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Fox and martens – are they really opportunistic feeders? A case of beetles and other arthropods occurrence in carnivores' diet

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The main goal of the investigation was to assess and compare insects' abundance in diet of fox (*Vulpes vulpes*) and martens (*Martes martes, Martes foina)*. The research was carried out in three national parks and in the city of Kraków, all located in the southern Poland. The collection of carnivores' faeces took place between 2002 and 2007. The total number of samples was 517 for foxes and 747 for martens. 59 insects species were recognised in 19% of samples. Forward selection of canonical correspondence analysis revealed factors that were carnivore species, place of collection which both described 89% of variance of insect species environment relations. Martens as a variable seemed to be the most influential on the composition and relative abundance of all insect assemblages (Monte Carlo test F=3.94, P<0.001). Moreover, the place of collection was an important factor (Monte Carlo test F=3.03, P=0.002 and F=2.18, P=0.002, respectively for Kraków and the Tatra Mountains). Martens fed most often on nest insects species, whereas foxes chose large beetles. The diagram of canonical correspondence analysis confirmed that distribution of specific groups of arthropods depended on carnivore feeder as well as occupied habitat.

Key words: diet overlap, mesocarnivores, foraging strategies

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INTRODUCTION

Carnivores are a diverse group comprising 271 species (Macdonald & Kays 2005). They evolved a great number of morphological and behavioural adaptations which enabled them to live in every habitat. *Carnivora* includes animals of different dental and feeding types from typical meat eaters (e.g. felids, wolves), scavengers (e.g. hyenas), insectivores (aardwolf), omnivores (e.g. brown bear) and frugivores (e.g. kinkajou) (Van Valkenburgh 1989). Some species are monophagous, feeding specialists foraging upon only one main food type, whilst many others exhibit opportunistic behaviour and depend on various potentially available food categories (Kruuk 2002). A mixed diet including the most abundant and available food gives the predator a chance for better adaptation and survival as it may exploit different trophic niches and habitats.

A good example of opportunistic feeders are martens and red foxes. Their feeding habits were described in numerous papers across their geographical distribution (Goszczyński 1986, Jędrzejewski *et al.* 1993, Genovesi *et al.* 1994, 1996, Leckie *et al.* 1998, Padial *et al.* 2002, Sidorovich *et al.* 2005, Barrientos & Virgós 2006, Delibes-Mateos *et. al*. 2007, Posłuszny *et al.* 2007). These predators feed mainly on small vertebrates (e.g. voles, lagomorphs, birds) and supplement their diet with fruits and invertebrates among whom insects are the most abundant (Wilson 1987 after Macdonald & Kays 2005, López-Martin 2006).

In spite of their supplementary role in the diet of mesocarnivores, they can serve as an important tool in ascertaining habitat or food preferences such as type and selectivity (i.e. carrion, fresh prey, domestic food) of the carnivore (Skalski & Wierzbowska 2008). Insect communities have been shown to vary in abundance and species composition according to changes in vegetation and soil conditions (McIntyre *et al.* 2001, Niemela 1997). Many species have strict ecological requirements and are used as bioindicators (Rainio & Niemela 2003).

Though, many studies focus on diet composition, only few provide a detailed evaluation of each trophic category. We found that in 90% (n=26) reviewed papers on diet habits of red fox (*Vulpes vulpes*) and martens (*Martes foina, Martes martes*) the insects were scarcely described. Thus, our main aim was to investigate the relationship between sympatric medium-sized carnivores *Martes martes* and *Martes foina* represented as *Martes* spp. and red fox *Vulpes vulpes*. We explored their foraging behaviour with regard to the use of similar ecological resources as sympatric species.

MATERIALS AND METHODS

The study areas comprises ca 650 km2 of southern Poland, among them three national parks: the Ojcow National Park (ONP) (50°12´N, 19°46´E), the Gorce National Park (GNP) (49°32´N, 20°06´E), the Tatra National Park (TNP) (49°13'N, 19°58'E), and city of Krakow (50° 03'41'' N 19° 56'18'' E). The national parks are located at 30km, 80 km and 100 km, respectively apart from Krakow. TPN is the biggest national park in our study area (21.164 ha) covered mainly by spruce mountain boreal forest and dwarf pine shrubs (70%) and alpine meadows (30%). ONP is a quite small deciduous forest complex of approximately 2.200 ha of patchily distributed woods, surrounded by many semi-natural and anthropogenic habitats, whereas GNP consists of large beech and spruce forest complex (6.585 ha) with small patches of semi-natural meadows (Matuszkiewicz 2007). Krakow occupies 327.000 ha and two study sites were depicted i.e. city centre (covered by old apartment houses with scarce greenery) and suburb terrain (covered by semi-detached houses with wide green spaces such as gardens and surrounding forest remnants) (Szałach 2007).

