

Food habits and trophic niche overlap of the red fox and the stone marten in a Mediterranean rural area

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The food habits of the red fox *Vulpes vulpes* (Linnaeus, 1758) and the stone marten *Martes foina* (Erxleben, 1777) were studied in a rural hilly area in Siena county, central Italy, using faecal analysis. Both frequency of occurrence and volume of the different foods were quantified. Rodents, especially *Apodemus* sp., were an important prey for both species. Predation on poultry and game birds was nearly absent, whereas fruits and insects were seasonally taken by both species. *Rosaceae* fruits were the most eaten plant item. Within this category the fox fed mainly on *Malus* sp. and *Pyrus* sp., while the marten showed a preference for *Rubus* sp. and *Sorbus domestica*. Only fruits of *Prunus spinosa* were eaten in comparable quantities. Beetles were well represented in the diet of both carnivores, although they tended to concentrate on different species. Grasshoppers were preyed in small quantity. The overall diet overlap of foxes and stone martens was extensive: a surprising result, if the different body size, locomotor adaptations and living habits of these carnivores are considered.

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Introduction

Very few studies have been carried out on the food habits of the stone marten *Martes foina* (Erxleben, 1777), especially in southern Europe (Denmark: Rasmussen and Madsen 1985; France: Waechter 1975, Clement and Saint-Girons 1982; Germany: Ansoerge 1989; Italy: Pozio and Gradoni 1981, Lucherini and Crema 1993; Mongolia: Chotolchu *et al.* 1980; Poland: Romanowski 1989; Spain: Delibes 1978) and in no area its diet has been compared with that of the red fox *Vulpes vulpes* (Linnaeus, 1758) to find out their ecological relationships.

The red fox and the stone marten have different body size (red fox weight: 6 – 7 kg; stone marten weight: 0.7 – 1.0 kg), different social organisation (one male and one to several female foxes may share the same territory, e.g. Macdonald 1987, whereas martens seem to be intrasexually territorial, e.g. Krüger 1990), and partly different activity rhythms (foxes are less nocturnal than martens although apparently both species tend to be active mostly at sunset and sunrise, e.g. Kalpers

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1984, Harris 1986, Cavallini and Lovari 1991, Posillico *et al.* 1992). Furthermore, the stone marten is a much better rock and tree climber than the red fox. Food habits could then be expected to show little similarity. Accordingly, Ciampalini and Lovari (1985) found out an extensive overlap of food habits between two similar-sized carnivores, the red fox and the Eurasian badger *Meles meles*, but almost no overlap was revealed between two different-sized ones, the red fox and the wolf *Canis lupus* (Patalano and Lovari 1993). Conversely, it could be argued that two species of different morphology and other adaptations may feed on the same food resource without ever coming into open conflict with each other. This may lead to a diffuse scramble competition. Whether such a competition leads to niche separation or just limitation of population densities, it will presumably depend on the specific circumstances. In fact, Goszczyński (1986) and Cantini (1991) found out a rather extensive overlap in the food habits of sympatric red foxes and martens, but these authors could not discriminate between scats belonging to the stone and pine martens (see also Lindström 1989). According to the principle of competitive exclusion (e.g. Odum 1983), sympatric stone and pine martens are likely to specialise on different food resources to coexist, thus expanding the overall trophic niche of *Martes sp.* to overlap with that of the fox (Marchesi *et al.* 1989, Cantini 1991). Cantini (1991) concluded that the remarkable dietary similarity between foxes and martens may then be more apparent than actual. Our study area was not inhabited by pine martens, which prevented errors of scat identification between these closely related mustelids.

The aims of our research were the following: (1) to find out the food habits of the stone marten and the red fox in a rural Mediterranean area, (2) to assess the extent of their diet overlap in a region where pine martens are not present, (3) to test the hypothesis that widely different species are likely to fill separate trophic niches.

