

Feeding resource partitioning among four sympatric carnivores in the Peneda-Gerês National Park (Portugal)

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Abstract

The Iberian Peninsula comprises two distinct biogeographic areas: a temperate Atlantic Eurosiberian (north) and a Mediterranean (centre and south), and they provide very different biotopes, landscapes and prey for carnivores. One example is an abundance of the wild rabbit *Orytolagus cuniculus* in the Mediterranean zone, which contrasts with the Eurosiberian zone, where the rabbit is scarce. The feeding resource partitioning among four sympatric predators (red fox *Vulpes vulpes*, wild cat *Felis silvestris*, genet *Genetta genetta* and stone marten *Martes foina*) was analysed in the Peneda-Gerês National Park (north-west Portugal), located in the Eurosiberian region. Data on the spatial distribution of three important prey species (*Apodemus sylvaticus*, *Microtus lusitanicus* and *Talpa occidentalis*) were also collected to investigate their possible relationships with the feeding habits of each predator. Rodents are the staple prey for this guild of carnivores. Predators are able to supplement their diets with one or two secondary prey types: rabbits and arthropods by the largest carnivores (the red fox and the wild cat); insectivores by the small predators (the genet and the stone marten). These results contrast with the characteristic Mediterranean predator–prey features, where rabbits are the main support of carnivore communities. The feeding resource partitioning revealed a complex structure characterized by a dynamic niche differentiation and overlap, according to a seasonal pattern. To explain this pattern of resource exploitation two hypotheses are discussed in the light of the body size of predators and their use of space.

Key words: diet, niche overlap, carnivores, feeding strategy, Portugal

INTRODUCTION

The investigation of the food-web relationships among predators, their prey and the environment is important for an understanding of the mechanisms that influence vertebrate community structure (Jedrzejewska & Jedrzejewski, 1998). Food is a critical resource for carnivore predators and its partitioning among sympatric species is crucial for their coexistence (Jedrzejewski, Jedrzejewska & Szymura, 1989; Lodé, 1991).

The Iberian Peninsula is an interesting region to study carnivores, since it comprises two distinct biogeographic areas: a temperate Atlantic Eurosiberian (north) and a Mediterranean (centre and south). This situation provides very different biotopes, landscapes and prey for carnivores. One remarkable example is the abundance of rabbits *Oryctolagus cuniculus* in the Mediterranean Iberia, contrary to the Atlantic zone, where rabbits are scarce (Blanco & Villafuerte, 1993).

In the Iberian Peninsula, the majority of published studies on diet dealt with only one predator and were realized in Mediterranean Iberia. It seems to be a general rule that the trophic importance of fruits and small mammals tends to decrease southwards, whilst the rabbits, reptiles and insects generally increase (for a revision see Delibes, 1983).

In this study, trophic relationships were examined among four sympatric carnivores (red fox *Vulpes vulpes*, wild cat *Felis silvestris*, common genet *Genetta genetta* and stone marten *Martes foina*) in north-west Portugal (Eurosiberian region). The study of this guild of carnivores is particularly interesting because it allows us to compare different predators with different body sizes and distinct degrees of specialization. The red fox (5–7 kg) and the wild cat (3.5–7 kg) are medium-sized predators. Red fox is a well known generalist (Amores, 1975), whilst wild cat is closer to a selective predator on rabbits (Gil-Sánchez, Valenzuela & Sánchez, 1999). The genet (1.7–2.0 kg) and the stone marten (1.1–2.5 kg) are small predators. The stone marten is a generalist species (Amores, 1980), whilst the genet is between typical generalists and typical specialists (Virgós, Llorente & Cortés, 1999).

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The mechanisms that regulate the feeding resource partitioning between sympatric predators in Eurosiberian Iberia are practically unknown. Certainly, the feeding choices of predators will reflect the lower abundance of wild rabbits in comparison with the Mediterranean habitats of the southern Iberian Peninsula. Therefore, as a general hypothesis one would expect that this guild of predators will depend much more on other prey types, namely, rodents. A high trophic niche overlap between red fox/wild cat and genet/stone marten would also be expected as a consequence of their morphological similarity.