Red fox 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 national parks (TNP, GNP, ONP), whilst only stone marten occupies urban ecosystems. It is not possible to differentiate between the scats of marten species using visible features, we recorded their scats as belonging to *Martes* spp. (Wierzbowska *et al.* 2005, Posłuszny *et al.* 2007). The climate is mainly temperate and in the mountains (TNP, GNP) with mountain climatic zones (Hess 1965).

Twice a month we walked along transects and collected only fresh faeces of free-living carnivores. With regard to the study areas there are different mammal carnivore guilds (e.g. only in the TNP live brown bears (*Ursus arctos*), wolf (*Canis lupus*) and lynx (*Lynx lynx*), however, martens and red foxes are present in all sites (Wierzbowska *et al.* 2005, Suchy 2006, Szałach 2007) As for martens it is impossible to distinguish between stone marten and pine marten by external features of the faeces (Posłuszny *et al.* 2007). Both species may live as sympatric in Poland (Posłuszny *et al.* 2007). Yet, urbanized areas are inhabited only by stone marten, whereas pine marten lives mainly in woods and avoids human neighbourhood (Goszczyński, *et al.* 1994). This is the case of our study where stone marten inhabits Krakow and its suburbs. Both species live in the ONP, and in the mountains of GPN and the TPN there lives probably only pine marten as it was confirmed by our previous studies (Wierzbowska *et al.* 2005) as well by the harvest statistics of the Polish Hunting Association (data only available on the official website www.pzlow.pl). Both species are game animals in Poland. Nonetheless, in our studies we described both species in genus as *Martes* spp.

Scats were collected along three transects in the ONP of a total length 12 km, four transects in the GNP of 42 km and 9 transects in the TNP of 80 km length, respectively. Scat collection was conducted twice a month, from October 2002 to December 2007. In Krakow, samples were collected randomly on attics and in gardens. During that period, 517 scats of red fox and 747 scats of martens were collected, 110 and 135 of which contained arthropods non-digested remains, respectively.

After collection the material was preserved in plastic bags stored at -20ŗC prior to dietary analysis. Scats were oven dried (40-50 ŗC), soaked for 24h, broken in water, washed through a 0.5 mm nylon sieve and searched for macroscopic remains (Reynolds & Aebischer 1991, Skalski & Wierzbowska 2008). We separated bones and teeth, feathers, hair, scales, arthropods, vegetal material and other material (e.g. garbage). For analysing dietary samples of vertebrate prey we used keys (Pucek 1981, Teerink 1999) and reference materials including skulls and skeletons as well guard hairs (and their microscopic slides), scales and feathers.

The frequency of occurrence of specific food category and biomass consumed calculated with digestibility coefficients were estimated (Litvaitis 2000, Jędrzejewska & Jędrzejewski 2001).

Yet in our study we focused on insects remnants and did not include results on all food categories which appeared in the scats of carnivores. All material was separated into particular morphospecies parts using stereoscopic microscope NIKON SMZ 1500 and compared with reference collection from given region (Skalski & Wierzbowska 2008). Abundance of particular species was estimated on basis of countable parts of body (e.g. heads, legs or abdominal appendages). In each case when the remnants were uncountable we calculated the abundance as 1.

The arthropods data were subjected to multivariate statistical analyses methods such as indirect method i.e. detrended correspondence analysis (DCA) used for raw data on the mesocarnivore-site data. This method helps to test dependence of analysed insect species composition on the type of carnivore. We have also used partial canonical correspondence analysis (pCCA) to test the influence of independent variables (type of predator and regional factors) on the abundance of arthropods in the fox and the martens' food (ter Braak 1986). Forward selection was also used to reduce the minimum number of variables and to improve the clarity of the ordination diagrams. The statistical significance of each selected variable was judged by the Monte- Carlo permutation test.

To understand the effect of carnivore species on arthropod body size classes, we used redundancy analysis (RDA) (Verdonschot & ter Braak 1994). We chose RDA because the body size classes related to the environmental variables in our data could not be normalized. Forward selection of RDA used permutation test to find the significance of variables and to order the variables in rank of significance.

