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Differential use of food and habitat by sympatric carnivores in the eastern Italian Alps

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Abstract

In an Alpine area, scat analysis and marking activity were used to assess the feeding habits, habitat preference and the degree of overlap of trophic niche and habitat use in sympatric carnivores: the red fox ($n=133$ faecal samples), the badger ($n=177$), the pine and the stone marten (*Martes* sp., $n=382$). Fruits were the main trophic resource for all species. The diet of martens differed from those of the red fox and badger by means of a higher consumption of garbage and non-Rosaceae fruits. The red fox preyed on more lagomorphs and roe deer and relied almost exclusively on two fruit species, rose-hips and whitebeam berries. Badgers ate few invertebrates, with cultivated fruits and pine seeds forming the bulk of their diet. On the whole, trophic niche overlap was kept low by the exploitation of different species of berries and mammals and, secondly, by seasonal differences in the use of same items by the three carnivores. Badger trophic niche overlapped to a wider extent than those of the other two predators in summer, when fruit availability is higher. Foxes used all habitats according to their availability, except for villages, which were avoided. Badgers used mainly open habitats, particularly Alpine meadows, avoiding villages and mixed woods. Martens selected the habitats avoided by the other two predators and avoided all the others. The narrow range of habitat used by martens and diet evidence suggest that, within the context of interspecific competition, they could play the role of sub-ordinate species, segregating in fox-free urban environments.

Keywords: Vulpes vulpes, Meles meles, Martes *sp., niche overlap, competition, habitat preference, Italian Alps*

Introduction

The role played by interspecific competition in structuring communities has been recognized since the pioneering works of Volterra (1926) and Lotka (1932). The use of a limited resource (exploitation) or its non-consumptive pre-emption (interference) by one species is expected to reduce the resource availabilty to the other species (Wiens 1989), implying resource partitioning and niche differentiation in sympatric species occupying the same trophic level (Pianka 1969; Schoener 1974, 1982; Pimm & Rosenzweig 1981; Begon et al. 1986; Ricklefs, 1990).

Food, habitat and time have been suggested to be the most important niche dimensions in resource partitioning between species (Pianka 1969; Schoener 1986): coexisting species should reduce competition shifting to different diets, selecting different habitats, carrying out different patterns of activity or, more probably, showing a specific combination of the former three modes imposed by local environmental conditions and their intra- and inter-specific densities (Guthrie & Moorhead 2002).

A further and lesser investigated (Palomares & Caro 1999) layer of complexity is introduced by interspecific killing between potential competitors (“intraguild predation”; Polis et al. 1989), inducing weaker species to seek for habitats avoided by their competitors (“refuges”) so as to escape being killed (Durant 1998).

The red fox *Vulpes vulpes*, the badger *Meles meles*, the stone marten *Martes foina* and the pine marten *M. martes* are medium-sized generalist carnivores widespread in the Italian Alps (Spagnesi & De Marinis 2002).

Foxes are considered to be prototypical generalists, feeding on a wide variety of food resources according to their local and seasonal availability (Ables 1975; Lloyd 1975, 1980; Macdonald 1977; Doncaster et al. 1990). In the Alps the fox shows carnivorous feeding habits relying on mammals, mainly ungulates and rodents, and, only secondly,

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on fruits and invertebrates (Leinati et al. 1960; Cantini 1991; Lucherini & Crema 1994; Cagnacci et al. 2003).

The badger is considered a "forager" (Neal 1986) rather than a predator. In NW Europe Lumbricidae comprise the main item of badger diet, such that badgers have been considered as earthworm specialists (Kruuk & Parish 1981; Kruuk 1989). Nonetheless, within its wide distribution range, the badger is better described as an opportunistic food generalist relying mainly on cereals, fruits and invertebrates (Roper 1994; Neal & Cheeseman 1996; Revilla & Palomares 2002; Balestrieri et al. 2004; Virgós et al. 2004; Rosalino et al. 2005). In the Alps, invertebrates—Coleoptera, Orthoptera and earthworms—form the bulk of badgers' diet (Rinetti 1987; Lucherini & Crema 1995), followed by rodents and carrion. Occasionally, fruits are intensively used (Kruuk & de Kock 1981).

Martens show much flexibility in their diet (stone marten: Marchesi et al. 1989; Libois & Waechter 1991; Romanowski & Lesinski 1991; Genovesi et al. 1996; Rödel et al. 1998; Padial et al. 2002; Lanszki 2003; pine marten: Marchesi & Mermod 1989; De Marinis & Massetti 1995; Russel & Storch 2004). Where the two species occur sympatrically, the pine marten is associated primarily with coniferous and mixed wood forest habitats, whilst the stone marten selects rocky open areas and urban areas (Frenchkop 1959; Novikov 1962; Delibes 1983). Differential habitat use has repercussions on the diet of martens, pine martens relying mainly on forest-dwelling trophic sources and stone martens widely using food associated with human activity (Marchesi & Mermod, 1989; Marchesi et al. 1989; Lanszki 2003). Their feeding habits in their Italian Alpine range are poorly known. Fruits and rodents form the bulk of *Martes* diet in the central (Cantini 1991) and western Italian Alps (Prigioni et al. 1998, unpublished report), whilst a high frequency of occurrence of insects has been occasionally reported (Lucherini & Crema 1993; Pedrini et al. 1995a).