Study area

This study has been carried out in a rural hilly area of about 900 ha in Siena county, central Italy (43°18'N, 11°05'E), at an altitude of 150–370 m a.s.l. Twenty five to thirty foxes were estimated to live in our study area, with a density of about 3 individuals/100 ha. Territory size could be estimated around 100 ha, with a sex ratio of 1 male : 2 females / territory. Territory size of stone martens ranged around 350–400 ha, with an approximate density of 0.7 individuals/100 ha. The area is covered with mixed oakwood (*Quercus ilex*, *Q. cerris*, *Q. pubescens*, *Fraxinus ornus*, *Carpinus betulus*, *Juniperus communis*, *J. oxycedrus*, *Spartium junceum*), interspersed with fallow and cereal fields. *Prunus spinosa*, *Pyrus pyraster*, *Malus sylvestris*, *Cornus mas*, *Rosa canina*, *Rosa sp.*, *Rubus sp.* were common in the wood margins, whereas *Prunus domestica*, *P. avium*, *Pyrus communis*, *Malus domestica*, *Ficus carica*, *Sorbus domestica* occurred in the neighbourhoods of 4 inhabited and 14 abandoned farms of the area. Hunting was allowed over about 450 ha, mainly aimed at pheasants and wild boars. So-called "fox control" operations also occurred (some 20 foxes, cubs included, were killed over the study area from mid-February to May 1991), as well as some songbird poaching. Several hundreds sheep were grazing over ca 400 ha. Mean temperatures during the research period ranged between 19.2°C (range: 12.4–24.8°C) in May/October, and 6.8°C (range: 2.4–9.9°C) in November/April.

Methods

Between July 1990 and June 1991 a total of 340 scats of red fox and 378 scats of stone marten were collected in weekly excursions along a ca 16 km itinerary crossing the study area. The excrements were stored in polythene bags, deep-frozen and later analyzed as described by Kruuk and Parish (1981), Ciampalini and Lovari (1985), and Calisti *et al.* (1990). Each sample was washed in a tea-sieve (1.3 mm mesh) and the fine sediment was examined under a binocular microscope to detect the presence of earthworm chaetae. The food remains in scats were identified by comparison with reference material (e.g. hair, bones, feathers, seeds). The recognition of hair was also based on the analysis of taxon-specific microscopical features (Faliu *et al.* 1980, Debrot *et al.* 1982). The identification of the small mammals was made by teeth characteristics (Toschi 1965). We called "unidentified material" what appeared in the scats as mostly homogeneous, often amorphous, components whose origin could not be traced. The few items (e.g. minute bone spikes, hair fragments) sometimes detected in such a matrix did not provide any useful clue for identification.

The relative volume (% vol.) of each kind of food was assessed as described in Kruuk and Parish (1981), and Kruuk (1989).

The data were analysed on: (1) a monthly basis, as a percent frequency of occurrence (% occ.) in the total sample and as percent of the total estimated volume. Only few scats of red foxes were found in January ($n = 6$) and February ($n = 6$), which we pooled together in our analysis. For purpose of comparison, marten scats underwent the same treatment. (2) a seasonal basis, combining the percent volume with the percent frequency.

Statistics

To evaluate the trophic niche breadths of the fox and the marten, we used the standardized Levins index (B_{sta}) (Colwell and Futuyma 1971). Their overlap was measured through Pianka index (O) (1973), cf Ricklefs (1980). Both indices were applied to the percent occurrence and estimated volume of food categories in the whole diet.

The Levins index formula is:

$$B = 1 / \sum_{i=1}^n p_i^2$$

where n is the number of food categories and p is the proportion of records in each food category (i) set at 100%. The standardized Levins index formula is:

$$B_{sta} = B - 1 / B_{max} - 1$$

where B is the Levins index (Levins 1968) and B_{max} is the total number of food categories recognised (lowest niche breadth = 0, greatest niche breadth = 1).

The Pianka index formula is:

$$O_{jk} = \sum_{i=1}^n p_{ij} p_{ik} / \sqrt{(\sum_{i=1}^n p_{ij}^2 \sum_{i=1}^n p_{ik}^2)}$$

where p_{ij} (or p_{ik}) is the proportion of the food category i recorded in the diet of the species j (or k).

The differences in diet of the main food categories (rodents, *Rosaceae*) eaten by both species were evaluated using the Mann-Whitney U -test, two-tailed (Siegel 1956). Correlations between environmental variables and occurrence/volume of food items in the diet were tested using the Spearman rank correlation coefficient (Siegel 1956).