All the analyses were made using the Canoco for Windows v. 4.52 statistical computer package (ter Braak & Šmilauer 2003).

RESULTS

With comparison to fox diet insect species are more numerous in the marten scats (Table 1).

Rank-abundance curves of general samples for the mesocarnivores are presented in figures 1 and 2. The majority of the invertebrate fractions which were present in the scats of martens were nesting insects, occurring in aggregation (i.e. *Forficula* or social hymenopterans). Whilst, the fox seemed to prefer large and easily visible beetles such as Carabus auronitens (more than 90% of insects fraction in general set) (Fig. 2). 44.9% of variance was described by the first two axes of detrended correspondence analysis of invertebrates in the fox and the marten. The biplot of the first two axes and mesocarnivore faunal composition in their diet with regard to different regions showed a close relationship between predators and the invertebrates appearing in their food as well as habitat type where the carnivore fed (Fig. 3).

When we treat the specific study area and the type of the carnivore as dummy variables, which potentially explain invertebrate compositions in the scats, direct gradient of the canonical correspondence analysis might be applied. In addition, in order to rank the importance of the independent variables, a forward selection of independent variables was tested. Results are presented in table 2.

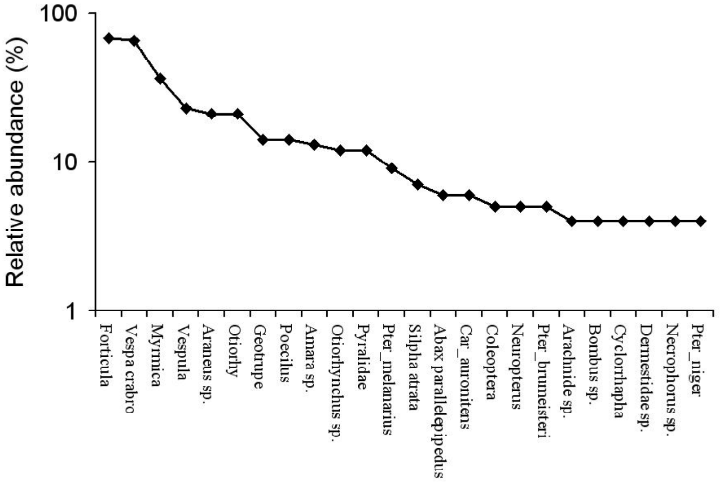

Fig. 1. Rank-abundance curve of the invertebrates in the diet of martens. Singletons, doubletons and tripletons were excluded from the diagram

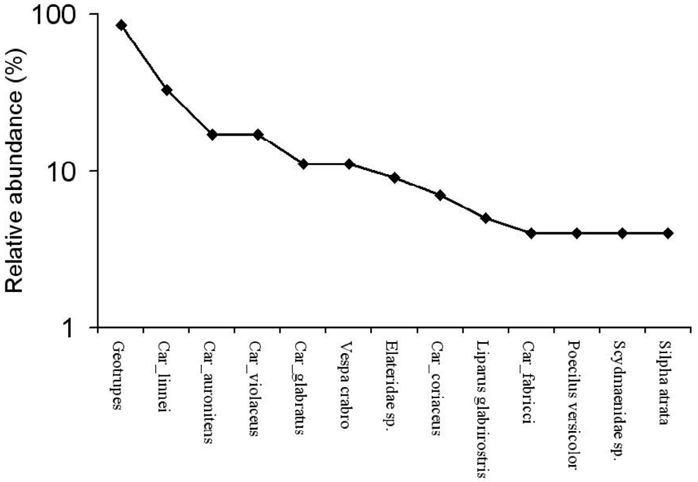

Fig. 2. Rank-abundance curve of the invertebrates in the diet of fox. Singletons, doubletons and tripletons were excluded from the diagram

Table 1. Composition and total abundance of arthropod species and morphospecies in the diet of the fox and martens. Letters denote respectively: habitat preferences – f – forest species, m – meadow species, e – eurytopic species and trophic groups: c – carnivore, p – phytophagous, n – necrophagous, o – omnivorous