Available information about direct interactions between pairs of these carnivores has been reviewed by Palomares and Caro (1999). Interspecific killing occurs between foxes and badgers, each one being able to kill only non-adult individuals of the other species, but rates of killing are likely to be quite low if we consider that they can share the same burrows (Neal & Cheeseman 1996). Diet data from several Italian studies support this hypothesis (reviewed by Remonti et al. 2005). Foxes may kill adult martens (American martens *Martes americana* and pine martens), even sharply limiting their population density (Thompson 1994; Lindström et al. 1995), as suggested by pine marten recovery following an epidemic of scabies among red foxes (Lindström et al. 1995; Smedshaug et al. 1999). On the contrary, no attacks are known between badgers and martens, predatory habits probably being a factor influencing interspecific killing at least as much as the relative body size of the interacting species (Donadio & Buskirk 2006).

We investigated the feeding habits of the above mentioned carnivores in an Alpine area of NE Italy with the aim of estimating (i) the relative importance of the different food items and their seasonal variation, (ii) the degree of interspecific diet overlap, (iii) carnivore preference for different Alpine habitats and (iv) the degree of interspecific overlap in habitat use.

We hypothesized that niche overlap would be larger between martens and foxes (badgers preying mostly on earthworms and other invertebrates), and that foxes, having a body weight ratio between foxes and martens about 3:1, would behave as the dominant species, exploiting a broader range of habitats and, consequently, a wider range of food resources. Also, if martens were victims of attacks by foxes, they would be expected to reduce the chances of encountering competitors using, as much as possible, different habitats for hunting and/or resting, this habitat selection determining qualitative and/or quantitative differences in food items exploitation.

Materials and methods

Study area

The Fiemme Valley is a wide east–west-oriented valley, located in the eastern Italian Alps (NE Trentino region). The study area (23.77 km^2) covers its central part, i.e. the surroundings of the village named Cavalese (about 3200 inhabitants), between 840 m a.s.l. (River Avisio) and 1550 m a.s.l. The climate is typically alpine-continental, with annual rainfall averaging 828 mm (with a wet period in mid-summer and a dry one in winter) and annual temperature 7.5°C at 900 m a.s.l. Vegetation consists of four main types:

(a) mixed woods (13.3% of the study area), dominated by beech *Fagus sylvatica*, hazel *Corylus avellana*, alders (*Alnus viridis*, *A. incana*, *A. glutinosa*) and spruce fir *Picea excelsa*;
(b) coniferous forest (60.6%), consisting in a mosaic of several stands of coeval spruce firs and larches (*Larix decidua*) as a consequence of timber harvesting activities;
(c) shrubs (2.8%), occurring mainly at the wood–Alpine prairie transition, with *Rosa canina*,

Berberis vulgaris, *Ligustrum vulgare* and *Corylus avellana*;

(d) Alpine meadows (8.1%), probably originated by tree-cutting in the first half of the 20th century.

Regularly mowed grasslands and orchards (10%) lie next to villages (5.2%).

Three fox dens and as many badger setts were found active during the study period in the area. In the urban area of Cavalese, Prigioni and Sommariva (1997) assessed the presence of 52 stone martens by radiotelemetry. No sound information was available about pine martens, which have been reported as the least common mustelid of the western Trentino region (Pedrini et al. 1995b).

Diet analysis

Faeces were collected monthly from June 1994 to June 1996 along four transects crossing the main habitats of the study area (Table I). Badger scats were collected from typical latrines. Shape and dimensions (martens scats diameter <10 mm, foxes scats diameter >15 mm; Bang & Dahlström 1974) were considered when distinguishing fox faeces from those of martens. The scats of pine martens are not distinguishable by eye from those of stone martens; anyway, pine marten scats are mainly found on branches or tree bases beneath arboreal dens (Kleef 1997), and at low densities pine martens may not defecate on trails and paths (Balharry et al. 1996). As a consequence, a quite higher proportion of stone marten scats was probably collected. None the less, scats were cautionary classified as *Martes* sp.

A total of 692 faecal samples (fox: 133; badger: 177; *Martes* sp.: 382) was stored in polythene bags and refrigerated until processing.

Scat analysis was performed according to Kruuk and Parish (1981). Samples were washed with three sieves of 1.5, 0.3 and 0.1 mm mesh and food remains were inspected to count or estimate the total numbers of each item.

