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Authors: Lanszki, József, Zalewski, Andrzej, and Horváth, Győző

Source: Wildlife Biology, 13(3) : 258-271

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/0909-6396(2007)13[258:CORFVV]2.0.CO;2

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Comparison of red fox *Vulpes vulpes* and pine marten *Martes martes* food habits in a deciduous forest in Hungary

József Lanszki, Andrzej Zalewski & Győző Horváth

Lanszki, J., Zalewski, A. & Horváth, G. 2007: Comparison of red fox *Vulpes vulpes* and pine marten *Martes martes* food habits in a deciduous forest in Hungary. - Wildl. Biol. 13: 258-271.

Feeding habits and interspecific trophic niche overlap of two sympatric predators, the pine marten *Martes martes* and the red fox *Vulpes vulpes*, were studied in a deciduous forest habitat in Hungary with conditions of differing abundance and dominance in the rodent community. The main food source of the predators consisted of small mammals, mainly rodents. Consumption of small mammals was higher during bank vole *Clethrionomys glareolus* dominated years than in *Apodemus* mice dominated years. Both predators preferred bank voles as prey and consumed less *Apodemus* mice and shrews (Soricidae) than expected by availability. The two opportunistic predators utilised different, seasonally-dependent food resources. Martens consumed more plants, reptiles, amphibians and fish, whereas foxes consumed more small mammals and ungulate carcasses. In summer and autumn, percent biomass of bank voles in marten diet and *Apodemus* mice in fox diet was positively correlated with the number of rodents in the available food resources. In winter and spring, the density of rodents varied slightly; therefore, variations in the diets of these two predators were not related to prey density. The prey consumed was characteristically terrestrial and small sized (< 50 g). There was no difference in prey weight distribution between martens and foxes, but martens consumed more arboreal and foxes more terrestrial prey. The standardised food niche breadth did not differ significantly between the two species. Food niche overlap between the two predators was higher in winter and spring, but the difference between seasons was not significant (mean overlap = 72%). In comparison with higher latitudes, we found a larger food niche overlap in our study.

Key words: feeding habits, functional response, Martes martes, prey preference, Vulpes vulpes

József Lanszki, University of Kaposvár, Ecological Research Group, 7401 Kaposvár, P.O. Box 16, Hungary - e-mail: lanszki@mail.atk.u-kaposvar.hu
Andrzej Zalewski, Polish Academy of Sciences, Mammal Research Institute, 17-230 Białowieża, Poland - e-mail: zalewski@bison.zbs.bialowieza.pl
Győző Horváth, University of Pécs, Department of Zootaxonomy and Synzoology, 7624 Pécs, Ifjúság u. 6, Hungary - e-mail: horvath@ttk.pte.hu

Corresponding author: József Lanszki

Received 25 September 2004, accepted 19 May 2006

Associate Editor: Piero Genovesi

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One way to understanding community organisations, could be to measure overlap in resource use among the different species in a community guild (Krebs 1989). The most common resources measured in order to calculate overlap are food and space (or microhabitat). Species can coexist with high overlap of food niche if: 1) food is abundant, 2) prey is partitioned by size (Rosenzweig 1966) or differential use (Mills 1984), and/or 3) diversity is greater in one species' diet than it is in other species' diets (White et al. 1995). The degree of overlap in diet and food habitats represents a major interspecific relation that strongly affects the potential for competition. Higher food overlap, however, does not necessarily mean competition. At the same time, knowledge on overlap in resource use is essential to understanding interspecific competition (Colwell & Futuyma 1971, Schoener 1974).

The European pine marten *Martes martes* is widespread in Europe, from northern Iberia and Italy to Fennoscandia and Russia, but less abundant in the Balkan Peninsula, and in a large part of its range it coexists with the red fox *Vulpes vulpes* (Corbet & Harris 1991). Pine marten and fox diets are composed mainly of small mammals, mostly rodents, and significantly change between geographical regions with a similar pattern in both predators (see review De Marinis & Asprea 2004, Zalewski 2004). In winter, the proportion of small mammals in marten diets increases from the Mediterranean to northern regions, and reaches a peak in the temperate deciduous and mixed woodlands although it declines further north in boreal forests (Zalewski 2004). Plant material and insects are more frequently consumed in southern Europe (Clevenger 1993, Serafini & Lovari 1993), whereas medium-sized mammals and large birds are consumed more often at higher latitudes (Nasimovich 1948, Pulliainen & Ollinmäki 1996, Helldin 2000). Similarly, red fox consumes fruits and insects more often in southern and central Europe (Ciampalini & Lovari 1985, Papageorgiou et al. 1988, Serafini & Lovari 1993, Lanszki et al. 1999, Padial et al. 2002) than in northern Europe (Englund 1965, Jędrzejewski & Jędrzejewska 1992, Lindström 1989). The food niche of the pine marten is wider in northern than in southern areas, whilst the opposite trend has been recorded for the red fox (De Marinis & Asprea 2004, Zalewski 2004).

Differences in morphological and ecological parameters can contribute to the food resource partitioning. Foxes and martens have different body sizes: foxes weigh on average 4-7 kg, whereas pine martens only weigh 0.6-2 kg (Corbet & Harris 1991, Gittleman 1985). Furthermore, pine martens are more nocturnal than foxes (Gittleman 1985, Weber et al. 1994, Zalewski 1997, 2000 and 2001), and they are adapted to tree climbing. Therefore, diet composition, size of prey and hunting locations should serve to separate the food niches of these two opportunist predators, resulting in long-term coexistence (Pulliainen 1981, Kurki et al. 1998).

Periods of reduced abundance of rodents (primary prey) are most difficult for predators (e.g. Hansson & Henttonen 1985, Marcström et al. 1988, Thompson & Colgan 1990). The central European populations of forest rodents, mainly bank voles *Clethrionomys glareolus*, are considered to be quite stable with small fluctuations in annual peak densities (Jensen 1982, Alibhai & Gipps 1985, Hansson & Henttonen 1985, Pucek et al. 1993), compared to *Microtus* voles, which exhibit 3-4 year cycles (Krebs & Myers 1974, Hansson & Henttonen 1985, Krebs 1996). Therefore, availability and dominance in the rodent community can affect variation in the food niche of predators and the degree of trophic overlap between species. When the main prey populations decline, predators turn to less abundant alternative food items (Angelstam et al. 1984, Goszczyński & Wasilewski 1992, Jędrzejewski et al. 1993, Norrdahl & Korpimäki 2000, Hanski et al. 2001, Elmhagen et al. 2002). Both predators may coexist during lean periods if they choose different buffer food items or buffer food items that are very abundant. In northern and central Europe, both predators consume various buffer food items; pine martens consume birds, squirrels *Sciurus vulgaris*, frogs and fruit (Jędrzejewski et al. 1993, Pulliainen & Ollinmäki 1996, Helldin 1999), whereas red foxes prey on hares *Lepus* spp. and birds, and eat carrion or fruit (Angelstam et al. 1984, Goszczyński 1986, Marcström et al. 1988, Reynolds & Tapper 1995). Consequently, the food niches of the predators should overlap less when their main food sources decline in numbers.

Despite the fact that the diet composition of both predators have been extensively studied in Europe, no information about pine marten diet in the Pannonian ecoregion is available in the literature (Zalewski 2004), and there are no data on trophic overlap between these predators, or on interactions between the predators and their main prey from this intermediate region. The objectives of our research were: 1) to study the interspecific and intraspecific (seasonal and inter-year) differences in feeding hab-

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its of the red fox and pine marten; 2) to examine the responses of both predators to variations in the small-mammal community and to monitor changes in preferences for rodents preyed upon in relation to their biomass in the areas studied; 3) to analyse the trophic niche separation between these sympatric predators based on diet composition, with assessments of the weight and zonation of prey species distribution in their diet; and 4) to test the hypothesis that the larger fox would take larger prey and would show a larger variation in food item types (wider food niche breadth) than the smaller pine marten.