Data on the distribution of three prey species (*Apodemus sylvaticus*, *Microtus lusitanicus* and *Talpa occidentalis*) were also collected to find potential relations with predatory strategies. The distribution and abundance of wild rabbits were also assessed in a previous study performed in the study area (Carvalho, 2001; Carvalho & Gomes, in press).

Hence, the aims of our research were: (1) to describe diet patterns, at the guild level, in the Eurosiberian Iberia; (2) to identify the resource partitioning patterns among predators in this part of the Iberian Peninsula.

METHODS

Study area

The study was carried out in a 4606-ha area near the city of Montalegre (41°49'N, 07°47'W), in the Peneda-Gerês National Park (PGNP), situated in north-western Portugal. The area is located in the Eurosiberian biogeographic region, near the transition with the supra-Mediterranean region (Ozenda & Borel, 2000). The area ranges between 800 m and 1400 m in altitude and granite is the lithological dominant type. Annual rainfall is *c.* 2000 mm and the annual average temperature is between 7.5 and 10 °C. This region is a typical mountain agricultural–forest mosaic habitat of north-west Portugal, comprising two distinct landscape systems: low matorral and agricultural–forest mosaic. The low matorral (<1 m) is distributed throughout an extensive plateau and is formed mainly by *Erica cinerea*, *Ulex* sp. and *Chamaespartium tridentatum*, interspersed with rocks and patches of tall scrubs (> 1 m) of *Genista* sp. and *Cytisus* sp. An agricultural–forest mosaic pattern of patches of oakwood (*Quercus pyrenaica* and *Quercus robur*), interspersed with pastures, agricultural fields and small villages, is scattered along valleys and lower altitude locations.

Diet composition

Between January 2000 and December 2000, 582 scats were collected (193 of red fox, 131 of wild cat, 151 of genet and 107 of stone marten). Genet faeces were collected from their latrines; samples of the other carnivores were searched for along paths distributed throughout the entire study area. To reduce bias on the assignment of the scats to the different predators, two researchers independently

identified each sample, and only those that were assigned to the same species were considered for analysis.

The methodology of scat analysis was based on the standard procedure of drying and washing through a sieve (0.36 mm mesh). More detailed description can be found in Putman (1984) and Reynolds & Aebischer (1991). Prey items were identified by their remains in scats (hair, feathers, scales, teeth, bones, etc.). The categories considered in the analysis were rodents, insectivores, lagomorphs (wild rabbit only), birds, reptiles, arthropods, carrion and fruits. Rodents and insectivores were identified to species level from their teeth (Blanco, 1998a,b) and hair (Teerink, 1991).

The contribution of each group of prey to the diet is presented as the frequency of occurrence, defined as the percentage of presences of a given prey item in the total scat sample. Confidence limits were generated for sample estimates by the bootstrap technique (1000 repetitions) as described in Reynolds & Aebischer (1991).

Since diet composition was expressed as frequency of occurrence, trophic niche breadth could not be estimated by the traditional measures of diversity. Therefore, a statistical approach was used consisting of the calculation of a coefficient of variation (CV). The CV is defined as the ratio of the standard deviation against the mean of a given statistical population (Sheskin, 2000). Here the frequency of each prey item per season was taken as a sample, and the mean and the standard deviation were calculated for the total prey items. The CV varies between 0, when all prey items are consumed equally (maximum diet diversity) and 4 (for 16 prey categories; rodents and insectivores considered at the specific level), when only 1 prey item is consumed (minimum diet diversity). A bootstrap approach (1000 repetitions) was performed to generate confidence limits for the CV values.

Structure of feeding resource partitioning

Trophic niche overlap was measured using Pianka's index:

$$O_{jk} = \sum p_{ij}p_{ik} / \left(\sum p_{ij}^2 \sum p_{ik}^2 \right)^{1/2},$$

where p_i is the frequency of occurrence of prey item i in the diet of species j and k (Pianka, 1973). Pianka's index varies between 0 (total separation) and 1 (total overlap). Food niche overlap was calculated considering rodents and insectivores at the specific level (*Apodemus sylvaticus*, *Microtus lusitanicus*, *Microtus agrestis*, *Arvicola sapidus*, *Eliomys quercinus*, *Crocidura russula*, *Talpa occidentalis*, *Sorex granarius*, *Sorex minutus* and *Neomys anomalus*) and the major prey groups (lagomorphs, birds, reptiles, arthropods, fruits and carrion). Confidence limits were generated for Pianka's index by the bootstrap procedure (1000 replications).