Mammal hairs were compared at 20 × and 40 × magnification with the keys provided by Debrot et al. (1982) and Teerink (1991), while reptiles and amphibians were detected by the keys of Di Palma and Massa (1981). Bird feathers were identified with reference to Day (1966). The undigested remains of insects (wings, legs and cuticle parts) and wild or cultivated fruits (seeds) were identified using personal collections. Sediment remained in the sieve with the thinnest mesh was examined under a binocular microscope to detect earthworm *chetae*. Food remains of human origin—generally including packing paper, tin foil, string, etc.—were recorded as "garbage".

The level of prey identification affects food-niche relationships among sympatric predators (Greene & Jacsíc 1983). According to Krebs (1989), prey were categorized to the lowest possible systematic level, attaining 34 items (see Tables II and III). Results were expressed as per cent frequency of occurrence (F% = number of faecal samples containing a specific food items/total number of faecal samples × 100), per cent volume (V% = total estimated volume of each food item "as ingested"/number of faecal samples containing that item) and per cent mean volume (Vm% = F% × V%/100) which, combining frequency and volume information, reflects the proportional contribution of each food item to the overall diet. The F% of main food items was plotted against their V%, connecting points with equal Vm% values by isopleths (Kruuk & Parish 1981).

Data were pooled seasonally (winter: I–III; spring: IV–VI; summer: VII–IX; autumn: X–XII) in order to investigate seasonal variations in carnivores diet.

A Principal Components Analysis (PCA) was used to describe the main sources of variation in the seasonal diet (Vm%) of the three species. PCA was performed on an arcsine transformed $3 \times N$ matrix, where N was, for each season, the number of items scoring Vm%>5% for at least one carnivore (i.e. those items scoring Vm%<5% for all carnivores

Table I. Habitat composition (%) and total length of the four transects used to collect faecal samples in the study area.

	Transects				
Habitat	1	2	3	4	Total
Villages		9.0	19.9	10.2	11.2
Grass-lands and orchards		15.9	30.4		14.5
Alpine meadows			40.7	20.2	18.6
Coniferous woods	79.6		9.0	69.6	34.3
Mixed woods	20.4	75.1			21.4
Total length (m)	4650	4750	7600	4100	21,100

Table II. Diet composition for the three carnivores in the study area (N=number of analysed faeces; I=overall number of items found; F%=per cent frequency of occurrence; V%= per cent volume).

	Red fox		Badger		*Martes* sp.	
Items	F%	V%	F%	V%	F%	V%
Fruits	66.2	74.1	89.8	81.5	78.8	73.4
Rosaceae	63.9	72.7	79.1	67.1	50.8	55.1
Pirus communis			5.1	26.1	3.1	46.2
Malus sylvestris	0.7	25.0	31.6	38.9	10.5	43.3
Sorbus aucuparia	31.6	80.1	7.9	47.0	3.9	39.7
Rubus saxatilis			1.1	65.0	4.4	47.0
Rubus idaeus	1.5	40.0	16.4	63.2	2.4	61.1
Fragaria vesca	3.0	31.2	11.3	26.5	12.8	46.2
Rosa sp.	34.6	51.6	3.9	27.6	4.7	22.5
Prunus avium	3.8	38.0	15.2	47.1	10.2	70.8
Prunus domestica			16.9	69.1	1.0	55.0
Prunus spinosa	1.5	12.5	4.5	35.6	6.0	34.8
Other fruits	15.8	16.2	54.2	37.2	47.6	62.7
Pinus cembra			18.6	57.6	0.3	20.0
Corylus avellana			4.5	19.1		
Berberis vulgaris	1.5	10.0	0.6	15.0	3.9	33.7
Ribes rubrum			1.1	10.0		
Rhamnus frangula					0.3	10.0
Vaccinium vitis-idaea	4.5	34.2	3.9	25.0	11.3	55.8
Vaccinium myrtillus			2.8	31.0	2.6	59.5
Ligustrum vulgare			0.6	5.0	22.5	79.6
Sambucus nigra			3.9	40.7	0.5	65.0
Undetermined fruits	10.5	8.2	26.5	18.3	12.6	19.0
Earthworms	0.7	10.0	20.9	7.1		
Gasteropods			4.5	6.5	1.3	11.0
Insects	27.8	63.0	48.0	20.7	29.1	25.6
Orthoptera	9.8	26.1	14.1	11.4	9.7	19.2
Coleoptera	24.1	60.3	33.9	23.4	11.5	28.1
Hymenoptera	1.5	27.5	5.6	6.6	12.8	16.7
Diptera	0.8	5.0	0.6	5.0	1.6	12.5
Birds	4.5	66.7	3.9	52.1	6.8	72.9
Passeriformes	3.8	67.0	3.9	52.1	4.7	69.2
Columbiformes	0.8	65.0			2.1	81.2
Mammals	36.1	74.5	8.5	77.0	14.1	73.1
Insectivores	5.3	41.4	1.7	28.3	2.9	63.2
Sorex sp.	5.3	41.4	1.7	28.3	2.9	63.2
Rodents	8.3	49.1			10.5	75.8
Muscardinus avellanarius	3.1	45.0			3.9	73.0
Apodemus sp.	5.3	51.4			1.3	71.0
Mus domesticus					5.2	79.1
Lagomorphs	11.3	86.7			0.5	100
Lepus sp.	11.3	86.7			0.5	100
Ungulates	11.3	96.3	6.8	89.2	0.3	20.0
Capreolus capreolus	11.3	96.3	6.8	89.2	0.3	20.0
Garbage	30.1	11.5	44.6	14.4	44.0	43.8
	N=133; I=267		N=177; I=555		N=382; I=821	