Results

Red fox

Rosaceae fruits, ungulates (sheep carrion), rodents and beetles made the staple of the fox diet (Figs 1, 3 and 4). The use of *Rosaceae* fruits (*Malus* sp., *Pyrus* sp., *Prunus spinosa*) increased rapidly from early summer to the autumn (Table 1, Figs 3 and 4), when most fruits are available on the ground, after falling from the trees. In late summer and early autumn *Cornaceae* fruits (*Cornus mas*, mainly) and, to a lesser extent, figs were also taken (Figs 3 and 4). In late winter and

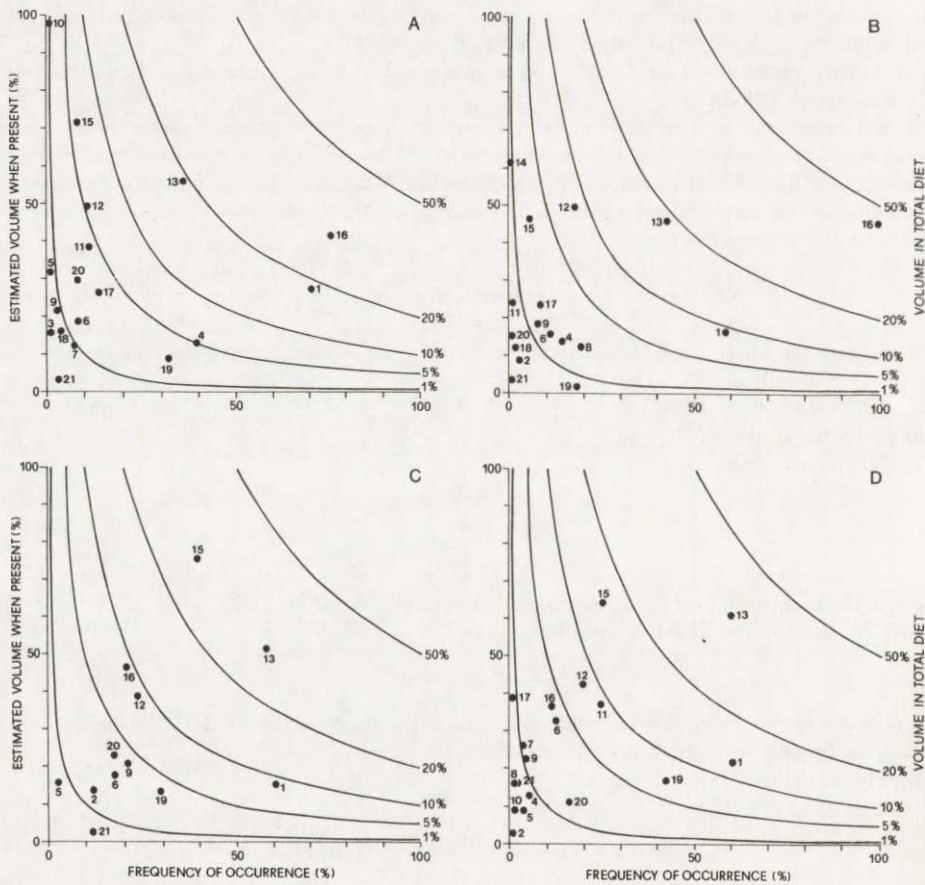


Fig. 1. Estimated volume of red fox food categories versus their frequency of occurrence. A – summer (J-A-S), B – autumn (O-N-D), C – winter (J-F-M), D – spring (A-M-J). Isopleths connect points of equal relative volume in the overall diet. 1 – *Coleoptera*, 2 – *Dermoptera*, 3 – *Hymenoptera*, 4 – *Orthoptera*, 5 – other insects, 6 – larvae, 7 – *Myriapoda*, 8 – *Arachnida*, 9 – *Mollusca*, 10 – other invertebrates, 11 – *Reptilia*, 12 – *Aves*, 13 – *Rodentia*, 14 – *Lagomorpha*, 15 – *Artiodactyla*, 16 – *Rosaceae*, 17 – *Cornaceae*, 18 – *Moraceae*, 19 – other plant material, 20 – garbage, 21 – unidentified material.