To further analyse the structure of feeding resource partitioning among predators, a multivariate technique called correspondence analysis was used. This is an ordination procedure that permits the arrangement of species (in this case predators) and samples (in this case

food items) in a low dimensional space, in a way that similar entries are close by and dissimilar entries are far apart (Gauch, 1982). Since predators and their prey are represented in the same space, the feeding strategies of each predator could be evaluated more clearly. The technique was applied to a predators-by-prey matrix where values were the frequencies of occurrence.

Spatial distribution of prey

The distribution of *Apodemus sylvaticus*, *Microtus lusitanicus* and *Talpa occidentalis* was investigated in order to establish possible relationships between the diet composition of each predator and the spatial distribution of their main prey. Therefore, the study area was stratified in the main landscape/vegetal formations (oakwood forest, matorral, tall scrubland and pastures/agricultural fields) and distribution and relative abundance data were collected in each stratum following a stratified random sampling procedure.

For *Apodemus sylvaticus* a standardized technique was used consisting of trap lines (INRA model) of 100 m (Spitz *et al.*, 1974). Each line was composed of 34 traps placed every 3 m and baited with seeds. In spite of a possible bias introduced by baiting, the use of seeds was to keep the animals alive during the trapping period. Each trapping session lasted for 3 nights. The rodents were live-trapped and released far from the trapping point. Relative abundance of *Apodemus sylvaticus* was expressed as the number of individuals caught per trap line during 3 nights.

To estimate the relative abundance of *Talpa occidentalis* and *Microtus lusitanicus* an adaptation of the protocol described by Giraudoux *et al.* (1995), which is based in counting surface signs of the burrowing activity of these species along transects, was used. The distinction between surface signs of the 2 species was easy because *Talpa occidentalis* form typical molehills and deeper tunnels than *Microtus lusitanicus*. Several transects of 400 × 4 m were set in each landscape/vegetation formation and presence/absence of each species was recorded at 4-m intervals. An abundance index was estimated using the ratio of the number of inhabited (where surface indices were detected) 4 × 4 m squares to the total number of squares (100) along the transect.

The non-parametric analysis of variance (Kruskal–Wallis test) was chosen for detecting statistical differences between relative abundances of *Apodemus sylvaticus*, *Talpa occidentalis* and *Microtus lusitanicus* among landscape/vegetation formations. Pairwise comparisons were made by the Dunn test (Sheskin, 2000). In all calculations the significance level considered was 0.05.

RESULTS

Diet composition

Frequencies of occurrence for each food resource, obtained by the bootstrap procedure (1000 simulations), are presented in Table 1. Confidence limits are in general

Table 1. Results of bootstrap simulation (1000 repetitions) to generate 95% confidence limits for the frequency of occurrence of each food item in the diet of red fox *Vulpes vulpes*, wild cat *Felis silvestris*, genet *Genetta genetta* and stone marten *Martes foina*. The coefficients of variation (CV) calculated using the occurrences of each prey type are also presented (95 percentile range obtained by bootstrap). Spr, Spring; Sum, Summer; Aut, Autumn; Win, Winter