simultaneously were considered unable to distinguish their diets).

Trophic niche breadth was estimated by Levins' B index (Feinsinger et al. 1981), using the proportions of occurrence (p_i) of food categories in terms of Vm%. Trophic niche overlap between pairs of the three species was assessed by Pianka's O index (1973), p_{ij} and p_{ik} being the per cent mean volume (Vm%) in the diet of the species *j* and *k*. The same 34 food categories used for the PCA were used for processing the two indexes.

$$B = \frac{1}{R \sum_{i=1}^{n} p_i^2} \qquad O_{jk} = \frac{\sum_{i=1-n} p_{ij} p_{ik}}{\sqrt{\sum_{i=1-n} p_{ij}^2 \sum_{i=1-n} p_{ik}^2}}$$

Table III. Seasonal variation (Vm%) in the diet of the three carnivores (RF: red fox, B: badger, M: *Martes* sp.; N: number of analysed faeces; in bold: values considered for PCAs).

	Spring			Summer			Autumn			Winter	
Items	RF	B	M	RF	B	M	RF	B	M	RF	M
Pirus communis	–	–	0.1	–	0.6	0.8	**–**	**5.0**	**2.1**	–	3.4
Malus sylvestris	**–**	**10.2**	**7.6**	**–**	**7.4**	**3.3**	**–**	**29.8**	**3.2**	0.8	4.8
Sorbus aucuparia	–	–	–	1.9	1.1	0.7	**50.1**	**16.1**	**3.5**	27.3	1.2
Rubus saxatilis	–	–	–	–	1.3	2.1	–	–	4.5	–	–
R. idaeus	–	–	–	**2.5**	**17.8**	**5.3**	–	–	–	–	–
Fragaria vesca	**3.3**	**9.4**	**20.1**	1.7	1.5	4.0	–	–	–	–	–
Rosa sp.	**15.5**	**0.6**	**1.3**	1.1	–	0.1	**27.2**	**4.9**	**1.1**	21.9	2.5
Prunus avium	–	–	–	**5.9**	**12.3**	**26.5**	–	–	–	–	–
P. domestica	–	–	–	**–**	**17.5**	**1.3**	**–**	**7.9**	**0.7**	–	–
P. spinosa	–	–	0.2	–	1.4	3.9	0.5	4.2	2.9	–	–
Pinus cembra	**–**	**39.4**	**–**	–	1.6	0.2	–	4.7	–	–	–
Corylus avellana	–	0.9	–	–	–	–	–	3.5	–	–	–
Berberis vulgaris	–	–	0.6	0.2	0.1	0.6	0.3	–	2.0	–	2.3
Ribes rubrum	–	–	–	–	0.2	–	–	–	–	–	–
Rhamnus frangula	–	–	–	–	–	–	–	–	0.1	–	–
Vaccinium myrtillus	–	–	–	**–**	**1.5**	**5.4**	–	–	0.2	–	–
V. vitis-idaea	–	–	–	–	–	1.9	**1.4**	**5.1**	**12.6**	4.3	1.0
Ligustrum vulgare	**–**	**–**	**5.3**	–	–	0.8	**–**	**0.1**	**36.1**	–	28.4
Sambucus nigra	–	–	–	–	2.8	1.2	–	–	–	–	–
Earthworms	–	4.6	–	0.3	0.7	–	–	0.1	–	–	–
Gasteropods	–	0.1	0.4	–	0.5	0.1	–	–	–	–	–
Orthoptera	1.4	0.1	1.1	**8.6**	**0.7**	**2.9**	**0.7**	**6.2**	**2.4**	–	–
Coleoptera	**34.0**	**11.9**	**9.9**	**38.0**	**8.3**	**2.7**	–	2.3	0.3	–	–
Hymenoptera	–	0.7	3.4	1.7	0.3	3.2	–	0.2	1.3	–	–
Diptera	–	–	0.3	0.2	0.1	–	–	–	0.1	–	0.6
Passeriformes	**11.2**	**6.123**	**5.9**	–	1.2	4.5	2.0	–	1.5	–	0.8
Columbiformes	–	–	3.5	–	–	0.4	1.3	–	0.7	–	3.5
Sorex sp.	3.8	0.6	2.2	0.9	0.6	0.5	3.3	–	3.4	0.6	–
M. avellanarius	**–**	**–**	**5.2**	1.2	–	–	–	–	3.2	4.5	3.5
Apodemus sp.	1.7	–	1.6	–	–	1.3	1.1	–	0.5	8.7	–
Mus domesticus	–	–	3.8	–	–	3.9	–	–	2.9	–	8.1
Lepus sp.	**11.4**	**–**	**1.1**	2.8	–	–	**5.5**	**–**	**–**	22.6	1.7
C. capreolus	**13.3**	**4.1**	**–**	**27.1**	**8.0**	**–**	2.0	2.5	0.2	6.4	–
Garbage	**3.6**	**4.2**	**23.8**	**4.7**	**8.0**	**16.9**	**3.2**	**4.2**	**13.5**	2.5	29.2
N	21	40	92	32	103	104	49	34	129	31	57

