

Variation of insect assemblages in fox and marten faeces collected in southern Poland

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Remains of invertebrates, especially insects, are frequently found in carnivores' faeces. Invertebrates are generally restricted to a given area and many factors such as land-use pattern, vegetation structure or even moisture can separate different groups; thus, invertebrates can be used as bioindicators. Forty-five samples of marten and fox scats were analysed for the presence of insect species. Thirty insect species — which were expected to be found — were identified. Canonical correspondence analysis indicated that the factor 'species' (i.e., marten and fox) was the main factor determining invertebrate species variation. Redundancy analysis allowed us to identify invertebrate ecological groups associated with these two carnivores. Martens prefer nest-building insects as a supplementary source of food and mainly forage in meadows, whereas foxes foraged in forest with high volumes of insects as well as necrophages. Martens preferred smaller, while foxes preferred larger insects. We conclude that insects found in faeces might play an important role in understanding food and habitat relationships between sympatric predators.

Introduction

A large number of carnivore species coexist in the same territory and exploit similar resources (e.g. food, habitat). Scat analysis helps us to understand feeding behaviour and habitat preferences as well as niche separation of sympatric species (Jędrzejewska & Jędrzejewski 1998). Most dietary analyses focus on the frequency distribution, fresh biomass and source of prey. In case of opportunistic carnivores such as martens (*Martes martes*, *M. foina*) and the red fox (*Vulpes vulpes*), the main sources of food are

very similar (Fedriani *et al.* 1999).

Remains of insects, or broadly speaking invertebrates, frequently occur in carnivore faeces. Their occurrence in the consumed food depends on the predator (Kauhala *et al.* 1998, Fedriani *et al.* 1999, Russell & Storch 2004), on available resources (Zielinski *et al.* 1983, Reynolds & Aebisher 1991) and on season (Lanszki & Körmendi 2000, Genovesi *et al.* 1996). This kind of food is mostly supplementary (Carvalho & Gomes 2004), but may also constitute a valuable proportion of food for foxes, badgers and raccoon dogs (Kauhala *et al.* 1998, Fedriani *et*

al. 1999, Lanszki & Körmendi 2000), reaching up to 21% of fresh biomass of faeces. Stomach analysis of foxes showed that up to 92% of the fresh weight of insects can be digested by this carnivore (Reynolds & Aebischer 1991).

In spite of the high frequency and, sometimes, important role in dietary supplementation, information on insect composition and group preferences is scarce. Kožená (1988) recognized carabid beetles in 18% of samples of fox scats.

The treatment of this fraction as 'unrecognizable' seems to be an oversimplification. Lanszki and Körmendi (2000) and Russell and Storch (2004), who identified some insect remains to species level, indicated a rich variety of insect groups in particular samples and between analysed carnivores. Only Skłodowski and Pośluszny (2005) analysed dietary differences between pine and stone martens on the basis of beetle composition.

Individual invertebrates are generally restricted to a given area and many factors such as land-use pattern, vegetation structure or moisture can separate different species groups, and are, subsequently, of great use in bioindication (Boscaini *et al.* 2000, Raino & Niemelä 2003). Information on the presence of specific insects in the diet of carnivores might be useful for assessing not only food preferences, but also habitat preferences and the behaviour of predators. On the basis of variation in the composition of invertebrates in the diet of carnivores, we might be able to separate niche dimensions such as a meadow–forest gradient, nocturnal–diurnal activity, etc.

Our main goal was to show variation in food preferences and invertebrate species composition in relation to habitat use by two sympatric carnivores: foxes and pine and stone martens. One of our aims was to show that high variation in invertebrate composition and abundance in the food of carnivores depends not only on food availability but also on specific preferences of the consumers in the type of supplementary food consumed.

Material and methods

The collection of carnivore faeces was carried out in 2003–2004 in two areas, i.e. Ojców

National Park (ONP) (50°12'N, 19°46'E) and Gorce National Park (GNP) (49°32'N, 20°06'E) located in southern Poland, each differing in habitat use and land cover. ONP is a small deciduous forest complex of approximately 1528 ha of patchily distributed woods, surrounded by many semi-natural and anthropogenic habitats, whereas GNP consists of a large beech and spruce forest complex (6585 ha) with small patches of semi-natural meadows. Red fox (*Vulpes vulpes*) and both species of martens, i.e. beech or stone marten (*Martes foina*) and pine marten (*Martes martes*) are commonly distributed mesocarnivores in Poland. They are abundant in both study areas and as it is not possible to differentiate between the scats of marten species using visible features, we recorded their scats as belonging to marten spp. (Wierzbowska *et al.* 2005).