Material and methods

Study area

Our study area is situated in the Pannonian ecoregion, southwestern Hungary (46°24'N, 17°27'E) in the Boronka Nature Conservation Area (BNCA; 78.3 km^2). The BNCA district is characterised by extensive forests of hornbeam and oak *Fraxino pannonicae-Carpinetum*, which contain island-like formations of beech *Leucojo verno-Fagetum*, Austrian oak *Quercetum petraeae-cerris* and Scots pine *Pinus silvestris* within a mixed oak stock. The forests surround eutrophic fish ponds. Detailed information on the vegetation and the water habitats of the BNCA is given by Lanszki et al. (2001). All interventional forestry procedures are performed in an environmentally sound manner, because the area was declared a protected zone in 1991 and part of the forest is a strictly protected core area. Thus, no logging and only a minimum of fish pond management was carried out, and consequently the degree of human influence in the area was kept at a minimum. The nearest plough-lands are at least 1.5 km away and the closest villages 4-5 km away from the study area. Between 1996/97 and 2000/01 the population densities of game species (individuals/km^2, mean ± SE) were the following: red deer *Cervus elaphus* 3.0 ± 0.35, fallow deer *Dama dama* 0.2 ± 0.02, roe deer *Capreolus capreolus* 2.4 ± 0.25, wild boar *Sus scrofa* 2.9 ± 0.35, brown hare *Lepus europaeus* 0.5 ± 0.11 and pheasant *Phasianus colchicus* 1.9 ± 0.49 (Csányi 1999, 2000, 2001). The climate is continental and during our study the mean (± SE) winter temperature was 1.7 ± 0.6°C (range: -0.4 - +3.2°C). Duration of snow cover was 33.4 ± 11.9 days (range: 7-71 days) and snow depth was 6.5 ± 1.1 cm (range: 3.1-8.8 cm). Summer temperature was 20.7 ± 0.5°C (range: 20.0-22.2°C), and mean annual precipitation was 711 ± 104 mm (range: 563-943 mm).

Rodent community

During April 1998-February 2001, 26 small mammal trapping sessions were carried out (one period in winter and two or three periods each season from spring to autumn). In each session, trapping was conducted at two stations for four consecutive nights using glass-doored wooden live traps. The traps (180 ×70 × 70 mm) were distributed in a grid 10 × 10 (at the first site: 100 traps) and 7 × 7 (at the second site: 49 traps). Quadrate grid points were marked for every 10 metres and a given trap was placed on the same point in each period during the study. The first station was situated in hornbeam and oak forests, characteristic of the BNCA; the second in a mixed forest (oak and pine). Walnuts, maize and ham were used as bait. The traps were checked twice daily: at 06:00 and 20:00 (with eight consecutive checks per session). For individual identification of captured animals we removed the terminal knuckle of the toes (Begon 1979), and recorded the sex, age and weight of the animal. Minimum number alive (MNA) was determined from capture-mark-recapture data (Krebs 1989). Biomass of small mammals living in the forest (in kg/ha) was calculated from summarised capture data (from individual weights and MNA) in each season. Data obtained from small mammal trapping, performed over three years, were averaged according to season for the preference calculations. All small mammal examination was permitted by the Directorship of the Danube-Drava National Park.

Scat collection and diet analysis

Diet composition of the red fox and pine marten was studied by analysis of scats collected during December 1996-February 2001. Scats were collected twice a month, on a standard route (approximately 5 km long). Pine marten and fox scats were distinguished on the basis of size, shape and smell characteristics. Scats of stone martens *Martes foina* and pine martens can be misclassified, as they are very similar and both species can inhabit the same habitat (Herrmann 1994, Pedrini et al. 1995a,b, Genovesi et al. 1996). Stone martens, however, in general tend to prefer agricultural land and small forest patches close to villages, whereas pine martens tend to select larger forest complexes. For example, stone marten sightings were rarely made far

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(≥ 10 km) away from urban areas in the central Italian Alps (Pedrini et al. 1995b). In larger forested areas of central Europe, like the Białowieża Forest (which is similar to the area examined in our study), stone martens mostly occur in villages and seem to avoid large forest complexes. Radiotracked stone martens in the Białowieża Forest mostly lived in villages, while movements between villages were very uncommon (1-2 nights per year; A. Zalewski, unpubl. data). Our study area in BNCA is distant from any human settlement, and only pine martens were recorded in the area during our study period both by direct observation and by snow tracking. On the basis of the above considerations and data, we assume that stone martens did not occur in our study area during the period of sample collection; if some stone martens did occur in the area, we assumed that it was an occasional presence with little or no effect on the results of our study.

A total of 1,010 fox and 332 pine marten scats were analysed using a standard procedure (Jędrzejewska & Jędrzejewski 1998). Scats were soaked in water, washed through a sieve (0.5 mm mesh) and dried. All food remains were separated and identified with the aid of keys from Teerink (1991), März (1972), Brown et al. (1993) and our own reference collection. Diet composition of the predators was expressed in two ways: relative frequency of occurrence (%Occ) and percentage of biomass consumed (%Bio). To calculate the relative frequency of occurrence the number of occurrences recorded for the given food source was multiplied by 100 and then divided by the total number of food types identified. All dry food remains were weighed and multiplied by coefficients of digestibility (insectivores and small rodents 23, medium-sized mammals 50, wild boar 118, deer 15, birds 35, amphibians and reptiles 18, fish 25, insects, crayfish and molluscs 5, fruit, seed and other plant material 14) to obtain an estimate of the percentage of fresh weight (biomass) of food consumed (Jędrzejewska & Jędrzejewski 1998). For wild boar and cervids we used various coefficients of digestibility as was suggested by Jędrzejewski & Jędrzejewska (1992). Wild boar meat eaten by fox and marten were from whole carcasses (mortality caused by disease), and medium-sized predators mostly consume meat and less frequently bones or skin with hairs. In contrast to wild boar, remains of cervids were mainly left by hunters (limbs and internal organs), and thus corresponded to what would have been left over from wolf kills where the prey is utilised almost completely. Therefore, scavengers often eat bones and skin, and coefficients of digestibility are likely to be lower (see Jędrzejewski & Jędrzejewska 1992). The prey species were classified according to weight (Clevenger 1993) and on their characteristic zone of occurrence recorded for predatory species (Gittleman 1985). We selected three prey zonation categories: 1) terrestrial and mainly terrestrial but sometimes arboreal, 2) arboreal and mainly arboreal but sometimes terrestrial, and 3) aquatic or water-linked (Gittleman 1985; for more detail see Appendix I). We used log-linear likelihood tests on frequency of occurrence data to test for dietary differences among seasons and years. Owing to the large number of comparisons (eight dietary categories), we adjusted the level of significance to 0.0064 with a Bonferroni correction. χ^2-test was applied for distribution analysis of prey consumption on the basis of weight and characteristic zonation.

Trophic niche breadth was calculated in accordance with Levins (Krebs 1989): $B = 1/\Sigma p_i^2$, where p_i = the relative frequency of the i^{th} food item; and standardised across food items: $B_A = (B-1)/(n-1)$, rating from 0 to 1. The following food categories were used in the calculations related to trophic niche and the comparative analysis of diet composition for predator species: 1) small mammals, 2) medium-sized mammals, 3) carcasses, 4) birds, 5) other vertebrates (reptiles, amphibians and fish), 6) invertebrates, and 7) fruits, seeds and other plant matter. Trophic niche overlap was calculated by means of the Renkonen index: $P_{jk} = [Sn(\text{minimum } p_{ij}, p_{ik})]100$, where P_{jk} = percentage overlap between species j and species k; p_{ij} and p_{ik} = proportion of resource i represented within the total resources used by species j and species k; n = total number of food items (Krebs 1989). The standardised food niche breadths were compared with general linear models (GLM procedure in SPSS). One-way analysis of variance was used for seasonal niche-overlap calculation. Ivlev's index (E_i) of preference according to small mammal dominance was applied as follows: $E_i = (r_i - n_i)/(r_i + n_i)$, where r_i = percentage biomass of the given (i^{th}) food category in the diet and n_i = percentage of biomass of the given (i^{th}) taxon in the environment (Krebs 1989). Electivity varies from -1.0 to +1.0. T-test was applied to compare the Ivlev's indices in two, bank vole or *Apodemus* mice dominated, periods. We used the SPSS 10 for Windows (1999) statistical package to process data.