Food categories	<i>Vulpes vulpes</i>				<i>Felis silvestris</i>				<i>Genetta genetta</i>				<i>Martes foina</i>			
	Spr	Sum	Aut	Win	Spr	Sum	Aut	Win	Spr	Sum	Aut	Win	Spr	Sum	Aut	Win
Rodents	44.4–71.1	15.4–35.4	28.9–60.5	76.1–95.7	37.8–70.3	12.5–43.8	66.7–92.6	68.6–94.3	49.0–76.5	74.4–93.0	87.0–100	63.6–90.0	22.2–55.6	16.7–46.7	36.8–78.9	68.2–95.5
<i>Apodemus sylvaticus</i>	4.4–20.0	1.5–12.3	5.3–28.9	17.4–43.5	2.7–24.3	6.3–34.4	18.5–55.6	28.6–60.0	27.5–54.9	41.9–69.8	78.0–100	24.2–60.6	5.6–30.6	0.0–16.7	15.8–63.2	13.6–50.0
<i>Microtus lusitanicus</i>	15.6–42.2	3.1–16.4	5.3–26.3	23.9–52.2	27.0–56.8	0.0–21.9	33.3–70.4	40.0–68.6	3.9–23.5	9.3–23.5	8.7–43.5	12.1–39.4	0.0–16.7	0.0–20.0	5.3–47.4	18.2–54.5
<i>Microtus agrestis</i>	6.7–28.9	3.1–16.9	5.3–26.3	13.0–34.8	2.7–18.9	0.0–21.9	7.4–37.0	20.0–54.3	17.6–41.2	18.6–46.5	0.0–13.0	18.2–48.5	2.8–27.8	0.0–20.0	10.5–47.4	13.6–50.0
<i>Arvicola sapidus</i>	–	–	0.0–7.9	–	–	–	0.0–11.1	–	0.0–11.8	–	–	0.0–15.2	–	–	–	–
<i>Eliomys quercinus</i>	0.0–11.1	0.0–4.6	–	–	0.0–8.1	0.0–9.4	–	0.0–8.6	0.0–9.8	0.0–11.6	–	–	–	0.0–16.7	0.0–15.8	–
Insectivores	6.7–28.9	9.2–27.7	–	4.3–23.9	18.9–48.6	25.0–56.3	11.1–44.4	14.3–40.0	37.3–64.7	34.9–62.8	13.0–52.2	48.5–78.8	41.7–72.2	23.3–56.7	10.5–52.6	9.1–45.5
<i>Crocodyra russula</i>	0.0–15.6	–	–	0.0–15.2	0.0–13.5	0.0–15.6	0.0–25.9	2.9–28.6	–	0.0–16.3	0.0–21.7	–	–	0.0–20.0	0.0–26.3	0.0–22.7
<i>Talpa occidentalis</i>	2.2–17.8	9.2–27.7	–	0.0–15.2	8.1–35.1	18.8–50.0	3.7–29.6	5.7–31.4	5.9–25.5	0.0–7.0	–	3.0–24.2	25.0–58.3	6.7–33.3	0.0–26.3	0.0–22.7
<i>Sorex granarius</i>	0.0–6.7	–	–	0.0–6.5	2.7–24.3	0.0–9.4	0.0–11.1	0.0–14.3	19.6–45.1	7.0–30.2	0.0–26.1	21.2–54.5	0.0–19.4	0.0–10.0	0.0–26.3	0.0–22.7
<i>Sorex minutus</i>	0.0–6.7	–	–	–	0.0–13.5	–	–	0.0–14.3	2.0–17.6	7.0–30.2	0.0–21.7	6.1–30.3	0.0–16.7	0.0–16.7	0.0–15.8	–
<i>Neomys anomalus</i>	–	–	–	–	–	–	–	–	0.0–9.8	2.3–20.9	0.0–21.7	0.0–15.2	–	–	–	–
Lagomorphs	8.9–33.3	18.5–38.5	0.0–7.9	2.2–19.6	13.5–43.2	15.6–46.9	11.1–40.7	20.0–48.6	0.0–13.7	–	–	0.0–9.1	0.0–13.9	0.0–10.0	0.0–15.8	0.0–27.3
Birds	6.7–13.3	1.5–15.4	7.9–31.6	4.3–23.9	0.0–16.2	6.3–34.4	0.0–11.1	–	23.5–51.0	9.3–32.6	–	0.0–15.2	2.8–22.2	10.0–40.0	0.0–31.6	0.0–22.7
Reptiles	0.0–6.7	6.2–15.4	0.0–7.9	–	2.7–21.6	3.1–25.0	0.0–11.1	0.0–20.0	13.7–35.3	7.0–27.9	0.0–26.1	3.0–27.3	8.3–33.3	6.7–36.7	–	–
Arthropods	17.8–44.4	43.1–67.7	18.4–50.0	2.2–17.4	13.5–40.5	25.0–56.3	14.8–48.1	0.0–14.3	0.0–9.8	0.0–7.0	–	0.0–9.1	0.0–8.3	0.0–20.0	0.0–31.6	–
Carrion	2.2–22.2	0.0–7.7	0.0–7.9	–	0.0–8.1	0.0–15.6	0.0–11.1	0.0–14.3	–	–	–	–	–	–	–	0.0–13.6
Fruits	0.0–6.7	0.0–10.8	65.8–92.1	6.5–21.1	–	0.0–18.8	7.4–40.7	–	0.0–5.9	14.0–41.9	–	–	–	–	10.5–52.6	0.0–13.6
No. of scats	44	65	38	46	37	32	27	35	51	44	23	33	36	30	19	22
CV	0.87–1.34	1.26–1.81	1.51–2.06	1.10–1.49	0.84–1.31	0.84–1.40	0.92–1.40	1.08–1.41	0.89–1.17	0.93–1.21	1.73–2.66	0.97–1.39	1.07–1.78	0.85–1.37	0.85–1.43	1.11–1.70