	Species name	Abreviation	Average body size (mm)	Habitat preferences	Trophic group	Fox	Marten
1	*Abax parallelepipedus*	Abax par	20	f	c	1	6
2	*Ceutorhynchus* sp.	Ceutor	5	f	p	0	3
3	*Amara* sp.	Amara sp.	6	m	o	0	13
4	*Aphodius sphaecelatus*	Aphodius	7	e	n	3	0
5	*Apis mellifera*	Apis mel	9	m	p	0	3
6	*Araneus* sp.	Araneus	14	m	c	1	21
7	*Arachnida* sp.	Arachnid	9	m	c	0	4
8	*Bombus* sp.	Bombus	18	m	p	0	4
9	*Byrrhus* sp.	Byrrhus	6	e	n	0	2
10	*Carabus auronitens*	Car_auro	30	f	c	17	6
11	*Carabus cancellatus*	Car_canc	30	m	c	3	1
12	*Carabus convexus*	Car_conv	20	m	c	1	1
13	*Carabus coriaceus*	Car_cori	40	f	c	7	1
14	*Carabus fabrici*	Car_fab	25	f	c	4	0
15	*Carabus glabratus*	Car_glab	34	f	c	11	3
16	*Carabus linnaei*	Car_linn	22	f	c	33	3
17	*Carabus silvestris*	Car_silv	25	f	c	2	0
18	*Carabus violaceus*	Car_vio	35	f	c	17	1
19	*Chrysomelidae* sp	Chrysome	6	m	p	0	1
20	*Chorthippus* sp.	Chrothip	9	m	p	0	1
21	*Coleoptera* not ident.	Coleopte	3	m	p	0	5
22	*Cychrus caraboides*	Cych_car	19	f	c	2	0
23	*Cychrus attenuatus*	Cychrus	17	m	c	0	2
24	*Cyclorthapha* not ident.	Cyclorth	8	m	n	0	4
25	*Dermestidae* sp.	Dermesti	5	m	n	0	4
26	*Elateridae* sp.	Elaterid	10	m	p	9	3
27	*Forticula auriculata*	Forticul	9	e	o	0	68
28	*Geotrupes stercorosus*	Geotrupe	15	e	n	85	14
29	*Geotrupinae*	Geotrupi	17	f	n	2	0
30	*Gyrinidae*	Gyrinida	4	e	p	0	2
31	*Tenthredinidae*	Tentr	10	f	p	3	0
32	*Julus* sp.	Julus	23	f	o	1	2
33	*Liparus glabrirostris*	Liparus	21	f	p	5	0
34	*Lycosidae* sp.	Lycosida	9	m	c	1	0
35	*Lymexylon* sp	Lymexylo	12	f	p	0	1
36	*Monochamus* sutor	Monocham	42	f	p	1	0
37	*Myrmica* sp	Myrmica	4	m	c	0	36
38	*Nebria brevicollis*	Nebria b	13	m	c	2	2
39	*Necrophorus* sp.	Necropho	15	e	n	1	4
40	*Neuroptera* sp	Neuropte	11	e	c	0	5
41	*Nymphalidae* sp	Nymphali	19	m	p	1	0
42	*Orthoptera* sp.	Orthopte	25	m	p	1	2

Table 1. *Continuation*

	Species name	Abreviation	Average body size (mm)	Habitat preferences	Trophic group	Fox	Marten
43	*Otiorhynchus morio*	Otior_m	11	m	p	1	0
44	*Otiorhynchus ovatus*	Otior_o	5	m	p	0	21
45	*Otiorhynchus* sp.	Otiorhyn	8	m	p	2	12
46	*Poecilus versicolor*	Poecilus	12	m	c	4	14
47	*Pseudoophonus rufipes*	Pseudoop	16	m	o	0	1
48	*Porcelio scaber*	Porcelio	7	f	n	0	3
49	*Pterostichus burmeisteri*	Pter_bru	15	m	c	3	5
50	*Pterostichus melanarius*	Pter_mel	19	m	c	3	9
51	*Pterostichus niger*	Pter_nig	27	f	c	3	4
52	*Ptinide* sp	Ptinide	1	f	c	0	3
53	*Pyralidae* sp	Pyralida	14	m	c	0	12
54	*Scydmaenidae* sp.	Scydmaen	3	m	c	4	1
55	*Selatosomus aeneus*	Selatoso	11	m	p	1	2
56	*Silpha atrata*	Silpha a	12	e	n	4	7
57	*Silpha thoracica*	Silpha t	14	e	n	2	0
58	*Vespa crabro*	Vespa cr	24	m	c	11	65
59	*Vespula germanica*	Vespula	13	m	c	0	23