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Results

Density and biomass of rodents

Apodemus mice species in BNCA were the yellow-necked mouse *Apodemus flavicollis* (51.4%), common field mouse *A. sylvaticus* (46.3%) and striped field mouse *A. agrarius* (2.3%). The various *Apodemus* species were grouped together because it was not possible in every case to identify the species on the basis of the hair or teeth found in predator scats. The trapping results showed that bank vole and *Apodemus* mice were the dominant rodent species in the forests of BNCA (Fig. 1), and they comprised on average 99.2 ± 0.4% (mean ± SE) of the small mammal community. Their number and dominance in the community varied both annually and seasonally. Based on the dominance of the small mammal species two periods were distinguished: 1) dominance of bank voles and 2) dominance of *Apodemus* mice (see Fig. 1). The density of small mammals increased from 19.9 ± 6.9 individuals/ha in spring to 69.3 ± 12.5 individuals/ha in autumn and decreased during winter. Small mammal numbers were highest in 1999, and, due to the mild winter weather of 1999/2000, a large proportion of them survived the winter (see Fig. 1). Despite this, no conspicuously high small-mammal density was observed in the autumn of 2000 (see Fig. 1).

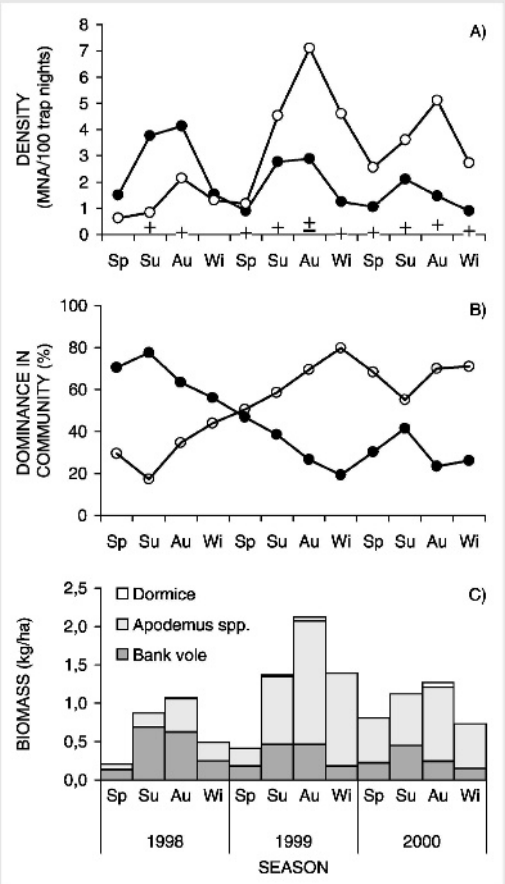


Figure 1. Availability of small mammals in the Boronka Nature Conservation Area, Hungary, expressed as abundance (A), dominance (B) and biomass (C). Data are based on minimum number alive (MNA) obtained using the mark-recapture technique. ● = bank vole; ○ = *Apodemus* spp.; + = shrews; - = dormice.

Predator diets

Two main food items were most important in predator diets: small rodents and plant material; together they comprised 69-93% of the food biomass of foxes and 55-79% of the food biomass of pine martens. The predators supplemented their diets with birds, ungulate carcasses and invertebrates. Generally, pine martens preyed more often on reptiles, amphibians and fish ($\chi^2 = 32.62$, df = 1, $P < 0.0001$) and consumed more plant material ($\chi^2 = 19.27$, df = 1, $P < 0.0001$), whereas red foxes preyed more often on small mammals ($\chi^2 = 36.80$, df = 1, $P < 0.0001$) and fed more often on carcasses ($\chi^2 = 14.21$, df = 1, $P < 0.0002$).

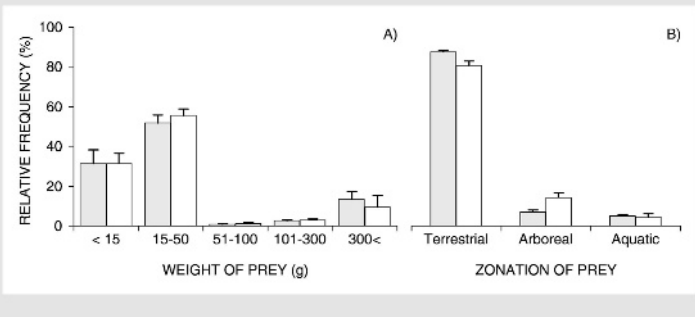


Figure 2. Distribution of the frequency of prey in the diet of red foxes (■) and pine martens (□) on the basis of weight (A) and zonation (B), in the Boronka Nature Conservation Area, Hungary.

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Prey weighing < 50 g comprised up to 83% of fox diet and 87% of marten diet (Fig. 2) and both predators hunted prey weighing 51-300 g. The highest prey weight category (> 300 g) proved to play an important role in fox diets (13%). Prey weight did not differ significantly between fox and marten diets ($\chi^2 = 9.27$, df = 4, P = 0.055). The majority (88%) of prey species consumed by the terrestrial fox lived at ground level (see Fig. 2). Foxes seldom ate arboreal species, or species associated with aquatic habitats (7 and 5%, respectively). The pine marten, despite its outstanding capacity for climbing, also preyed primarily on terrestrial species (frequency: 81%). In total, 14% of pine marten prey species were typically arboreal and only 5% were associated with aquatic habitats. The diets of the two predators differed significantly ($\chi^2 = 33.27$, df = 2, P < 0.001) on the basis of zonation of prey.

Seasonal and inter-year variation in the predator diets

Predator diet compositions showed significant differences between seasons (Tables 1 and 2). Percent occurrence of rodents in both predators' diets was higher in winter and autumn and lower in summer (see Table 1). Both predators hunted more bank voles than *Apodemus* mice. The proportion of both bank voles and *Apodemus* mice in fox diets did not

Table 1. The diet of red fox and pine marten in the Boronka Nature Conservation Area, Hungary. Data were collected during December 1996-February 2001. %Occ = percent relative frequency of occurrence; %Bio = percent of biomass consumed; - = occurring in proportions of < 0.05%.