early spring rodents and ungulates (sheep carrion and offal, 75% occ.; wild boar carcasses, 15.4% occ.; undetermined carcasses, 9.6% occ.) peaked in the fox diet, while fruits were absent (Figs 3 and 4). Among rodents, field mice *Apodemus* sp. were the most preyed upon species (37.8% occ., 35.1% vol.) in spring. Bank voles *Clethrionomys glareolus* built up 7.6% in occ., and 6.7% in vol., of the diet. Beetles were taken throughout the year, but their bulk was rarely more than 20% in diet (Figs 1, 3 and 4). *Lamellicornia* (mainly *Scarabaeidae*) were taken in late spring and summer, whereas *Carabidae* peaked in late summer and early autumn. The consumption of reptiles (colubrid snakes, 50% occ.; lizards, 27.5% occ.; undetermined, 22.5% occ.), grasshoppers and garbage was restricted to the warm months, but no category appeared important (Figs 3 and 4). In the cold season occasionally foxes preyed on slugs (*Limax limax*). Earthworms did not show up in the diet, but in one sample (one chaeta). While the use of grasshoppers was positively associated

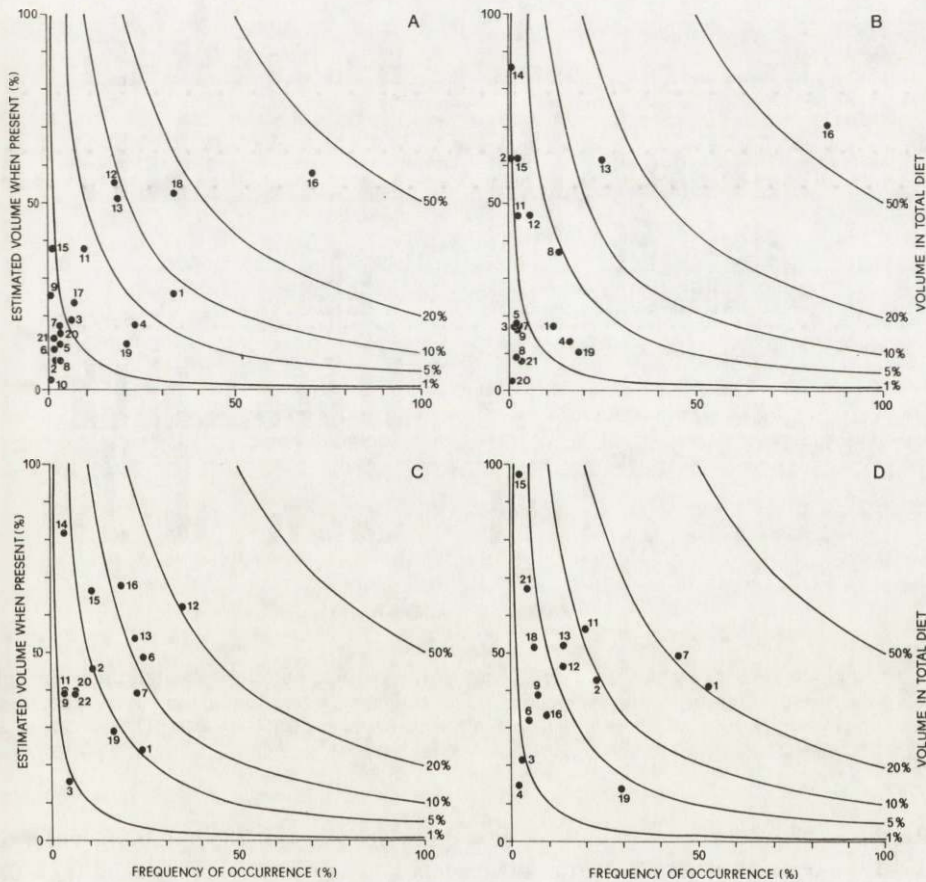


Fig. 2. Estimated volume of stone marten food categories *versus* their frequency of occurrence. 22 - eggs. Other denotations as in Fig. 1.