Table 2. Results of bootstrap simulation (1000 repetitions) to generate 95% confidence limits for the trophic niche overlap, expressed as Pianka's index, between all possible predator pairs. The rodents and insectivores categories were considered at the specific level

Predator pairs	Spring	Summer	Autumn	Winter
<i>Vulpes vulpes/Felis silvestris</i>	71.9–94.2	71.5–95.7	39.4–75.8	75.7–93.3
<i>Vulpes vulpes/Genetta genetta</i>	33.4–62.0	15.9–37.1	9.9–33.8	53.2–81.2
<i>Vulpes vulpes/Martes foina</i>	25.5–61.7	32.4–72.0	45.0–89.4	75.5–95.8
<i>Felis silvestris/Genetta genetta</i>	39.9–72.0	26.4–58.6	38.1–75.0	57.2–84.2
<i>Felis silvestris/Martes foina</i>	38.8–78.1	44.0–84.0	58.5–89.4	64.9–88.8
<i>Genetta genetta/Martes foina</i>	51.4–85.3	33.3–70.7	36.3–80.9	53.5–77.7

high in consequence of the low sample size. Nevertheless, the diet patterns for each predator are evident.

In the diet of the red fox, rodents were consumed all year round, but particularly in winter (sample estimate = 87.0%). Lagomorphs were consumed most often in spring (sample estimate = 20.0%) and summer (sample estimate = 26.7%). During this period, insectivores were a supplementary food resource (sample estimate: 17.8% in spring, 18.5% in summer). Arthropods were frequently found throughout the year (sample estimates > 30%), except during winter. A high consumption peak of fruits was observed in autumn (sample estimate = 78.9%).

Rodents dominated the diet composition of the wild cat all year-round (sample estimates varied between 28% in summer and 83% in winter). Lagomorphs were regularly consumed throughout the year (sample estimates varied between 26% in autumn and 34% in winter). Insectivores were an important secondary food category (sample estimates varied between 25.9% in autumn and 40.6% in summer). Arthropods were eaten throughout the year (sample estimates > 25%), except during the winter period. Other foods were minor dietary components.

In the diet of the genet, rodents were the dominant year-round component (sample estimates varied between 62.7% in spring and 95.7% in autumn). Insectivores were the most important secondary prey category (sample estimates ranged between 30.4% in autumn and 63.6% in winter). Birds were also an important seasonal resource, namely in spring (sample estimate = 37.3%). The other food sources were scarcely represented.

The main food categories of the stone marten, throughout the year, were rodents (sample estimates varied between 30.0% in summer and 82.0% in winter) and insectivores (sample estimates varied between 27.3% in winter and 55.6% in spring). Secondary components consumed seasonally were reptiles (sample estimate = 20.0% in summer), birds (sample estimate = 23.3% in summer) and fruits (sample estimate = 31.6% in autumn). The other prey items were consumed only sporadically.

Low CV values were observed for all predators throughout the year, which is indicative of high diet diversity (Table 1). This reflects a small preponderance of one or two prey categories in the diet of each predator and small differences in the occurrence of the other prey types. The red fox and genet diets, during the autumn period, were an exception to this pattern. In this season a strong preponderance of one prey type was observed,

fruits in the case of the red fox and *Apodemus sylvaticus* in the case of the genet.