Habitat selection

Marking ratio (M%)—i.e. the ratio between the number of faeces found in each habitat and the overall number of faeces found × 100—was considered an index of habitat utilization. This method, an adaptation of that carried out for otter surveys (Lenton et al. 1980) has been widely used for assessing the abundance and habitat preferences of many terrestrial mammals (reviews by Putnam 1984; Kohn & Wayne 1997; Gese 2001). Its reliability has been disputed (e.g. Kruuk et al. 1986; Messenger & Birks 2000), the survey interpretation involving several assumptions about marking activity and droppings identification (see Sadlier et al. 2004). None the less, scat counts still represent an effective and low-cost method to derive an index of carnivore relative abundance at different times or habitat of a same region (Sadlier et al. 2004).

To assess habitat selection M% was compared to the per cent availability of habitat types by the χ^2 test, using the sequential Bonferroni's technique to determine the level of significance (Rice 1989). Expected frequencies were calculated considering the overall relative length of transects covered in each habitat (Table I).

Pianka's O index (1973) was used to assess the overlap in habitat use, p_{ij} and p_{ik} being the proportions of use (M%) of habitat i by the species j and k.

Results

Diet analysis

Fruits were the main trophic resource for all the investigated species, reaching 49% (Vm%) in the diet of the red fox (almost exclusively Rosaceae), 73.2% for the badger (53% Rosaceae, 20.2% other fruits) and 57.9% for martens (Rosaceae and other fruits in similar proportions; Figure 1). Insects, mainly ground-living Coleoptera, and roe deer (*Capreolus capreolus*) were a secondary food source for foxes and badgers, the foxes relying also on hares (*Lepus europaeus* and *L. timidus*). Food of human origin ("garbage") formed a relatively large part of martens' diet (19.3%) and was also exploited by badgers. Rodents were rarely preyed upon by foxes (F%=8.3) and martens (F%=10.5) and apparently avoided by badgers (Table II).

Seasonal variation in the diet of all the three species was large. The bulk of fox diet consisted of Rosaceae fruits in autumn (Vm%=77.9) and winter (50.1%), and of insects in spring (35.3%) and summer (48.4%). Mammals were more important in winter (42.9%) except for roe deer which predominated in summer (27.0%), whilst birds were preyed on in spring (11.2%). Rosaceae, mainly cultivated fruits, were the main food item for badgers both in summer (60.8%) and autumn (68%), partially substituted by pine seeds (*Pinus cembra*) in spring (40.3%). Earthworms occurred almost exclusively in spring, amounting to only 4.65% of badger diet in that season. In winter no badger faeces was found, this being a period of heavy snow cover and least badger activity. Martens relied on wild Rosaceae in spring (29.3%) and summer (48.1%) and on other fruits in autumn (51.1%) and winter (40.7%); garbage was an important resource all year long (Vm% ranging between 13.5 and 29.2), whilst insects predominated in spring (14.7%).

Wider seasonal differences emerged when considering food items at species level, as shown by PCAs (Figure 2; Table III). Foxes ate almost exclusively rowan berries (*Sorbus aucuparia*), widespread in mixed woods, and rose-hips (*Rosa* sp.) and preyed more on medium-sized mammals, i.e. roe deer in spring and summer and hares in autumn and winter. Cultivated fruits—apples (*Malus sylvestris*), plums (*Prunus domestica*) and pears (*Pirus communis*)—and raspberries (*Rubus idaeus*) marked badger diet in summer and autumn, whilst a higher consumption of pine seeds characterized its diet in spring. Foxes relied on Coleoptera and Orthoptera in spring and summer, whilst Orthoptera were exploited by badgers in autumn. Strawberries (*Fragaria* sp.) peaked in marten diet in spring, cherries (*Prunus avium*) in summer, cranberries (*Vaccinium myrtillus* and *V. vitis-idaea*) in summer and autumn and privet fruits (*Ligustrum vulgare*) from autumn to spring. Garbage was significant in the diet of martens throughout the year.