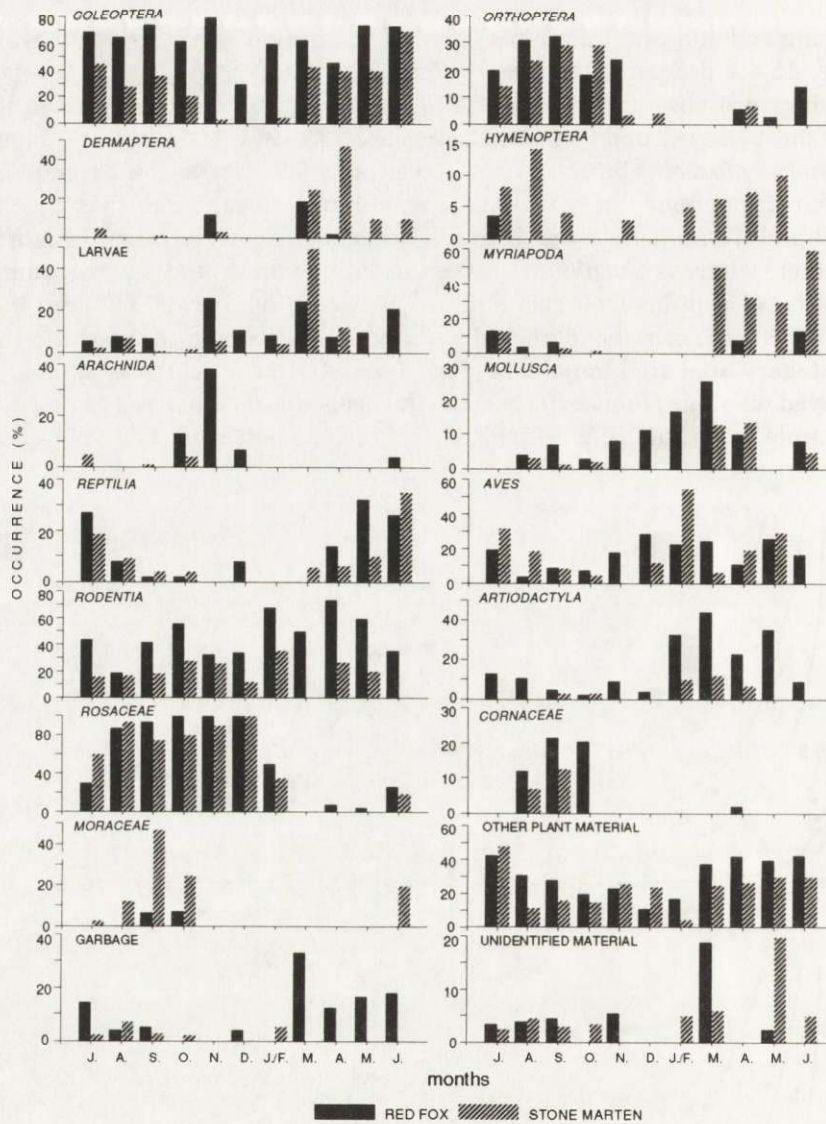


Fig. 3. Percentage of occurrence of food categories in the red fox and stone marten diets throughout the research period. Monthly sample size (n_1 refers to fox; n_2 refers to marten): J, $n_1 = 30$, $n_2 = 38$; A, $n_1 = 26$, $n_2 = 43$; S, $n_1 = 43$, $n_2 = 99$; O, $n_1 = 40$, $n_2 = 61$; N, $n_1 = 34$, $n_2 = 31$; D, $n_1 = 27$, $n_2 = 25$; J-F, $n_1 = 12$, $n_2 = 20$; M, $n_1 = 16$, $n_2 = 16$; A, $n_1 = 52$, $n_2 = 15$; M, $n_1 = 37$, $n_2 = 10$; J, $n_1 = 23$, $n_2 = 20$.

to the mean temperature ($r_s = 0.64$, $p < 0.05$, occ.; $r_s = 0.73$, $p < 0.05$, vol.), only the beetle percent volume (but not occurrences) was directly correlated ($r_s = 0.77$, $p < 0.05$).