	Red fox								Pine marten							
	Winter		Spring		Summer		Autumn		Winter		Spring		Summer		Autumn	
Items	%Occ	%Bio	%Occ	%Bio	%Occ	%Bio	%Occ	%Bio	%Occ	%Bio	%Occ	%Bio	%Occ	%Bio	%Occ	%Bio
Shrews (Soridae)	0.9	0.5	1.5	2.5	0.6	0.2	0.5	0.3	1.4	0.8	0.9	2.7	2.3	3.2		
Apodemus spp.	19.2	23.4	12.4	13.9	9.0	12.9	15.3	21.4	10.9	15.5	8.6	11.4	12.5	7.5	16.1	26.9
Bank vole	23.7	35.5	20.5	51.1	14.3	28.9	19.2	37.6	26.1	34.2	20.3	39.8	10.6	15.1	19.0	20.9
Microtus spp.	1.4	2.7	0.8	0.7	0.5	1.8	1.1	1.2	0.7	1.3	0.5	1.9				
Other small rodents	1.8	2.3	0.6	1.8	0.9	1.1	2.0	0.5	0.7	-	1.0	0.3	2.3	0.5	0.8	0.1
Small rodents total	47.0	64.4	35.8	70.0	25.3	44.9	38.1	61.0	39.8	51.8	31.3	56.1	27.7	26.3	35.9	47.9
Medium sized rodents			0.2	0.9	0.4	0.9	0.5	0.8	0.7	1.4	1.4	-	0.4	0.1	0.7	1.5
Brown hare			0.2	0.2	0.4	0.5	0.2	0.3					0.4	0.1		
Mustela spp.			0.4	0.1	0.1	-										
Domestic cat and dog	0.4	0.9			0.2	0.1										
Wild boar carcass	6.7	17.0	3.8	10.0	0.6	2.0	0.5	0.2	9.3	23.2	2.2	3.9	0.4	0.1		
Cervidae carcass	10.9	4.6	7.3	2.3	2.9	2.1	3.5	1.6	13.8	6.4	5.9	2.5	0.4	0.8	0.7	0.3
Small birds (Passeriformes spp.)	5.9	5.0	5.7	3.1	6.3	4.8	2.0	0.8	5.8	5.9	13.5	26.3	12.8	21.2	9.1	16.0
Pheasant	0.9	1.2	1.1	6.2	0.8	4.4	0.7	1.6								
Other birds	0.9	1.7	1.4	1.5	1.1	2.1	0.6	0.4	0.7	2.2	1.0	0.3				
Birds total	7.7	7.9	8.2	10.8	8.2	11.3	3.3	2.8	6.5	8.1	14.5	26.6	12.8	21.2	9.1	16.0
Reptiles, amphibians and fish	2.2	0.6	4.2	1.8	2.2	1.2	2.0	0.4	6.6	5.1	8.9	5.3	1.2	0.8	4.2	1.8
Carabid beetles	3.1	0.1	18.1	0.1	24.3	1.7	16.9	0.8	5.8	0.1	15.8	1.4	15.8	1.5	14.9	0.7
Other Coleoptera	2.8	0.2	7.8	0.1	6.2	0.3	4.7	0.3	2.9	-	8.0	0.6	6.4	0.6	4.2	0.1
Other invertebrates	1.7	-	1.4	-	1.3	-	2.0	0.1	4.4	0.3	6.2	0.2	3.7	0.3	0.7	-
Invertebrates total	7.6	0.3	27.2	0.3	31.6	2.0	23.6	1.2	13.1	0.4	30.0	2.2	26.0	2.4	19.8	0.8
Wild raspberry (*Rubus* spp.)	0.2	-	0.2	-	9.3	12.3	2.3	0.7	1.5	0.2			13.2	18.9	4.9	1.2
Cherry (*Cerasus* spp.)			1.7	2.0	3.4	5.8					0.9	3.3	7.5	20.5		
Wild plum (*Prunus spinosa*)					2.5	3.0	1.8	2.7					1.1	1.0	2.1	7.5
Pear (*Pyrus* spp.)	0.2	-			8.0	12.9	8.1	16.2			0.5	-	3.8	7.1	10.6	14.9
Other fruits			0.4	0.1	1.2	0.4	2.2	0.3	1.5	0.4	2.3	0.1	1.8	0.5	2.9	0.6
Seeds and other plants	17.1	4.3	10.4	1.5	3.7	0.6	15.4	11.8	7.3	3.0	2.3	-	3.4	0.3	9.1	7.5
Plant material total	17.5	4.3	12.7	3.6	28.1	35.0	29.7	31.7	10.2	3.6	5.9	3.4	30.8	48.3	29.6	31.7
No. of scats analysed	294		211		259		246		71		96		103		62	
Items per scat	1.9		2.2		2.8		2.3		1.9		2.3		2.6		2.3	

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Table 2. Summary of log-linear analysis of the variation in red fox and pine marten diets during four seasons and four years (1997-2000) from Boronka Nature Conservation Area, Hungary. Numbers in italics indicate significant values.

			Red fox		Pine marten	
Item	Effect	df	χ^2	P	χ^2	P
Bank vole	Season	3	8.2	0.043	17.9	*0.0005*
	Year	4	38.6	*<0.0001*	12.5	0.0137
	Interaction	12	34.0	*0.0007*	7.1	0.85
Apodemus spp.	Season	3	8.2	0.041	7.2	0.73
	Year	4	22.6	*0.0001*	2.0	0.07
	Interaction	12	18.7	0.096	7.1	0.85
Small mammals total	Season	3	28.6	*<0.0001*	5.1	0.17
	Year	4	13.3	0.0099	16.3	*0.0027*
	Interaction	12	39,3	*0.0001*	10.7	0.55
Carcasses	Season	3	57.3	*<0.0001*	50.7	*<0.0001*
	Year	4	12.4	0.015	5.7	0.22
	Interaction	12	14.0	0.23	8.8	0.72
Birds	Season	3	24.1	*<0.0001*	15.6	*0.0013*
	Year	4	12.7	0.013	5.6	0.23
	Interaction	12	18.3	0.11	16.0	0.19
Other vertebrates	Season	3	6.2	0.10	16.5	*0.0009*
	Year	4	2.5	0.64	5.9	0.20
	Interaction	12	17.8	0.12	11.1	0.52
Invertebrates	Season	3	277.4	*<0.0001*	28.1	*<0.0001*
	Year	4	14.5	*0.0058*	9.9	0.041
	Interaction	12	38.7	*0.00012*	25.6	0.011
Plant material	Season	3	243.5	*<0.0001*	114.8	*<0.0001*
	Year	4	83.8	*<0.0001*	13.3	0.0099
	Interaction	12	43.7	*<0.0001*	26.2	0.010

vary between seasons (see Table 2). Pine martens preyed upon bank voles significantly more in winter than in summer. In both predators' diets, carcasses, birds, invertebrates and plant material varied significantly between seasons. Invertebrates and plant materials (mainly fruits and maize *Zea mays*) were more often consumed in summer and autumn, carrion in winter and spring, and birds in spring and summer (see Tables 1 and 2). Pine martens preyed upon reptiles, amphibians and fish significantly more in winter and spring than in summer and autumn.

Diets of both predators changed between years (see Table 2). Occurrence of bank voles in fox diet decreased with decreasing density of this rodent (see Table 2 and Fig. 1). However, the season*year interaction was significant, indicating that fox diet did vary between seasons in various years (see Table 2): the occurrence of bank voles was higher in summer and autumn in the first two years (high vole density), and in the next two years (low vole density) foxes hunted more voles in winter and spring. The frequency of occurrence of *Apodemus* mice showed an opposite trend. These rodents were often eaten by foxes in 1999 and less often in 1997. Therefore, the occurrence of small mammals in total was relatively stable between years in the fox diet (see Table 2). However, red foxes ate more small rodents in the autumns and winters of 1997 and 1998 than in the winters and springs of 1999 and 2000. Carcasses, birds and other vertebrates (frogs, reptiles and fish) occurred equally often in scats from different years. Invertebrates were eaten by foxes more often in 1997 and 1998 than in the following two years. The occurrence of invertebrates in 1998 and 1999 decreased in summer and increased in winter, whereas in 1997 and 2000 the opposite occurred. Plant materials were eaten more by foxes in 1999 and 2000 than in the first two years. A significant three-way interaction (see Table 2) showed that the degree of differences varied among years and seasons. In years of lower consumption of plants (i.e. 1997 and 1998), this type of food was consumed more often in autumn, whereas in years of higher consumption (i.e. 1999 and 2000) plants were found more often in summer.

Diets of pine martens varied much less between years than did fox diets. The frequency of occurrence of bank voles and *Apodemus* mice in pine marten diets varied only slightly between years

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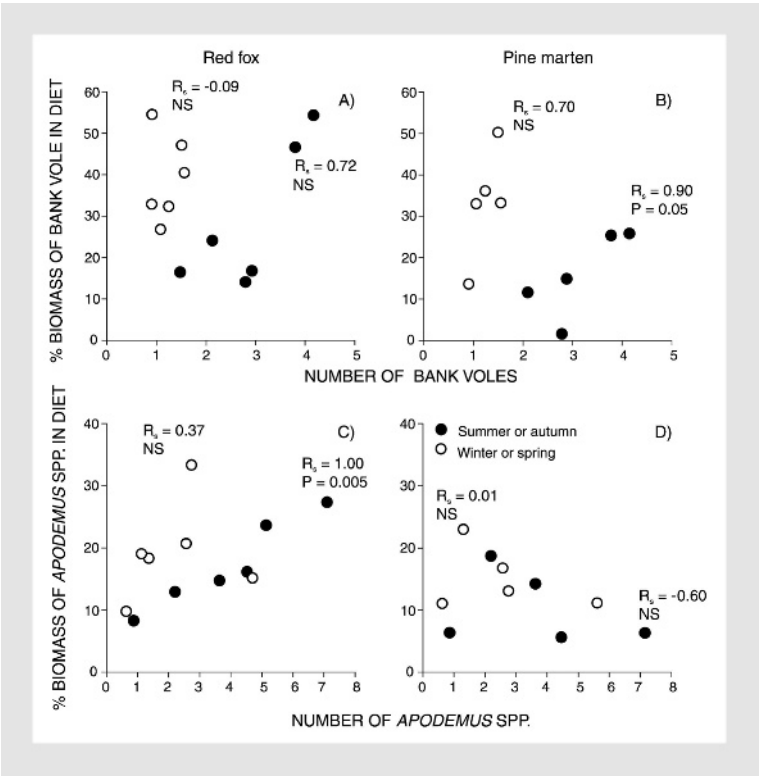


Figure 3. Relationship between bank voles (A,B) and *Apodemus* mice (C,D) densities (MNA/100 trap nights) and percent biomass of these rodents in red fox (A,C) and pine marten (B,D) diets during 1997-2000.