Trophic niche breadth showed little seasonal variation for foxes, a bimodal pattern for martens and a peak in summer for badgers, whose overall yearly (three seasons) diet was the most diversified (B=0.36; Table IV). Fox trophic niche width was the narrowest, as a consequence of the small number of fruit species exploited and of a more carnivorous diet (mammals+birds Vm%: fox=29.9%, martens=15.3%, badger=8.5%).

Overall food overlap values were the greatest between badgers and martens (O=0.40) and the smallest between foxes and martens (O=0.20; Table IV); in summer, badger trophic niche overlapped those of the other two predators to a wider extent (Table IV), fruits and insects being intensively used by all species.

Habitat selection

Foxes avoided villages, using all other habitats according to their availability. Badgers used mainly open habitats (herbaceous areas and coniferous woods, whose undergrowth is scarce), showing a

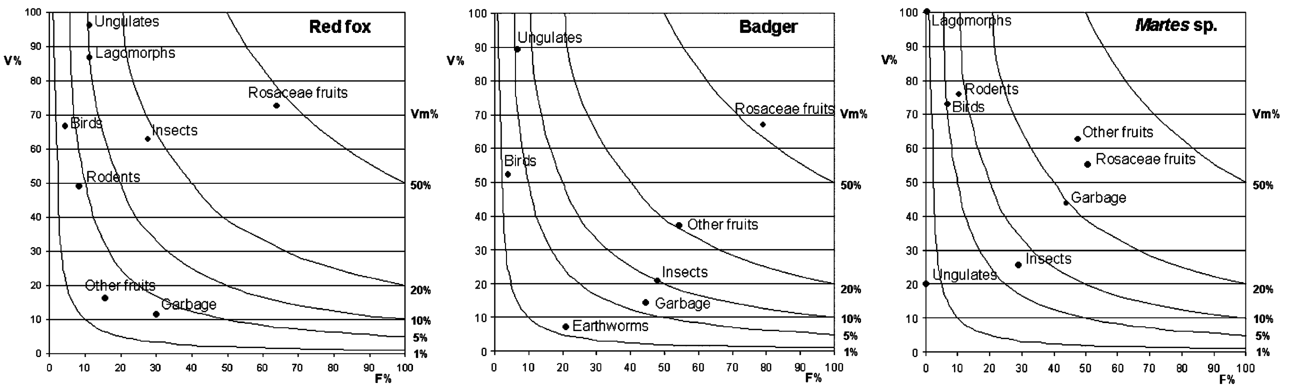

Figure 1. Estimated volume (V%) of the main food categories, whenever eaten, vs. their frequency of occurrence (F%) for the overall diet of the three species. Isopleths connect points of equal overall volume in the diet (Vm%, see methods).

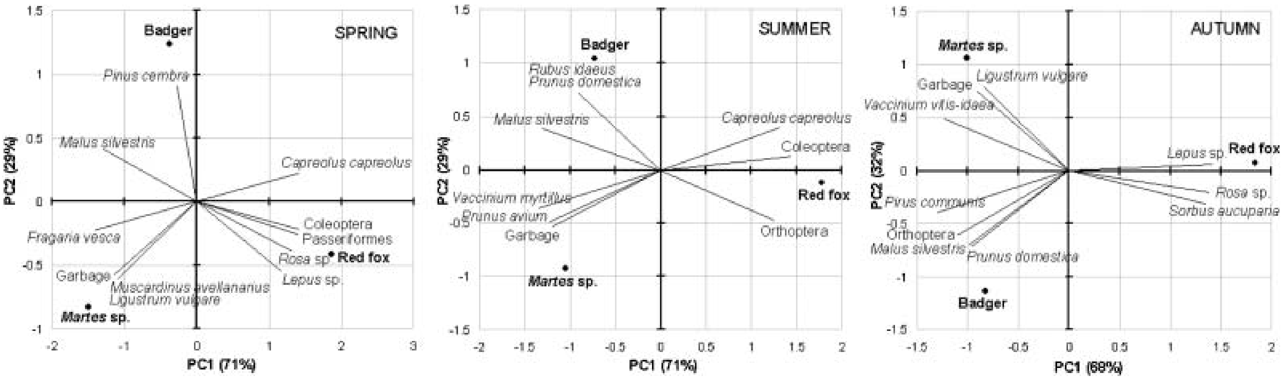

Figure 2. Plot of carnivore seasonal diet in relation to the first two Principal Components extracted from Vm% data of 34 food categories, excluding a priori, for each season, those items scoring Vm%<5% simultaneously for all carnivores. Items are represented by lines that approximately point towards the direction of maximum variation of each factor. The length of each line is proportional to the importance of the item in the assemblage arrangement. In brackets are the per cent explained variance of each Principal Component; coordinates of the carnivores species on PCs axes not in scale.

sharp preference for meadows, whilst avoiding villages and mixed woods. Martens showed an opposite pattern, selecting urban areas and mixed woods and avoiding open areas (Table V). The overlap in habitat use was maximal between badgers and foxes and minimal between badgers and martens. In summer all overlap indices between pairs were higher than in the other seasons (Table VI).