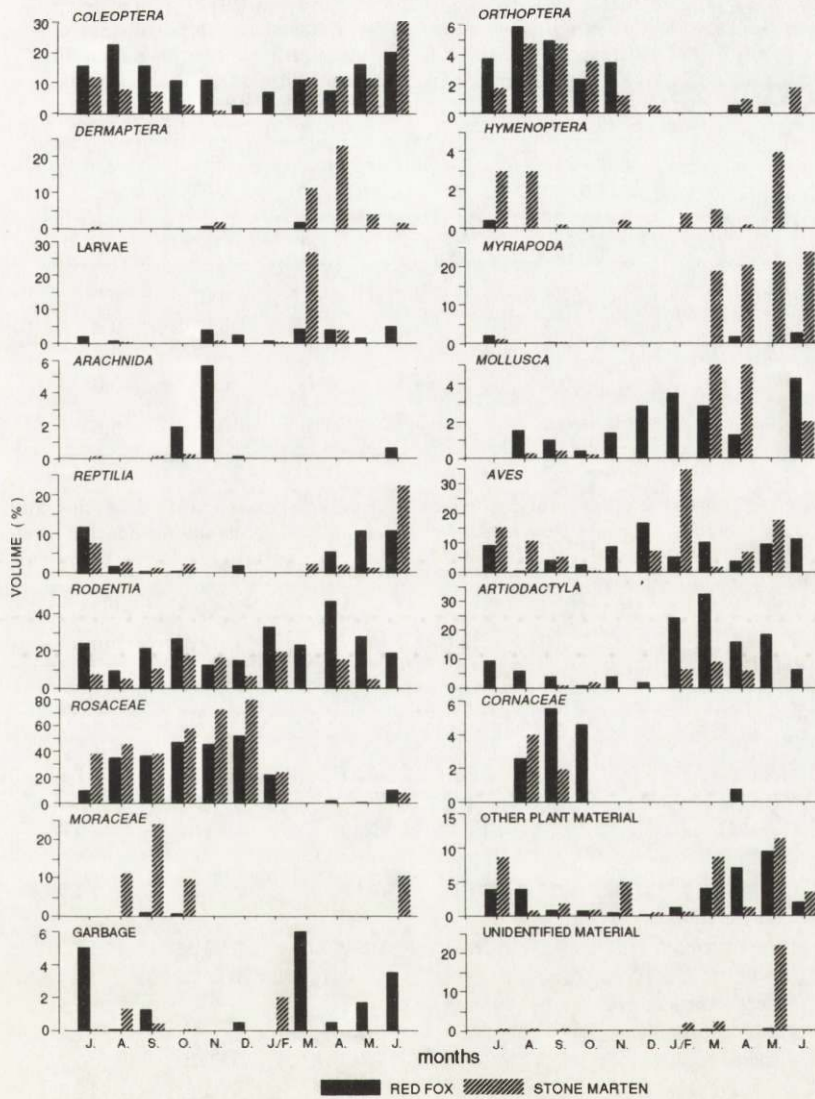


Fig. 4. Percentage of volume of food categories in the red fox and stone marten diets throughout the research period. Scat sample sizes as in Fig. 3.

Stone marten

Fruits were the staple of the stone marten diet for most of the year, showing a clear seasonality (Fig. 2). The use of *Rosaceae* fruits (Figs 2, 3 and 4) increased sharply from June to December becoming, together with figs, one of the main components of the diet. Birds (*Passeriformes*, 52.8% occ.; *Galliformes*, 11.3% occ.;

Table 1. Trophic niche breadth (Colwell and Futuyma 1971) and overlap (Pianka 1973) of *Vulpes vulpes* and *Martes foina*, based on the percentage of occurrence and estimated volume. $B_{sta\ f}$ – standardized Levins index, in occurrences; $B_{sta\ v}$ – standardized Levins index, in volume; O_f – Pianka index, in occurrences; O_v – Pianka index, in volume; n – number of food categories.

Season	<i>Vulpes vulpes</i> ($n = 35$)		<i>Martes foina</i> ($n = 37$)		O_f	O_v
	$B_{sta\ f}$	$B_{sta\ v}$	$B_{sta\ f}$	$B_{sta\ v}$		
Summer	0.4	0.4	0.4	0.4	0.8	0.5
Autumn	0.4	0.4	0.2	0.1	0.5	0.4
Winter	0.6	0.4	0.6	0.6	0.7	0.6
Spring	0.4	0.3	0.4	0.4	0.7	0.6
Annual	0.3	0.4	0.4	0.3	0.8	0.6

Table 2. Differential frequency of occurrence of food categories (carabid beetles and rose fruits) used by *Vulpes vulpes* and *Martes foina*, split to genus and/or species level. Family sub-totals (in bold) refer to annual total diet; values for lower taxonomic categories refer to each family.

