just partially in accordance with) the general diet compositions of carnivores (CLEVINGER 1994, GOSZCZYNSKI *et al.* 2000, ZALEWSKI 2004), the diet of badgers did not contain many remains of very small-

sized (< 15 g) prey (mainly invertebrates). The majority of prey species weighted 15–50 g, thus the distribution of the studied predators according to categories of mass of prey did not show any difference.

These results, which are in accordance with the food specialist hypothesis (KRUUK 1989, ROPER & LÜPS 1995), also confirmed earlier experiences from studies performed in Hungary (LANSZKI *et al.* 1999, LANSZKI 2004). We examined if the badger and the marten separated their respective food niches by hunting prey in different microhabitats, i.e. if the tree-climbing marten preyed more on arboreal prey (CLEVENGER 1994, ZALEWSKI 2004) than the terrestrial badger (GOSZCZYNSKI *et al.* 2000). The results showed that both carnivores hunted basically on terrestrial prey (and ate from the same carcasses). We also examined the interspecific differences according to habitat types and this was not significant, as both carnivores preyed mainly on animals living in open fields. The use of open field food resources is further confirmed by the fact that both the badger and the marten significantly preferred open-field living *Microtus* voles and avoided forest-living bank vole. Between the predators only the preferences for habitat generalist *Apodemus* mice were considerably different. Results in the case of *Martes* sp. indicated that most samples might originate from stone marten and partially from pine marten.

High trophic niche overlap between the studied mustelids, which was independent of year, indicates that food changes depended on climatic variations. Namely, due to the cold winter in 2002/2003 and following a dry summer, biomass and consumption of small mammals declined. Habitat transformation (cultivation of abandoned fields) also influenced the feeding habits of mustelids. Under cultivation, both consumed less small mammals and more plants.

The badger and the marten consumed the same primary and buffer foods, preyed on similar sized, terrestrial and open-field living species and preferred open-field living and avoided forest-living small mammals. The carnivores can co-exist with high trophic niche overlap (COLWELL & FUTUYMA 1971, SCHOENER 1974, KREBS 1989) as was found in our area between sympatric golden jackal and red fox (LANSZKI *et al.* 2006), and with the lack of food niche partitioning, if the most important resources, e.g. food, are abundant and the competitive interaction between predators is weak. This explanation is supported by the fact that while intensification of agriculture pertained decline in biomass of the small mammal availability, no coherent relation was found between the primary prey type, the small mammal consumption by mustelids and biomass of small mammal availability. These results therefore demonstrate principally that the availability of primary and secondary food resources were unlimited in the agricultural study area during the studied period of time (CARBONE & GITTLEMAN 2002). The density of certain

predators can be determined by the internal regulation mechanisms of the given population, as has been confirmed for example in the case of foxes (e.g. LINDSTRÖM 1989). Another explanation is that there are other mechanisms of niche segregation, such as different selection of habitat or activity time, which may reduce competition. This could be further investigated by additional studies, e.g. using radio-telemetry. Further studies to distinguish scats of stone and pine martens, based on molecular techniques are also needed, to clarify a possible more significant habitat segregation between the three species living in this study area. Our results, in conclusion, give answers to the question of how it is possible that 10–12 sympatric carnivore species can co-exist (and even form a Carnivora community) in the Hungarian habitats.

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