Scats were collected from transects along forestry roads. Transects were walked twice a month and only fresh scats were collected. To eliminate the preferences of a few carnivores, we randomly selected 45 samples from a larger collection for a particular analysis. The total number of collected faeces was 200 in ONP and 150 in GNP. Scats were collected during different seasons and from different localities. Fresh scats were placed in plastic bags and frozen at –20 °C, and were prepared using the methodology of Goszczyński (1974), and Reynolds and Aebischer (1991).

Faeces were rinsed with tap water through a sieve with a mesh size of 0.5–1 mm. Microscopic and macroscopic fragments were separated into food categories. The dry mass of each food category was measured. Arthropod remains were then separated into orders and identified to species level using reference insect collections from each region. The number of specimens was counted for each species on the basis of replicable parts of the exoskeleton such as the head, the pronotum, abdominal appendages and legs.

The expected species number in the entire data set was estimated using the Bootstrap estimator of species richness (Smith & van Belle 1984):

$$S_{\text{bot}} = S_{\text{obs}} + \sum (1 - p_k)^m$$

where S_{bot} is estimated species richness, S_{obs} is

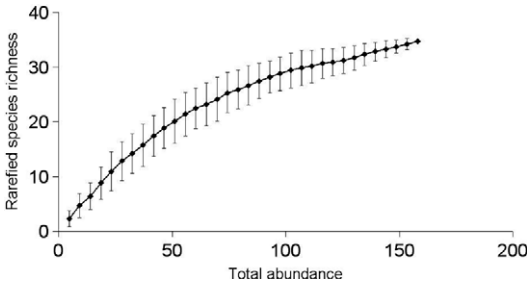


Fig. 1. Expected number of insect species collected in the carnivores faeces using the Bootstrap estimator (\pm SD) of species richness.

total number of observed species in all samples pooled, p_k is the proportion of samples that contain species k , and m is the total number of samples. The randomisation of samples was performed using the programme EstimateS 8.0 (Colwell 2005).

Biomass of the most frequent species was calculated using the formula in Jarosik (1989):

$$B = 0.03069a^{2.63885}$$

where a is mean body length an individual.

The selection of beetles of a particular carnivore was evaluated on the basis of the relative abundance of beetle species in a given community.

To determine the relationship between carnivores and the insect community collected from the faeces, redundancy analysis (RDA) and canonical correspondence analysis (CCA) were used (ter Braak 1986, ter Braak & Šmilauer 2002). RDA reveals if there exists a linear relationship between response variables (insect community structure parameters) and predictor variables (carnivores and site). The unimodal response model was selected in order to study particular relationships between species and environmental factors, which are included in the CCA, due to the fact that maximum abundance occurs under optimal environmental conditions. Insect abundances were $\log(n + 1)$ transformed to avoid the undue influence of outliers on the ordination. We used the programme CANOCO ver. 4.5 (ter Braak & Šmilauer 2002).

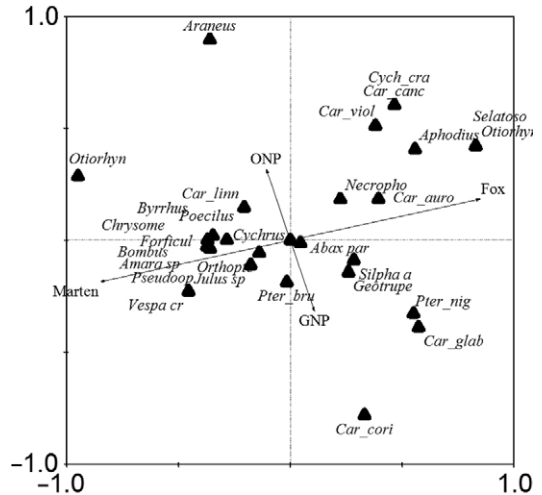


Fig. 2. A biplot of the first two canonical axes of a correspondence analysis of insect species (\blacktriangle) in relation to environmental variables. Arrows represent environmental dummy variables: main predators (marten and fox) and different landscapes (GNP = Gorce National Park, ONP = Ojcow National Park).