(see Table 2). However, the total of small mammals consumed was higher in the first two years than in the last two years. Other types of food did not vary significantly between years.

Throughout the years, rodents were the most important prey resource for both red foxes and pine martens. However, in periods of lower rodent consumption both predators supplemented their diet with other food items. In summer and autumn, with an increase in the percentage biomass of rodents in fox and marten diets, there was a decrease in consumption of plant material and birds (see Table 1). In winter and spring, birds and carcasses were the most important alternative food, and their consumption decreased with the predators' consumption of rodents.

Small mammal abundance and preference by predators

In summer and autumn, percentage biomass of bank voles in pine marten diet significantly correlated with the number of voles in the local populations (Fig. 3), but the correlation was non-significant for foxes. In winter and spring bank vole density varied to a minor degree (0.9-1.5 MNA/100 trap nights). Furthermore, percent biomass of *Apodemus* mice in fox diets was positively correlated with numbers of mice in the population in summer and autumn, but not in winter and spring (see Fig. 3). In pine marten diets this relationship was not significant in either period.

The red fox and pine marten ate bank voles primarily in winter, while in summer both predators generally consumed less of the various species of mice than expected by availability (Fig. 4). In 1998-1999, when bank vole numbers were greater or equal to the number of mice in the rodent community (see Fig. 1), both predators preyed on bank voles in proportion to their total biomass in the rodent community; the electivity index (E_i) was 0.12 ± 0.04 (range: 0.04-0.26) for fox and E_i = -0.12 ± 0.12 (range: -0.60 - +0.11) for pine marten (see Fig. 4). In this period, red fox ate less *Apodemus* mice (E_i = -0.30 ± 0.05; range: -0.39 - -0.15), but pine marten consumed this rodent in proportion to its abundance in the rodent community (E_i = -0.06 ± 0.06; range: -0.31 - -0.03). In the second period (from autumn 1999; see Fig. 1), when *Apodemus* mice outnumbered the other species, foxes and martens preferred bank voles (E_i = 0.35 ± 0.08 for fox and 0.25 ± 0.18 for marten) and ate less *Apodemus* mice (E_i = -0.28 ± 0.05 for fox and E_i

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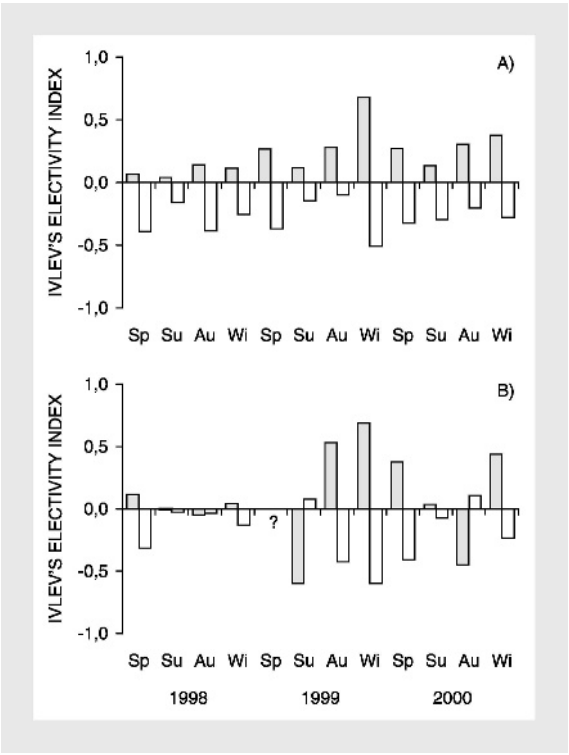


Figure 4. Preference by red foxes (A) and pine martens (B) for bank voles (■) and *Apodemus* mice (□) in spring (Sp), summer (Su), autumn (Au) and winter (Wi) during 1998-2000 in the Boronka Nature Conservation Area, Hungary.

= -0.27 ± 0.10 for marten). The difference in bank vole preference between the first and second periods was significant for both the red fox (t-test: P = 0.027) and pine marten (t-test: P = 0.015) and for *Apodemus* mice in respect of pine marten (t-test: P = 0.035). Red foxes and pine martens similarly consumed fewer shrews (E_i on average -0.12 for both predators), and various species of dormice (E_i = -0.06 for fox and -0.10 for marten) than expected by availability.

Food-niche breadth and food niche overlap

The number of food items in the diet of foxes living in the forest was 66 prey and 15 plant taxa, and for pine martens it was 62 and 11, respectively. The general linear model for the standardised trophic niche breadth, calculated with predator species, seasons and years as independent variables, was not significant ($F_{7,30}$ = 1.52, P = 0.21). Pine martens had a standardised trophic niche breadth similar to that of red foxes (F_1 = 1.12, P = 0.30) and both predators' food niche breadth did not vary significantly between seasons (F_3 = 1.55, P = 0.22; Table 3) and years (F_3 = 1.65, P = 0.21). Trophic niche overlap between the red fox and pine marten, proved to be of a high degree (71.6 ± 3.3%), but differed non-significantly between seasons (one-way ANOVA: F_3 = 1.14, P = 0.38; see Table 3).

Table 3. Seasonal standardised trophic niche breadths and overlaps (± SE) of the red fox and pine marten in the Boronka Nature Conservation Area. Calculated from the percent biomass of food types in the scats.

	Standardised food niche breadth		
Season	Red fox	Pine marten	Food niche overlap
Winter	0.16 ± 0.04	0.27 ± 0.09	76.0 ± 8.6
Spring	0.24 ± 0.04	0.24 ± 0.01	79.6 ± 3.8
Summer	0.29 ± 0.03	0.26 ± 0.04	65.4 ± 7.2
Autumn	0.16 ± 0.03	0.20 ± 0.06	67.2 ± 3.3

Discussion

Our results showed that food habits of the opportunistic red fox and the pine marten were very similar. The most important foods for both predators were small rodents. Foxes consumed more small mammals and ungulates, whereas martens consumed more plants, reptiles, amphibians and fish. Red fox diet varied more among years than did pine marten diet. Besides considerable small mammal consumption, both predators supplemented their diet with plant matter (primarily forest fruits) in summer and autumn and birds or carcasses in spring and winter. The general feeding habits appear to confirm the results of earlier studies that have found high seasonal variation in red fox and pine marten diets, and identified small mammals as the most frequent food item, with fruit also being an important food source (Jędrzejewski & Jędrzejewska 1992, Jędrzejewski et al. 1993, Serafini & Lovari 1993, Clevenger 1994, Sidorovich et al. 2000, Baltrunaite 2002, Zalewski 2004). In northern Europe, these predators increase their proportions of alternative prey species (e.g. hares, tetraonids and squirrels) in their diets when numbers of their main prey (voles) decreases (Angelstam et al. 1984, Marcström et al. 1988, Zalewski et al. 1995, Pulliainen & Ollinmäki 1996, Helldin 1999). At lower latitudes (e.g. in central Poland), foxes appear to compensate for a lack of small mammals in their diet by consuming more birds and hares. Pine and stone martens, however, compensated for a lack of small mammals by consuming fruit in summer and

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autumn, and birds in winter and spring (Goszczyński 1986). In eastern Poland, when *Microtus* vole numbers were low, foxes ate more hares, carrion and forest rodents (Jędrzejewski & Jędrzejewska 1992), whereas pine martens consumed more birds in spring-summer and insectivorous mammals and carrion in autumn-winter (Jędrzejewski et al. 1993). In southern Europe, seasonal abundance of plant material (mainly fruits) and insects affect the seasonal variation in predator diets, for example foxes and stone martens consumed fruit more often in summer and autumn (Papageorgiou et al. 1988, Herrera 1989, Cavallini & Lovari 1991, Serafini & Lovari 1993, Brangi 1995) similar to what was found in previous studies carried out near BNCA (Lanszki et al. 1999, Lanszki 2003). The recorded low consumption of hare or pheasant and the high winter consumption of ungulates is likely to be related to the low abundance of pheasants and hares and the high availability of carcasses in our study area.