Food category	<i>Vulpes vulpes</i>		<i>Martes foina</i>	
	n	%	n	%
<i>Coleoptera</i>				
Carabidae	169	49.7	83	21.9
<i>Carabus morbillosus</i>	5	2.7	–	–
<i>Carabus rossii</i>	45	20.5	10	9.6
<i>Carabus violaceus</i>	25	11.4	8	7.7
<i>Carabus</i> sp.	6	2.7	2	1.9
<i>Cychrus italicus</i>	1	0.5	–	–
<i>Percus payculi</i>	18	8.2	19	18.3
<i>Percus</i> sp.	–	–	7	6.7
<i>Procrustes coriaceus</i>	14	6.4	6	5.8
<i>Pterostichus bicolor</i>	–	–	1	1.0
<i>Scarites buparius</i>	–	–	7	6.7
<i>Zabrus tenebrioides</i>	31	14.2	17	16.3
Unidentified	74	33.8	27	26.0
Rosaceae	191	56.2	240	63.5
<i>Malus</i> sp.	83	34.9	17	6.0
<i>Prunus avium</i>	1	0.4	10	3.5
<i>Prunus spinosa</i>	76	31.9	93	32.6
<i>Prunus</i> sp.	3	1.3	12	4.2
<i>Pyrus</i> sp.	62	26.1	14	4.9
<i>Rosa</i> sp.	–	–	3	1.1
<i>Rubus</i> sp.	13	5.0	58	20.4
<i>Sorbus</i> sp.	–	–	78	27.4

Columbiformes, 3.8% occ.; undetermined, 32.1% occ.) and reptiles were eaten mainly in spring and summer, but rodents were a constant component of the diet throughout the year (Figs 3 and 4). Field mice *Apodemus* sp. were the rodent species most preyed upon (45.2% occ., 46.5% vol.). During summer *Orthoptera* peaked up. Larvae and adult beetles were found in the marten diet during the whole year, except the coldest months. Large *Lamellicornia* beetles (mainly *Lucanidae* and *Scarabaeidae*) were important food items in summer, whereas *Carabidae* peaked in spring (Table 1). *Myriapoda* and *Dermaptera* were also taken in the latter season (Figs 2, 3 and 4).

The use of reptiles (lizards, 62.1% occ.; colubrid snakes, 34.5% occ.; undetermined, 3.4% occ.) was directly associated to the mean temperature ($r_s = 0.78$, $p < 0.05$, occ.; $r_s = 0.81$, $p < 0.05$, vol.) and negatively correlated to precipitation ($r_s = -0.67$, $p < 0.05$, vol.). Positive correlations to the mean temperature were also found for beetles ($r_s = 0.66$, $p < 0.05$, occ.; $r_s = 0.65$, $p < 0.05$, vol.) and *Moraceae* ($r_s = 0.73$, $p < 0.05$, occ.; $r_s = 0.79$, $p < 0.05$, vol.). Garbage was rarely taken.

Trophic niche breadth and overlap

The annual value of the trophic niche breadth of the red fox ($B_{sta} = 0.3$ in occurrences; 0.4 in volume) is relatively low. Monthly values ranged from 0.4 to 0.7, in occurrences, and from 0.3 to 0.6, in volume, the cold months showing the highest value. The annual trophic niche breadth of the stone marten matches well those reported for two areas of the Alpine Arch (Cantini 1991, Lucherini and Crema 1993), and its values are the same of the fox's (Table 1). Monthly variation is great: 0.2–0.7, in occurrences; 0.1–0.6, in volume. Autumn values are the smallest and winter ones stand as the highest. The niche overlap is extensive, nearing total overlap (annual, in occurrences), and showing the smaller values in autumn (Table 1). If several food categories are broken down into smaller units (Table 2), some remarkable differences are detectable, e.g. *Carabus rossii* is preferred by the fox, while *Percus payculli* is mainly eaten by the marten; apples and pears are taken by the former, whereas the latter feeds on blackberries and sorb-apples (Table 2). If the food categories listed in Table 2 are not considered, the annual trophic niche overlap increases from 0.8 to 0.9 (in occurrences) and from 0.6 to 0.8 (in volume) (cf Table 1).