Results

We were able to determine 30 species of arthropods, mainly beetles and wasps (Table 1). Their frequencies varied between groups and samples. We wanted to determine the expected number of species in the area. The species rarefaction curve, based on the bootstrap analysis, indicates that the majority of the expected fauna in the area was collected (Fig. 1).

To determine the relationship between the arthropod species collected and large carnivore consumption, a canonical correspondence analysis was used. The ordination diagram (Fig. 2) indicated that the variation in species abundances among replicates (faeces) was associated mainly with carnivore species and habitat characteristics (altitude and land use type). The first four canonical axes described 18.3% of the variance of the species data and 86% of the species–environmental relation (Table 2). The insect species distribution on the ordination diagram can be classified into four groups in relation to carnivore and national park. Species in the upper right of the diagram are mainly consumed by foxes in the forest. Most of these belong to

the carabid beetle genera *Carabus* and *Pterostichus*, which were the most frequently collected taxa in the dataset. In addition, the presence of scavengers such as *Silpha atrata* indicates that

foxes more frequently eat decaying meat. Species in the lower right cluster are also consumed by foxes but in the meadow habitat. There are two large species in this group: the nest building

Table 1. The frequency of occurrence (freq) and abundance (abund) of insects in marten and fox faeces collected in Gorce National Park (GNP) and Ojcow National Park (ONP).

		Marten GNP		Marten ONP		Fox GNP		Fox ONP	
		freq	abund	freq	abund	freq	abund	freq	abund
1	<i>Abax parallelepipedus</i>	0	0	0.17	4	0	0	0.13	1
2	<i>Amara</i> sp.	0	0	0.08	12	0	0	0	0
3	<i>Aphodius sphaelatus</i>	0	0	0	0	0	0	0.13	2
4	<i>Araneus</i> sp.	0.17	1	0.08	1	0.13	1	0	0
5	<i>Bombus</i> sp.	0	0	0.17	4	0	0	0	0
6	<i>Byrrhus</i> sp.	0	0	0.08	2	0	0	0	0
7	<i>Carabus auronitens</i>	0.17	2	0	0	0.25	2	0.25	2
8	<i>Carabus cancelatus</i>	0	0	0	0	0	0	0.13	1
9	<i>Carabus coriaceus</i>	0	0	0	0	0.13	1	0	0
10	<i>Carabus glabratus</i>	0.17	1	0	0	0.13	1	0.25	2
11	<i>Carabus linnei</i>	0	0	0.17	3	0.13	1	0	0
12	<i>Carabus violaceus</i>	0	0	0	0	0.13	1	0.13	1
13	<i>Melasoma</i> sp.	0.08	1	0	0	0	0	0	0
14	<i>Cychrus craboides</i>	0	0	0	0	0	0	0.13	1
15	<i>Cychrus attenuatus</i>	0.17	1	0	0	0	0	0	0
16	<i>Forficula auriculata</i>	0	0	0.25	39	0	0	0	0
17	<i>Geotrupes stercorosus</i>	0.17	3	0.33	5	0.25	2	0.25	18
18	<i>Julus</i> sp.	0	0	0.08	2	0.13	1	0	0
19	<i>Necrophorus</i> sp.	0	0	0.08	1	0	0	0.13	1
20	<i>Orthoptera</i> sp.	0	0	0.08	2	0	0	0	0
21	<i>Otiorhynchus ovatus</i>	0	0	0.08	1	0	0	0	0
22	<i>Otiorhynchus</i> sp.	0	0	0	0	0	0	0.13	1
23	<i>Poecilus versicolor</i>	0.17	1	0.08	9	0	0	0	0
24	<i>Pseudoophonus rufipes</i>	0	0	0.08	1	0	0	0	0
25	<i>Pterostichus brumeisteri</i>	0.33	3	0	0	0	0	0.13	1
26	<i>Pterostichus melanarius</i>	0	0	0	0	0	0	0	0
27	<i>Pterostichus niger</i>	0	0	0	0	0.13	1	0.13	1
28	<i>Selatosomus aeneus</i>	0	0	0	0	0	0	0.13	1
29	<i>Silpha atrata</i>	0	0	0.08	2	0.25	2	0.13	2
30	<i>Vespa crabro</i>	0.33	2	0.17	5	0.13	1	0.13	1