In the deciduous forests of BNCA both predators hunted more voles (bank vole) than *Apodemus* mice, although all the mice were relatively well represented in the two species' diet. In boreal and temperate zones, inter-year variation in red fox diets was influenced by *Microtus* vole numbers (Goszczyński 1974, Macdonald 1977, Jędrzejewki & Jędrzejewska 1992). The high occurrence of *Apodemus* mice in the diet of foxes and pine martens in the BNCA, and in other locations in southern Europe (Ruiz-Olmo & Nadal 1991, Clevenger 1993, Serafini & Lovari 1993), is probably related to the high availability of these mice in many forested and open habitats in these areas (Canova & Fasola 1991, Horváth 1998, Horváth & Pintér 2000). This suggests that foxes living in forests shift their primary prey from *Microtus* voles in northern Europe to *Apodemus* mice in southern Europe. Similarly, pine marten diet changed from bank voles in northern Europe to *Apodemus* mice in southern Europe (Zalewski 2004). Therefore, red fox and pine marten in the Pannonian region showed intermediate characteristic in small-mammal predation.

Both red fox and pine marten preferred *Microtus* voles, especially in years of low bank vole abundance. Generally, the red fox showed a preference for *Microtus* voles, whereas the pine marten preferred bank voles (Goszczyński 1977, 1986, Macdonald 1977, Storch et al. 1990, Lindström & Hörnfeldt 1994, Jędrzejewski et al. 1993). Both predators, preferred slower-moving voles from the rodent community, and preferred less *Apodemus* mice which are characteristically a faster-moving, very agile species which can be difficult to prey upon (Jędrzejewski & Jędrzejewska 1992, Jędrzejewski et al. 1993).

The niche breadth of mammals and birds can be positively correlated with animal body mass (Jarman 1974, Marti et al. 1993, Gittleman 1985, Brändle et al. 2002); for example, in southern and central Europe sympatric stone martens (smaller species) had narrower food niches than foxes (larger species; Serafini & Lovari 1993, Brangi 1995, Lanszki et al. 1999, Padial et al. 2002). Indeed, in previous multi-predator studies, the pine marten had a narrower food niche than the red fox (Belarus: Sidorovich et al. 2000; Lithuania: Baltrunaite 2002; Germany: Ansorge 1989, 1991). However, different results have been obtained in the Białowieża Forest, where the red fox had a narrower food niche than the pine marten (Jędrzejewska & Jędrzejewski 1998). In our study, the smaller pine marten had a niche similar to that of the larger red fox.

In our study, niche overlap between the two predators was very high as compared to those found in other studies (Jędrzejewska & Jędrzejewski 1998, Sidorovich et al. 2000, Baltrunaite 2002, Ansorge 1989, 1991), and the niche overlap increased a little in winter and spring when food resources were scarce. This contradicts the hypothesis of niche segregation between the two predators. Moreover, our data do also not support a hypothesis of resource partitioning according to prey size, as the average prey size did not differ between the two predators. This is in contrast with the results of other studies which showed that larger predators generally rely on larger prey (e.g. Brangi 1995, White et al. 1995, Cypher & Spencer 1998, Kitchen et al. 1999, and discussed by Gittleman 1985). We also tested if predators separated their respective food niches by hunting prey in different microhabitats (tree climbing pine martens feeding more on arboreal prey than terrestrial foxes), but also in this case our data did not show any significant difference between the two species, both hunting mainly on terrestrial preys.

In conclusion, red fox and pine marten diets were very similar. Both species preferred bank voles, fed upon similarly-sized prey and ate the same buffer prey. There are two possible explanations for the lack of food niche partitioning between these two predators. First, food resources are overabundant in our study area and the competitive interaction between the predators was very weak. The second

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and more probable explanation is that there are other mechanisms of niche separation, such as different selection of habitat or activity time, which may reduce competition. Further studies of pine marten-red fox relations are, however, necessary to examine alternative potential mechanisms of niche separation other than food niche partitioning.

Acknowledgements - we express sincere thanks to Prof. J. Goszczyński and Drs J. Birks and J. Kamler for advice and comments on an earlier draft of the manuscript. We thank G. Yoxon and G. Telford for help with language and also the anonymous referees for constructive comments on the composition of the manuscript. The study was supported by the Hungarian Fund for Scientific Research (OTKA no. F 023057), the Bolyai scholarship (J. Lanszki) and Centre of Excellence in Biodiversity Conservation and Mammal Research in European Terrestrial Ecosystems 'BIOTER' Contract No EVK2-CT-2002-80011.

References

Alibhai, S.K. & Gibbs, J.H.W. 1985: The population dynamics of bank voles. - In: Flowerdew, J.R., Gurnell, J. & Gipps, J.H.W. (Eds.), The ecology of woodland rodents: bank voles and wood mice. - Symposia of the Zoological Society of London 55: 277-313.

Angelstam, P., Lindström, E. & Widén, P. 1984: Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. - Oecologia 62: 199-208.

Ansorge, H. 1989: Nahrungsökologische Aspekte bei Baummarder, Iltis und Hermelin (Martes martes, Mustela putorius, Mustela erminea). Populationsökologie marderartiger Säugetiere. - Wissenschaftliche Beiträge University of Halle, pp. 494-504. (In German).

Ansorge, H. 1991: Feeding ecology of red fox, Vulpes vulpes, in the Oberlausitz (SO Germany) during the winter season. - Abhandlungen und Berichte des Naturkundemuseums Görlitz 65: 1-24.

Baltrunaite, L. 2002: Diet composition of the red fox (Vulpes vulpes L.), pine marten (Martes martes L.) and raccoon dog (Nyctereutes procyonoides Gray) in clay plain landscape, Lithuania. - Acta Zoologica Lithuanica 12: 362-368.

Begon, N. 1979: Investigating animal abundance: capture-recapture for biologists. - Edward Arnold, London, 97 pp.

Brangi, A. 1995: Seasonal changes of trophic niche overlap in the stone marten (Martes foina) and the red fox (Vulpes vulpes) in a mountainous area of Northern Apennines (Italy). - Hystrix 7: 113-118.

Brändle, M., Prinzing, A., Pfeifer, R. & Brandl, R. 2002: Dietary niche breath for central European birds: correlations with species-specific traits. - Evolutionary Ecology Research 4: 643-657.

Brown, R., Ferguson, J., Lawrence, M. & Lees, D. 1993: Federn, Spuren und Zeichen der Vögel Europas: Ein Feldführer. - Aula-Verlag Wiesbaden, 232 pp. (In German).

Canova, L. & Fasola, M. 1991: Communities of small mammals in six biotopes of northern Italy. - Acta Theriologica 36: 73-86.

Cavallini, P. & Lovari, S. 1991: Environmental factors influencing the use of habitat in the red fox, Vulpes vulpes. - Journal of Zoology 223: 323-329.

Ciampalini, B. & Lovari, S. 1985: Food habits and trophic niche overlap of the badger (Meles meles L.) and the red fox (Vulpes vulpes L.) in a Mediterranean coastal area. - Zeitschrift für Säugetierkunde 50: 226-234.

Clevenger, A.P. 1993: Pine marten (Martes martes Linné, 1758) comparative feeding ecology in an island and mainland population of Spain. - Zeitschrift für Säugetierkunde 58: 212-224.

Clevenger, A.P. 1994: Feeding ecology of Eurasian pine martens and stone martens in Europe. - In: Buskirk, S.W., Harestad, A.S., Raphael, M.G. & Powell, R.A. (Eds.); Martens, sables and fishers biology and conservation. Cornell University Press, Ithaca and London, pp. 326-340.

Colwell, R.K. & Futuyma, D.J. 1971: On the measurement of niche breadth and overlap. - Ecology 52: 567-576.

Corbet, B.C. & Harris, S. 1991: The handbook of British Mammals. - Blackwell Scientific Publications, Oxford, 520 pp.