Discussion

The unusually scarce use of invertebrates, particularly earthworms, shown by badgers was unexpected. The local combination of rainfall (on average 828 mm/year for the period 1953–1980), temperature (7.5°C) and snow cover probably limits earthworm availability for badgers. Moreover, *Lumbricus terrestris*, the only species of the study area foraging on the surface in substantial numbers, represents only a small (17%) fraction of the earthworm fauna (Cavada 1997). According to their foraging habits, badgers shifted to other sources "lying on the ground", their diet turning decidedly frugivorous. Fruits seem to play an important role as alternative resources for Alpine carnivores, as already stressed for "rodent-specialist" mustelids, such as the stoat *Mustela erminea* and the weasel *M. nivalis* (Martinoli et al. 2001; Remonti et al. 2007).

As a consequence of diet shift, badger trophic niche was the widest and overlapped those of the other two carnivores to a wider extent than hypothesized at the outset of the research.

In accordance with competition theory (Schoener 1982), which predicts a convergence of the diet of coexisting consumers when resources are abundant, diet (and habitat) overlap was higher in summer, when most fruits ripen.

On the whole, diet overlap between species was lower than that reported by other authors (Serafini & Lovari 1993; Fedriani et al. 1999; Baltrûnaitë 2001; Padial et al. 2002), even if the number of items used for the calculation of Pianka's index is likely to influence the result and thus to invalidate comparisons between different studies (Prigioni 1991).

Overlap was limited by the use, at species level, of different items, whilst temporal differences, i.e. the use of the same resources in different seasons ("sequential use"; Barrientos & Virgos 2006), seemed to play a secondary role, even though the

Table IV. Annual and seasonal trophic niche breath (B) and overlap (O) indices for the three carnivores.

	B index			O index		
	Red fox	Badger	*Martes* sp.	Red fox–Badger	Red fox–*Martes* sp.	Badger–*Martes* sp.
Winter	0.14		0.15		0.14	
Spring	0.15	0.14	0.22	0.30	0.39	0.34
Summer	0.12	0.26	0.23	0.44	0.24	0.61
Autumn	0.10	0.19	0.16	0.45	0.12	0.21
Yearly	0.19	0.36	0.30	0.34	0.20	0.40

Table V. Seasonal and overall habitat selection for the three carnivores based on the proportion of faeces encountered in each habitat (M%). Expected frequencies: villages=11.2%; grasslands and orchards=14.5%; meadows=18.6%; coniferous woods=34.3%; mixed woods=21.4%. Selected habitats in bold, avoided ones in italic-bold; * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

	Winter		Spring		Summer		Autumn		Yearly	
	M%	χ^2	M%	χ^2	M%	χ^2	M%	χ^2	M%	χ^2
Red fox										
Villages	0	3.36	0	2.02	0	4.14	0	5.38	***0***	14.90***
Grass-lands	13.3	0.03	16.7	0.06	16.2	0.08	8.3	1.26	12.8	0.27
Meadows	23.3	0.36	33.3	2.10	13.5	0.51	22.9	0.48	21.8	0.73
Coniferous woods	26.7	0.51	5.6	4.34	43.2	0.86	47.9	2.59	36.1	0.12
Mixed woods	36.7	3.27	44.4	4.47	27.0	0.55	20.8	0.01	29.3	3.90
Badger										
Villages			0	3.47	***1.9***	8.21*	0	4.14	***1.1***	16.03***
Grass-lands			0	4.50	20.7	2.86	0	5.37	12.4	0.52
Meadows			**70.9**	45.71***	**37.7**	20.87***	**70.3**	53.11***	**49.7**	92.14***
Coniferous woods			22.6	1.24	24.5	2.95	21.6	1.73	24.8	4.60
Mixed woods			6.5	3.24	15.1	1.97	8.1	3.05	***11.8***	7.52*
Martes sp.										
Villages	**34.1**	20.59***	**33.7**	41.57***	**22.1**	12.04**	15.1	1.90	**23.7**	54.23***
Grass-lands	6.8	1.79	8.7	2.14	15.0	0.02	7.2	5.12	***9.8***	5.93*
Meadows	4.5	4.67	***1.1***	15.17***	***1.8***	17.21***	11.5	3.76	***5.4***	36.28***
Coniferous woods	***11.4***	6.75*	***13.0***	12.12***	***18.6***	8.14**	***10.1***	23.79***	***13.4***	49.40***
Mixed woods	**43.2**	9.75**	**43.5**	20.96***	**42.5**	23.46***	**56.1**	78.28***	**47.7**	125.2***

small seasonal samples available for foxes and badgers could have underestimated temporal shifts.