Table 2. Summary of canonical correspondence analysis (CCA) eigenvalues, and the cumulative percentage of variance explained on the first four canonical axes. Significance of canonical axes identified using the Monte Carlo permutation test. * $p < 0.1$.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.239	0.142	0.130	4.438
Species-environment correlations	0.892	0.836	0.686	0.818
Cumulative percentage variance				
of species data	6.80	12.2	15.4	18.3
of species-environment relation	32.0	57.3	72.2	86
F				
Significance of first canonical axis	1.98*			
Significance of all canonical axes	1.22*			

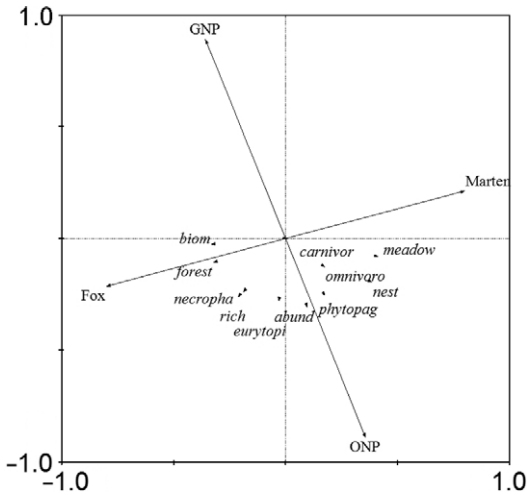


Fig. 3. Correlation biplots based on a redundancy analysis of the species groups and community structure parameter data from the faeces of martens and foxes in the two national parks (ONP and GNP). Names of the groups indicate insect preferences (necrophaga = scavengers, forest = forest species, eurytopi = eurytopous insects, carnivor = carnivores, omnivoro = omnivorous insects, phytopag = plant eaters, meadow = meadow preferring insects, nest = nest building insects) and community structure parameters (rich = species richness, abund = sample abundance).

Vespa crabro and the dung beetle *Geotrupes stercorosus*.

The upper left cluster contains small-sized arthropods consumed by marten, which are characteristic of the forest floor; for example the nest building earwig, *Forficula auriculata*, which always occurred in faeces in large numbers. The lower left group contains mostly meadow species such as a nest building *Bombus* sp. or large orthopterans.

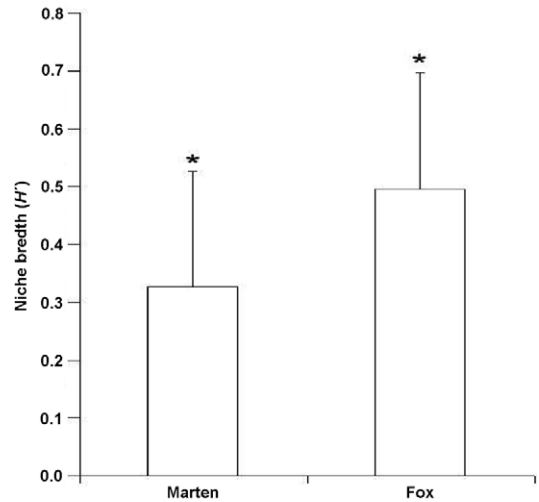


Fig. 4. Mean niche breadths of martens and foxes according to the Shannon-Wiener index. * $p < 0.05$

A redundancy analysis (Fig. 3) revealed that most of the variation of arthropod communities and the abundances of some characteristic ecological groups was explained by the predator species (fox or marten). The first four axes explained 24.2% of the community variance, while 99.6% of the community indices are related to environmental factors such as carnivore identity and site location (Table 3). The first and all four canonical axes are significant at $p < 0.05$ (Monte Carlo permutation test). These dummy variables i.e., marten and fox, were correlated with the first canonical axis, which indicates primary significance of these variables. The scatter plot of the data indicates two groups of arthropods indices. Martens prefer meadow and nest-building species, whereas foxes prefer forest species of greater biomass and necrophages. There was a

Table 3. Summary of redundancy analysis (RDA) eigenvalues, cumulative percent of variance explained on the first four canonical axes. Significance of canonical axes identified using the Monte Carlo permutation test. * $p < 0.05$.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.156	0.054	0.019	0.002
Species-environment correlations	0.665	0.484	0.462	0.187
Cumulative percentage variance				
of species data	16.3	22.0	24.0	24.2
of species-environment relation:	67.0	90.3	98.6	99.6
	<i>F</i>			
Significance of first canonical axis	5.45*			
Significance of all canonical axes	1.80*			