Csányi, S. (Ed.); Hungarian Game Management Database. 1994-1998/2001 hunting years. - Agricultural University, GödöllöAvailable at: http://www.vvt.gau.hu

Csányi, S. (Ed.); Hungarian Game Management Database. 1999/2000 hunting year. - St. Stephen University, Gödöllö. Available at: http://www.vvt.gau.hu

Csányi, S. (Ed.); Hungarian Game Management Database. 2000/2001 hunting year. - St. Stephen University, Gödöllö. Available at: http://www.vvt.gau.hu

Cypher, B.L. & Spencer, K.A. 1998: Competitive interactions between coyotes and San Joaquin kit foxes. - Journal of Mammalogy 79: 204-214.

De Marinis, A.M. & Asprea, A. 2004: The diet of red fox Vulpes vulpes and badger Meles meles in the Mediterranean ecosystems. - In: Aranoutsou, M. & Papanastasis, V.P. (Eds.); Proceedings of the 10th MEDECOS Conference, Rhodes, Greece, pp. 1-10.

Elmhagen, B., Tannerfeld, M. & Angerbjörg, A. 2002: Food-niche overlap between arctic and red foxes. - Canadian Journal of Zoology 80: 1274-1285.

Englund, J. 1965: Studies on food ecology of the red fox (Vulpes vulpes) in Sweden. - Viltrevy 3: 371-442.

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Genovesi, P., Secchi, M. & Boitani, L. 1996: Diet of stone martens: an example of ecological flexibility. - Journal of Zoology 238: 545-555.
Gittleman, J.L. 1985: Carnivore body size: ecological and taxonomic correlates. - Oecologia 67: 540-554.
Goszczyński, J. 1974: Studies on the food of foxes. - Acta Theriologica 19: 1-18.
Goszczyński, J. 1977: Connections between predatory birds and mammals and their prey. - Acta Theriologica 22: 399-430.
Goszczyński, J. 1986: Diet of foxes and martens in central Poland. - Acta Theriologica 31: 491-506.
Goszczyński, J. & Wasilewski, M. 1992: Predation of foxes on a hare population in central Poland. - Acta Theriologica 37: 329-338.
Hanski, I., Henttonen, H., Korpimäki, E., Oksanen, L. & Turchin, P. 2001: Small-rodent dynamics and predation. - Ecology 82: 1505-1520.
Hansson, L. & Henttonen, H. 1985: Gradients in density variations of small rodents: the importance of latitude and snow cover. - Oecologia 67: 394-402.
Helldin, J.O. 1999: Diet, body condition, and reproduction of Eurasian pine marten (Martes martes) during cycles in microtine density. - Ecography 22: 324-336.
Helldin, J.O. 2000: Seasonal diet of pine marten Martes martes in southern boreal Sweden. - Acta Theriologica 45: 409-420.
Herrera, C.M. 1989: Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. - Oikos 55: 250-262.
Herrmann, M. 1994: Habitat use and spatial organization by the stone marten. - In: Buskirk, R.A. (Ed.); Martens, sables and fishers biology and conservation. Cornell University Press, Ithaca and London, pp. 122-136.
Horváth, G. 1998: Population dynamics and trapability of four rodent species in a forest habitat. - Miscellanea Zoologica Hungarica 12: 107-119.
Horváth, G. & Pintér, V. 2000: Small mammal fauna of two abandoned field habitats, and a spatio-temporal analysis of four rodent populations. - Miscellanea Zoologica Hungarica 13: 105-121.
Jarman, P.J. 1974: The social organization of antelopes in relation to their ecology. - Behaviour 48: 215-267.
Jędrzejewska, B. & Jędrzejewski, W. 1998: Predation in vertebrate communities: the Białowieża Primeval Forest as a case study. - Ecological Studies vol. 135. Springer-Verlag, Berlin, Heidelberg, and New York, 450 pp.
Jędrzejewski, W. & Jędrzejewska, B. 1992: Foraging and diet of the red fox Vulpes vulpes in relation to variable food resources in Białowieża National Park, Poland. - Ecography 15: 212-220.
Jędrzejewski, W., Zalewski, A. & Jędrzejewska, B. 1993: Foraging by pine marten Martes martes in relation to food resources in Białowieża National Park, Poland. - Acta Theriologica 38: 405-426.
Jensen, T.S. 1982: Seed production and outbreaks of non-cyclic rodent populations in deciduous forest. - Oecologia 54: 184-192.
Kitchen, A.M., Gese, E.M. & Schauster, E.R. 1999: Resource partitioning between coyotes and swift foxes: space, time, and diet. - Canadian Journal of Zoology 77: 1645-1656.
Krebs, C.J. 1989: Ecological methodology. - Harper Collins Publishers, New York, 654 pp.
Krebs, C.J. 1996: Population cycles revisited. - Journal of Mammalogy 77: 8-24.
Krebs, C.J. & Myers, J.H. 1974: Population cycles in small mammals. - In: Macfadyen, A. (Ed.); Advances in ecological research. Academic Press, London, New York, pp. 267-399.
Kurki, S., Nikula, A., Helle, P. & Lindén, H. 1998: Abundances of fox and pine marten in relation to the composition of boreal forest landscapes. - Journal of Animal Ecology 67: 874-886.
Lanszki, J. 2003: Feeding habits of stone martens in a Hungarian village and its surroundings. - Folia Zoologica 52: 367-377.
Lanszki, J., Körmendi, S., Hancz, C. & Martin, T.G. 2001: Examination of some factors affecting selection of fish prey by otters (Lutra lutra) living by eutrophic fish ponds. - Journal of Zoology 255: 97-103.
Lanszki, J., Körmendi, S., Hancz, C. & Zalewski, A. 1999: Feeding habits and trophic niche overlap in a Carnivora community of Hungary. - Acta Theriologica 44: 429-442.
Lindström, E. 1989: The role of medium-sized carnivores in the Nordic boreal forest. - Finnish Game Research 46: 53-63.
Lindström, E.R. & Hörnfeldt, B. 1994: Vole cycles, snow depth and fox predation. - Oikos 70: 156-160.
Macdonald, D.W. 1977: On food preference in the red fox. - Mammal Review 7: 7-23.
Marcström, V., Kenward, R.E. & Engren, E. 1988: The impact of predation on boreal tetraonids during vole cycles: an experimental study. - Journal of Animal Ecology 57: 859-872.
Marti, C.D., Steenhof, K., Kochert, M.N. & Marks, J.S. 1993: Community trophic structure: the roles of diet, body size and activity time in vertebrate predators. - Oikos 67: 6-18.
März, R. 1972: Gewöll- und Rupfungskunde. - Akademie Verlag, Berlin, 398 pp (In German).
Mills, M.G.L. 1984: Prey selection and feeding habits of large carnivores in the southern Kalahari. - Koedoe 27: 281-294.
Nasimovich, A.A. 1948: Ekologiya lesnoi kunitsy. (In Russian with an English summary: Ecology of the pine marten). - Trudy Laplandskogo gasudarstvennogo zapovednika 3: 81-106.
Norrdahl, K. & Korpimäki, E. 2000: Do predators limit the abundance of alternative prey? Experiments with

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vole-eating avian and mammalian predators. - Oikos 91: 528-540.

Padial, J.M., Avila, E. & Gil-Sanchez, J.M. 2002: Feeding habits and overlap among red fox (Vulpes vulpes) and stone marten (Martes foina) in two Mediterranean mountain habitats. - Zeitschrift für Säugetierkunde 67: 137-146.

Papageorgiou, N.K., Sepougaris, A., Christopoulou, O.G., Vlachos, C.G. & Petamidis, J.S. 1988: Food habits of the red fox in Greece. - Acta Theriologica 33: 313-324.

Pedrini, P., Prigioni, C. & Volcan, G. 1995a: Distribution of mustelids in Adamello-Brenta Park and surrounding areas (Central Italian Alps). - Hystrix 7: 39-44.

Pedrini, P., Prigioni, C. & Volcan, G. 1995b: Use of trophic resources and forest habitats by the genus Martes in Adamello-Brenta Park (Central Italian Alps). - Hystrix 7: 127-135.