Table 2 Rank of the independent variables after evaluation of forward selection of canonical correspondence analysis

Variable	Lambda A	Monte Carlo permutation test
GNP	0.23	ns
ONP	0.46	P=0.0220, F-ratio= 1.59
TNP	0.55	P=0.0040, F-ratio= 1.85
Krakow	0.59	P=0.0020, F-ratio= 3.74
Fox	0.64	P=0.0020, F-ratio= 4.39
Marten	0.64	P=0.0020, F-ratio= 4.39

Table 3. Rank of the independent variables after evaluation of forward selection of redundancy analysis

Variable	Lambda A	Monte Carlo permutation test
Krakow	0	
GNP	0	
TNP	0.01	
ONP	0.01	P=0.022, F-ratio= 3.39
Fox	0.02	P=0.004, F-ratio= 3.90
Marten	0.02	P=0.004 F-ratio= 3.90

This statististical analysis showed that the type of the mesocarnivore species was the most significant variable which described variation of the invertebrate species (lambda A = 0.64, F ratio = 4.39, p=0.002) (Table 2).

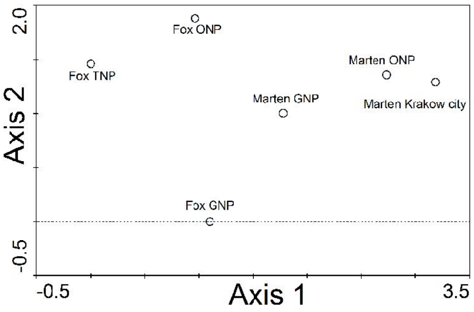

Fig. 3. DCA of invertebrate composition in scats from specific regions, biplot of the first two ordination axes.

The first two canonical axes described 74.8% of variance of relations between insect species data and environmental factors. The first axis corresponds to the type of the carnivore and divides the invertebrates into two groups i.e.: specific for the fox large beetles (A group) and specific for the martens small sized nesting insects (B group). It is also worth to mention that the invertebrates found in the carnivore food depend on regional variation and slightly vary between the specific study areas (group C of the invertebrates typical for urbanized areas).

In order to assign different food preferences of the carnivores to size groups of the insects, we adopted redundancy analysis. The results of this analysis are presented in figure 5.

As in previous analyses, the type of the carnivore was the most important factor describing variation in body size classes of the invertebrates (Table 3). There was a strong relation between the fox and the large (40-30 mm) invertebrate species. The martens, however, preferred smaller species (1-5 mm and 5-10 mm re4spectively). Medium sized insects were consumed by the two carnivores in the similar frequency.

DISCUSSION

Animals might be classified within a range of adaptations towards foraging strategies. Some species are highly specialised and feed only on particular species of prey, whereas the other ones feed on a broad spectrum of food items (Grier 1984). It is crucial that the animal develops optimal foraging strategy which maximises the benefits and minimises the potential costs. This might be explained by different foraging strategies in order to minimise foraging activities and potential energetic costs (Krebs 1978, Grier 1984).

The easy capture and high energy value makes invertebrates as a food resource of a great value for the carnivores. The frequency of occurrence of this food category in the carnivores diet (scats) was positively correlated with increasing number of insect in assemblages (Skalski & Wierzbowska 2008). This relationship was even more emphasized in the case of martens which fed on large assemblages of nest insects (Fig. 4). McNab (2000) highlighted that insects prey which occurred in sufficient large colonies might serve energetically feasible source of food in specific regions. However, invertebrate-eaters should not exceed body mass of 10 kg, which is the case both of the foxes and martens.

Invertebrates pose food item low in biomass. Yet their frequent contribution in the identified prey of the carnivore might prove the martens and foxes specialization as insectivores. This type of