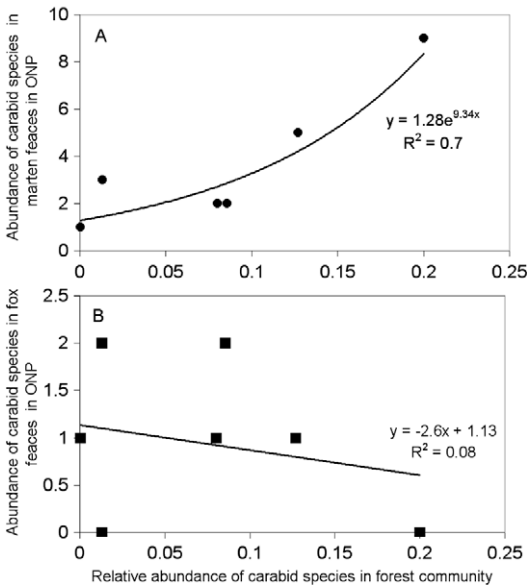


Fig. 5. Relationship between the abundance of ground beetles in the forest community and the abundance of carabid beetles in (A) marten and (B) fox faeces.

higher abundance and richness of insect species found in the scats collected in ONP.

Total niche breadths of martens and foxes in relation to arthropod consumption are presented in Fig. 4. Fox food is more diverse according to the Shannon-Wiener index ($t = 2.7, p < 0.05$).

There was a strong positive correlation between the relative abundance of ground beetles in the forest community and the occurrence of species in the faeces of marten (Fig. 5a). Such a relationship was not observed for foxes (Fig. 5b). This indicates that martens are more opportunistic feeders. Foxes are more selective, preferring only certain species, which (B) are not necessarily most abundant.

When we compare size classes in food consumed by foxes and martens, the distributions are different (Fig. 6). Foxes consume significantly more large carabids ($F = 7.07, p < 0.05$), while the diet of martens includes significantly more smaller beetles ($F = 5.06, p < 0.05$).

Discussion

Foxes and martens are generalist predators with broad food ranges and wide geographic distribu-

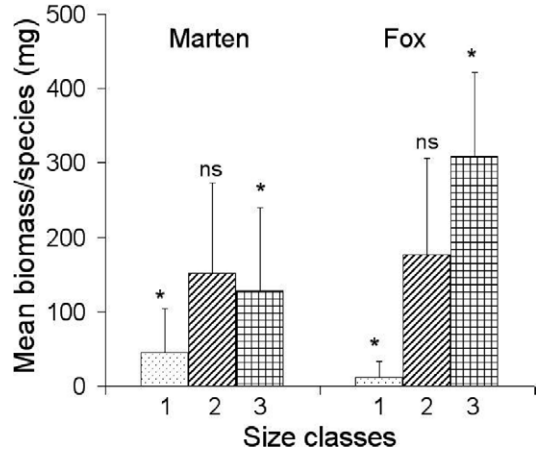


Fig. 6. The distribution of ground beetle biomass in relation to size classes (1: 5–15 mm, 2: 15–25 mm, 3: 25–35 mm) of marten and fox food. Significant differences between pairs of size groups are marked with asterisks (*).

tions (O'Mahony *et al.* 1999, Nowak 2005). As they are opportunistic feeders, their food preferences reflect local prey availability. Simultaneously these predators may switch to alternative prey (Ben-David *et al.* 1997, Baltrūnaitė 2006).

A large number of researchers have studied dietary exploitation by sympatric species, of which red foxes and martens are frequent examples (Serafini & Lovari 1993, Lanszki *et al.* 1999, Birks 2002, Russell & Storch 2004, Wierzbowska *et al.* 2005, Sidorovich *et al.* 2006). In spite of the fact that they show significantly overlapping habitat and food preferences, some authors believe that these carnivores do not compete. They share the same habitat and similar food resources but demonstrate minor discrepancies that allow them to coexist (Jędrzejewska & Jędrzejewski 1998, López-Martin 2006). Although martens and foxes are food generalists, there are distinct insect groups that appear more frequently in their individual diets. Yet, arthropods constitute a significant part of food of both species (Molsher *et al.* 2000, Carvalho & Gomes 2004). Most of the recent studies analysing the food of martens and foxes treat invertebrates as an unrecognisable fraction and focus only on its proportion in the whole diet. Few authors have observed that invertebrates might constitute a large proportion of the food of foxes and martens (Jędrzejewski *et al.* 1993, Lanszki *et al.*

1999). The contribution of invertebrates depends mainly on season and location. Insects constitute an important dietary supplement of carnivores during spring and summer in temperate areas (Lanszki *et al.* 1999, Wierzbowska *et al.* 2005), or during the whole year in warmer areas such as the Mediterranean (Serafini & Lovari 1993, Genovesi *et al.* 1996).