Pucek, Z., Jędrzejewska, W., Jędrzejewska, B. & Pucek, M. 1993: Rodent population dynamics in primeval deciduous forest (Białowieża National Park) in relation to weather, seed crop, and predation. - Acta Theriologica 38: 199-232.

Pulliainen, E. 1981: A transect survey of small land carnivore and red fox populations on a subarctic fell in Finnish Forest Lapland over 13 winters. - Annales Zoologici Fennici 18: 270-278.

Pulliainen, E. & Ollinmäki, P. 1996: A long-term study of the winter food niche of the pine marten Martes martes in northern boreal Finland. - Acta Theriologica 41: 337-352.

Reynolds, J.C. & Tapper, S.C. 1995: The ecology of the red fox Vulpes vulpes in relation to small game in rural southern England. - Wildlife Biology 1: 105-119.

Rosenzweig, M.L. 1966: Community structure in sympatric Carnivora. - Journal of Mammalogy 47: 602-612.

Ruiz-Olmo, J. & Nadal, J. 1991: Regime alimentaire de la martre (Martes martes L., 1758) en hiver et taille des portees a Menorca, Iles Baleares. - Mammalia 55: 639-642. (In French).

Schoener, T.W. 1974: Resource partitioning in ecological communities. - Science 185: 27-39.

Serafini, P. & Lovari, S. 1993: Food habits and trophic niche overlap of the red fox and the stone marten in a Mediterranean rural area. - Acta Theriologica 38: 233-244.

Sidorovich, V.E., Polozov, A.G., Lauzhel, G.O. & Krasko, D.A. 2000: Dietary overlap among generalist carnivores in relation to the impact of the introduced raccoon dog Nyctereutes procyonoides on native predators in northern Belarus. - Zeitschrift für Säugetierkunde 65: 271-285.

SPSS 1999: SPSS 10 for Windows. - SPSS Inc, Chicago, IL, USA.

Storch, I., Lindström, E. & de Jounge, J. 1990: Diet and habitat selection of the pine marten in relation to competition with the red fox. - Acta Theriologica 35: 311-320.

Thompson, I.D. & Colgan, P.W. 1990: Prey choice by marten during a decline in prey abundance. - Oecologia 83: 443-451.

Teerink, B.J. 1991: Hair of West-European mammals. - Cambridge University Press, Cambridge, 224 pp.

Weber, J-M., Meia, J-S. & Aubry, S. 1994: Activity of foxes, Vulpes vulpes, in the Swiss Jura mountains. - Zeitschrift für Säugetierkunde 59: 9-13.

White, P.J., Ralls, K. & White, C.A.V. 1995: Overlap in habitat and food use between coyotes and San Joaquin kit foxes. - Southwestern Naturalist 40: 342-349.

Zalewski, A. 1997: Factors affecting selection of resting site type by pine marten in primeval deciduous forests (Białowieża National Park, Poland). - Acta Theriologica 42: 271-288.

Zalewski, A. 2000: Factors affecting the duration of activity by pine martens (Martes martes) in the Białowieża National Park, Poland. - Journal of Zoology 251: 439-447.

Zalewski, A. 2001: Seasonal and sexual variation in diel activity rhythms of pine marten Martes martes in the Białowieża National Park (Poland). - Acta Theriologica 46: 295-304.

Zalewski, A. 2004: Geographical and seasonal variation in food habits and prey size of the European pine marten Martes martes. - In: Harrison, D.J., Fuller, A.K. & Proulx, G. (Eds.); Martens and fishers (Martes) in human-altered environments: an international perspective. Kluwer Academy Publishers, pp. 77-98.

Zalewski, A., Jędrzejewski, W. & Jędrzejewska, B. 1995: Pine marten home ranges, numbers and predation on vertebrates in a deciduous forest (Białowieża National Park, Poland). - Annales Zoologici Fennici 32: 131-144.

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Appendix I

Weight and zonation of prey eaten by red foxes and pine martens in the Boronka Nature Conservation Area, Hungary. Prey weight categories are indicated as: 1 = < 15, 2 = 15-50, 3 = 51-100, 4 = 101-300, 5 = > 300 g (Clevenger 1993), and prey zonation categories are indicated as: t = terrestrial and mainly terrestrial but sometimes arboreal, a = arboreal and mainly arboreal but sometimes terrestrial, and w = aquatic or water-linked (Gittleman 1985). Undetermined prey was classified to the closest identifiable taxa, e.g. undetermined Rodentia might be *Apodemus, Clethrionomys* or *Microtus* species.

Vertebrates:

Small and medium sized mammals: bicolour white-toothed shrew *Crocidura leucodon* (1 t), common shrew *Sorex araneus* (1 t), red squirrel *Sciurus vulgaris* (4 a), fat dormouse *Myoxus glis* (4 a), dormouse *Muscardinus avellanarius* (2 a), undetermined Myoxidae spp. (4 a), common field mouse *Apodemus sylvaticus* (2 t), yellow-necked field mouse *Apodemus flavicollis* (2 t), striped field mouse *Apodemus agrarius* (2 t), harvest mouse *Micromys minutus* (1 t), Norway rat *Rattus norvegicus* (4 t), bank vole *Clethrionomys glareolus* (2 t), common vole *Microtus arvalis* (2 t), water vole *Arvicola terrestris* (4 w), muskrat *Ondatra zibethicus* (5 w), undetermined Rodentia spp. (2 t), brown hare *Lepus europaeus* (5 t), weasel/stoat *Mustela* spp. (4 t)

Ungulates: wild boar *Sus scrofa* (5 t), roe deer *Capreolus capreolus* (5 t), red deer *Cervus elaphus* (5 t)

Domestic animals: cat *Felis catus* (5 t), dog *Canis familiaris* (5 t)

Birds: goldfinch *Carduelis carduelis* (1 a), nuthatch *Sitta europaea* (2 a), wren *Troglodytes troglodytes* (1 a), undetermined small passerines (Passeriformes) (2 a), pheasant *Phasianus colchicus* (5 t), moorhen *Gallinula chloropus* (4 w), duck *Anas* spp. (5 w), coot *Fulica atra* (4 w), grebe *Podiceps* spp. (4 w), medium-sized waterfowl (5 w), egret *Egretta* spp. (5 v), bird egg (2 a,t)

Reptiles and amphibians: European pond turtle *Emys orbicularis* egg (1 t), grass snake *Natrix natrix* (3 w), lizard *Sauria* spp. (1 t), undetermined reptile (3 t), frog *Rana* spp. (2 t), undetermined amphibians Anura spp. (2 t)

Fish: giebel carp *Carassius auratus gibelio* (4 w), grass carp *Ctenopharyngodon idella* (4 w), other Cyprinidae (2 w), sunfish *Lepomis gibbosus* (1 w), perch *Perca fluviatilis* (1 w), pike-perch *Stizostedion lucioperca* (4 w), pike *Esox lucius* (4 w), undetermined fish (4 w).

Invertebrate:

(1 t): acridoids Acridoidea spp., garden ground beetle *Carabus hortensis*, ground beetles *Carabus ullrichi*/*C. cancellatus*, violet ground beetle *Carabus violaceus*, other carabid beetles *Carabus scheidleri*, *Carabus coriaceus*, small-sized ground beetles *Pterostichus* and *Harpalus* spp., undetermined ground beetles (Carabidae), ground beetle larvae (Carabidae), ladybird *Coccinella* spp., stag beetle *Lucanus cervus*, lesser stag beetle *Dorcus parallelepipedus*, dor beetle *Geotrupes vernalis*, dor beetles *Geotrupes* sp., undetermined Scarabeidae, click beetles Elateridae spp., rose chafer *Cetonia* spp., cockchafer *Melolontha melolontha*, chafer *Melolontha* spp., burying beetles *Necrophorus* spp., bee beetle *Trichodes apiarius*, buprestid beetles *Buprestis* spp., beetle and beetle larvae *Coleoptera* spp., hornet *Vespa crabro*, social wasps and larvae (Vespidae), dragon-fly Odonata , chrysalis Lepidoptera, undetermined insects Insecta , millipedes Diplopoda, banded snail *Cepaea* spp., snails Gastropoda

(1 w): water beetles *Dytiscus marginalis*, great black water beetle *Hydrous piceus*, dragon-fly larvae Odonata, crayfish *Astacus* spp.

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