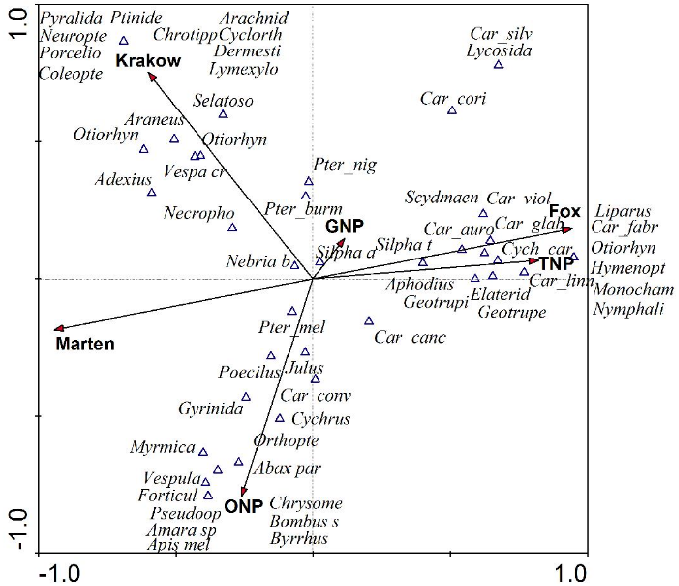

Fig. 4. Biplot based on canonical correspondence analysis of the invertebrates from scats with respect to the environmental variables extracted from forward selection. A, B, C denote the derived groups of insects after order analysis with similar environmental preferences

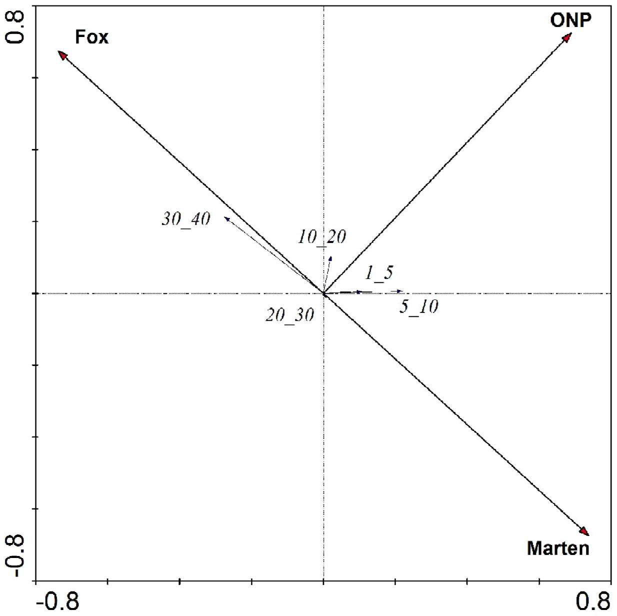

Fig. 5. Relationships between the type of the mesocarnivore and the body size of the invertebrate prey after evaluation of forward selection of redundancy analysis. (40_30 etc. denote body length range (mm) of the insects)

feeding behaviour was also documented by López-Martin (2006) but in the case of frugivory preferences.

Though strong competition relationship between red foxes and martens was described by many authors (eg. Storch *et al.* 1990, Serafini & Lovari 1993, Lindström *et al.* 1995, Sidorovich *et al.* 2006), we cannot support this argument regarding invertebrates as a food source. Whilst martens and foxes exploit the same food resource if more detailed evaluation of the material is done we cannot conclude that they compete (Skalski & Wierzbowska 2008, Figs 3 and 5). In the view of our results we may support the argument that predator size should be related to prey size. In other words, the larger the predator, the larger the prey (Curio 1976, Kruuk 2002). Smaller martens forage upon smaller insects, whereas larger foxes search for big and more nutritional beetles (Fig 5). The experiment on caloric values of fifty different insect species from *Coleoptera, Lepidoptera, Hemiptera, Hymenoptera* and *Orthoptera* showed that they had 50% higher caloric value than soybeans and 87% than corn (De Foliart 1992).

Moreover, Grier (1984) suggested that specific prey may provide different nutritional items and due to dietary needs carnivores more often switch to it. For example, some insects are a rich source of macro- and micro-elements and vitamins such as magnesium, iron, zinc, copper riboflavin important for proper growth (De Foliart 1992).

Our results seem to support the idea that predator species that appear to be generalists over large geographical ranges may be specialists and depend upon few prey categories at the local level (Grier 1984, Kruuk 2002). As predicted by Herrera (1989), López-Martin (2006) or Santos-Reis *et al.* (2004) mesocarnivores may develop low searching costs or habitat partitioning at the same range level to minimize the competition. It can be concluded, therefore, that fox and martens have similar diets due to their similar opportunistic behaviour, but demonstrating minor differences that might be of a significant value and enable them to coexist. Though both species are described as opportunistic feeders and their trophic niches overlap they differ significantly in the choice of insects as a food source. The martens feed mainly on colonising insects, whilst the foxes forage upon more nutritional and larger beetles (Skalski & Wierzbowska 2008).

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