CCA analysis revealed that most of the variation in invertebrate species in faeces is described by the factor 'species' (i.e. fox and marten). This information is very useful when comparing niche overlap and competitive exclusion of the carnivores. Preferences of particular insect species may indicate food selectivity, but in most cases it is a compromise between competitive effect and food availability. Only few insect species were consumed with the same intensity by both carnivores. This finding supports the hypothesis on discrimination between these two carnivores (Fedriani *et al.* 1999).

Giving the ecological preferences of insects we are also able to assign carnivores into particular microhabitats. The redundancy analysis showed that martens mostly feed in meadows, whereas foxes prefer forests. Cavallini and Lovari (1991) indicated that the beetles contributed mostly to the diet of foxes. Moreover, foxes exploring meadows feed on insects characteristic for this habitat, while forest preferring populations chose forest beetles. Correlation between fox habitat use and insect abundance was positive. Simultaneously, a strong correlation between seasonal food availability and food habits was observed by Cavallini and Lovari (1991). Our study revealed comparable results.

In contrast, martens prefer nest-building insects, which are often found in large numbers in the study area. Similar findings were recorded by Zielinski *et al.* (1983) who found a yellow jacked nest-building wasp in the faeces of martens and Lanszki (2003) who recorded social *Hymenoptera* in 23% of marten faeces. In addition, Russel and Storch (2004) found nest-building ants in the food of martens.

What do these results tell us about food preferences? Martens probably search for nests of insects that are a very rich food source. On the other hand, foxes choose larger specimens, mostly *Coleoptera*, whose biomass is sometimes

very significant in relation to all the food consumed (Reynolds & Aebisher 1991). Such a food type in the diet of foxes was also confirmed by other authors (Lloyd 1980, Kožená 1988). However, both authors believe that although the beetles appear more frequently in the diet of the red fox, their contribution is of little importance, with some seasonal exceptions.

How do we explain the presence of many carrion-feeding insects in the faeces of foxes? Foxes presumably feed on carrion more frequently than martens and the presence of such insects in fox faeces indicates the scavenging behaviour of this predator. However, some authors have also demonstrated that martens feed on carcasses (Ben-David *et al.* 1997, Sidorovich *et al.* 2006, Baltrūnaitė 2006). Yet, there is no method to distinguish between scavenging and predatory behaviour even though we analyse the stomach content of foxes (Molsher *et al.* 2000). The more frequent occurrence of carrion beetles in the diet of foxes indicates that this carnivore exploits carcasses. The decaying carrion of large animals is consumed by insects, whereas smaller carcasses are suitable for breeding (Wilson & Knollenberg 1984). The location and colonization of such patchily distributed food determines the reproductive success of insects (Eggert 1992). Carrion is therefore, in most cases, colonised fairly quickly by carrion feeding insects. As such, we are able to compare the importance of carrion in the diet of carnivores, and to estimate their importance in the whole diet.

Martens and foxes are regarded as food generalists. However, when we compare preferences for ground dwelling beetles, only the total abundance of carabids in the food of martens reflects their proportion in a habitat. It indicates that martens are opportunistic species and choose this source of food randomly. Foxes, on the other hand, prefer larger specimens of *Carabidae* as is shown in Fig. 6. Reynolds and Aebisher (1991) found large numbers of large sized ground beetles in the stomachs of foxes, which may indicate the selection of such larger food items. Also Kožená (1988), Lanszki and Körmendi (2000) and Russel and Storch (2004) found that among invertebrates, carabids are the most frequently chosen and dominant group in faeces. The importance of invertebrates in the

diet of the fox was also shown by Molsher *et al.* (2000). In most cases, invertebrates were frequent and represented up to 21% of the volume of food consumed.

Our data indicate that the identification of insect species in the food of carnivores is a useful tool in determining the diet and habitat preferences of carnivores. Particular analysis of insect remains may indicate more clearly what kind of habitat the carnivore selects and eventually what the differences in food supplementation between sympatric species are. Our study demonstrated that a detailed analysis of dietary habits may serve as a valuable tool for discrimination between sympatric species. We showed that even a small fraction of the food consumed by carnivores, believed by some authors to be of little importance, may provide additional information on the dietary and habitat preferences of these animals.

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