Discussion

Abundance, availability and dispersion of food resources are important factors underlying the food habits and habitat use of carnivores (e.g. Macdonald 1981, Doncaster *et al.* 1990, Cavallini and Lovari 1991). In turn, climatic/seasonal variation in the diet of both the red fox and the stone marten, two euriphagous species, is not surprising. The fox used mainly three food resources: *Rosaceae* fruits and, to a lesser extent, rodents (summer, autumn); rodents and scavenged larger mammals (winter, spring). The marten mostly based its diet on *Rosaceae* fruits, rodents as well as figs in summer and autumn, while wild birds and *Rosaceae*

fruits, in winter, and beetles as well as large centipedes, in spring, were the staple. Thus, the marten seemed to shift its food habits seasonally more than the fox (Figs 1 and 2), making use of a number of main (i.e. 10% isopleth in Figs 1 and 2) diet components twice as large as that of the latter, 8 *versus* 4, although the overall number of food categories differed little in the two species (see Table 1). The remarkable use which both carnivores made of fruits and other plant items may be explained as (A) a preference for it, or (B) a consequence of seasonal availability, or (C) an obligate diet when sources of animal proteins (e.g. rodents, carrion, insects) are scarce. Carnivores possess a short and simple digestive tract, unsuitable to process most vegetal food. They would then have difficulty meeting their energy and nutrient requirements on an exclusively vegetarian diet (Cavani 1991, Ball and Golightly 1992). Proteins are especially needed to build up and to restore body mass. In case of scarcity or unavailability of animal proteins, some carnivores can survive by taking plant food, e.g. fruits and berries, often in large quantities to compensate for limited actual digestion (the giant panda being an extreme example, Schaller *et al.* 1985). It may also be noted that the simple carbohydrates in fruits and berries do not require any special adaptation of the digestive system to be digested. Furthermore, both the stone marten and the red fox have been shown to be opportunistic species (e.g. Marchesi *et al.* 1989, Cavallini and Lovari 1991, Prigioni 1991), which tend to take what is most available. We think that a combination of reasons (B) and (C) may explain why their diet can be based so extensively on plant food, i.e. fruits and berries. Within this category, preferences are likely to occur.

In summer the trophic niche overlap of these carnivores tends to be greater than in the other seasons. In particular, while their diets are qualitatively similar, some differences can be detected in the quantity of the food categories used. In the warm months, reptiles tended to appear relatively more often in the fox's than in the marten's diet, while bird remains showed up more frequently in the scats of martens. The different climbing ability of these carnivores may partly have determined food selection: e.g. in summer, apples and pears can be found also on the ground where foxes can take them, but sorb-apples and wild plums are still on trees, where only martens may get access to them. The lowest value of diet overlap has been found in autumn: both species fed largely on fruits, most abundant in this season in Mediterranean countries, but, while the fox still went for apples and pears, the marten took figs and sorb-apples. Not surprisingly, the diet overlap grows again in the cold season, when the array of potential food resources decreases. However, within the animal food taken from December through March, the marten concentrated on invertebrates, while the fox used carrion and rodents. In particular, the marten fed steadily on bees and wasps throughout the year, although in limited amounts (Figs 3 and 4). Delibes (1978) suggests that stone martens feed on honey in all seasons and that often their scats smell of honey, show the presence of wax and sometimes contain bee remains. These characteristics are likely to be associated to honey consumption, but we could detect

traces of wax and honey only rarely in our sample (where, on the other hand, *Hymenoptera* were commonly found). This inconsistency may depend on the difficulty of detecting direct and indirect traces of a small quantity of honey in scats.

We cannot conclude that competition occurs between foxes and martens, but our data have shown that, when opportunist species are concerned, a large overlap of food habits can occur even if body size, locomotor adaptations, social organisation and activity differ widely. However, some of our results suggest that a greater trophic niche separation may not be ruled out, if food habits are analysed in fine detail, i.e. by breaking down the food categories into smaller units.

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