Foxes preyed on larger mammalian species than martens, as can be expected according to the positive correlation between predator and prey body size observed for a number of communities of predators (Jaksic & Braker 1983; Jedrzejewski et al. 1989).

As predicted, foxes exploited the widest range of habitats, avoiding only urban areas, in accordance to radio-tracking data from the Swiss Jura Mountains (Weber & Meia 1996). Martens were the most selective carnivores with regard to habitat, preferring those avoided by both of the other species (villages) or at least one (mixed woods), and avoiding all the others. *Martes* selection for mixed woods was reported also for the central Italian Alps (Pedrini et al. 1995a), whilst the avoidance of open areas, where the risk of predation would be higher, was reported for Mediterranean areas (Pittiglio 1996; Rondinini & Boitani 2002).

In the absence of competitors and predators, both pine (De Marinis & Massetti 1993; Clevenger 1994) and stone (Delibes 1978; Libois & Waechter 1991) martens are habitat generalists, even if stone martens have often been associated to human settlements (Waechter 1975; Hermann 1994). Delibes (1983) proposed that this preference could be a consequence of competition with the pine marten, but more recent studies have reported the two species as syntopic (Kruger 1990; Genovesi 1993; Pittiglio 1996). Then, the narrow range of habitat used by martens in our study area and their selection for competitor-free habitats could suggest the existence of asymmetrical competition (Wiens 1989) between martens and foxes (or, to a minor extent, both foxes and badgers).

Supporting this hypothesis, fox diet included a larger proportion of vertebrates. The energy content being equal, a diet including fruits provides less proteins and lipids than a largely carnivorous one, determining body fat loss and energy deficiency in carnivores (Larivière et al. 2001). In the context of optimal foraging theory (Krebs & Davies 1993), the dominant competitor is expected to exploit the most profitable food resource. Large-sized mammals like roe deer may be an important source of proteins for carnivores. About 40% (84% in summer) of the meat eaten by foxes consisted of roe deer, both fawns (in summer), which are exposed to fox predation (Lindstrom et al. 1994; Jarnemo 2004) and carrion (in winter/spring). To a lesser extent, roe deer were exploited also by badgers, probably exclusively as carrion, whilst martens' exploitation of this resource was negligible, as reported also by other studies comparing their diets in sympatry (Goszczynski 1986; Brangi 1995). More detailed research is needed to determine if the avoidance of dangerous interactions with larger competitors could be the

Table VI. Annual and seasonal overlap in habitat use between pairs of the three carnivores.

	O index		
	Fox–Badger	Fox–Martens	Badger–Martens
Winter		0.70	
Spring	0.64	0.66	0.15
Summer	0.81	0.75	0.55
Autumn	0.66	0.57	0.33
Yearly	0.81	0.72	0.40

cause of the lack of such a profitable resource from the diet of martens (DeVault et al. 2003; see also Cagnacci et al. 2003 about foxes in the western Italian Alps).

According to the hypothesis of asymmetrical competition, urban areas, avoided by both foxes and badgers, were selected by martens (probably almost exclusively *M. foina*; Prigioni & Sommariva 1997). Hermann (1994), reviewing several reports, suggested that stone martens select urban areas because they offer safe and warm resting places and trophic resources. Pine martens are said to rest in shelters above ground to avoid foxes (Pulliainen 1981; Webster 2001) and most dens of both *Martes* species are made on natural or artificial elevated places; in the urban environment of Cavalese village, attics and roofs of old houses are selected as resting places (Prigioni & Sommariva 1997), as reported elsewhere (Lachat Feller 1993; Brown 2004; Toth-Apathy & Szenczi 2004). Recent studies have suggested that food resources would play a minor role in stone martens' selection for urban habitats compared to the availability of fox-free shelters (Le Lay and Lodé 2004). Accordingly, as fruits formed the bulk of the diet of martens, this could explain their high selection for mixed woods.

Nonetheless, towns also offer unexploited (except for stray cats) human waste food, which may represent, particularly in conditions of food shortage, an important trophic source. The high stone marten density reported for Cavalese (0.87 ind./ha) together with the habitat composition of the home-ranges of three radio-tracked females, which almost totally included the village (Prigioni & Sommariva, 1997), suggest that urban areas and surroundings can satisfy all their ecological requirements. Stone marten adaptability to urban areas could represent a key factor in Alpine areas, where the decline of ecosystem productivity and the shrinkage of food resources with altitude may increase competition among top predators.

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