Structure of feeding resources partitioning

Confidence limits obtained by bootstrap simulation for the trophic niche overlap, expressed as Pianka's index, are presented in Table 2. Niche overlap values were in general medium/high indicating similar prey choices among predators. This was particularly evident between the red fox and the wild cat. Lower values were observed between red fox/genet all year round (except in winter), red fox/stone marten in spring and wild cat/genet during summer.

The correspondence analysis for the spring season generated two axes that explain 93.4% of the total variance. The first factor (69.0% of variance) characterizes an opposition between the pair red fox/wild cat, associated to a higher consumption of lagomorphs, arthropods and *M. lusitanicus*, and the pair genet/stone marten. The second axis (24.4% of variance) contrasts the genet, which exploits more birds, *S. granarius* and *A. sylvaticus*, to the stone marten, that preys more on *T. occidentalis*. The species *N. anomalus* and *A. sapidus* appear in the two-dimensional graph as outliers, only consumed by the genet (Fig. 1).

The first two factors extracted for the summer period account for 95.4% of the total variance. The first factor (74.8% of variance) opposes the pair red fox/wild cat to the genet. The second factor (20.6% of variance) differentiates the stone marten from the other predators. The two-dimensional plot presents a clear pattern, the pair red fox/wild cat prey more on lagomorphs, arthropods and carrion, while the genet takes more advantage from *S. granarius*, *A. sylvaticus*, *N. anomalus*, and fruits, and the stone marten exploits more *C. russula* and *E. quercinus* (Fig. 2).

For the autumn season, the first two factors represent 88.0% of the total variance. The first factor (63.8% of variance) mostly characterizes the opposition of the genet to the other carnivores. The second factor (24.2% of variance) contrasts the red fox and the wild cat. The two-dimensional plot reveals a distinct pattern: the genet preys more on *A. sylvaticus*, *S. granarius*, *S. minutus*, *N. anomalus* and reptiles, whereas the red fox exploits more birds and fruits, and the wild cat consumes more lagomorphs and *T. occidentalis*. Note the position of the

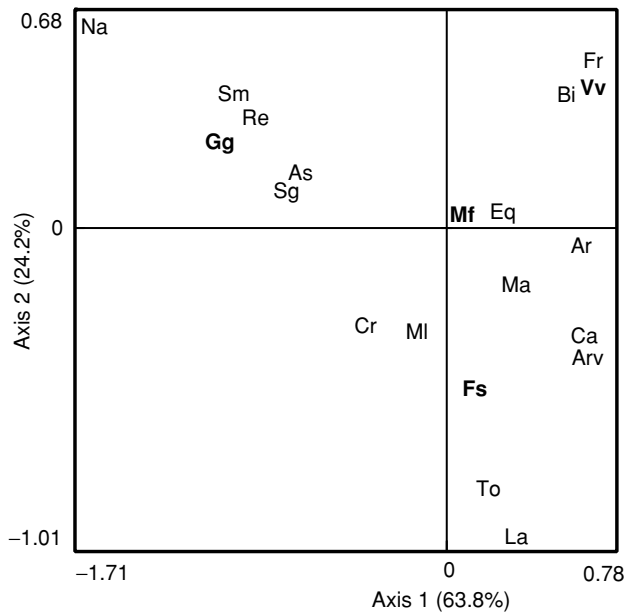


Fig. 3. Correspondence analysis ordination diagram (axes 1 and 2) obtained from the analysis of a predator–prey matrix, where values were the sample estimates of the frequency of occurrence for each prey type in the autumn season. Prey: As, *Apodemus sylvaticus*; Ml, *Microtus lusitanicus*; Ma, *Microtus agrestis*; Eq, *Eliomys quercinus*; Arv, *Arvicola sapidus*; Cr, *Crocidura russula*; To, *Talpa occidentalis*; Sg, *Sorex granarius*; Sm, *Sorex minutus*; Na, *Neomys anomalus*; La, lagomorphs; Bi, birds; Re, reptiles; Ar, arthropods; Ca, carrion; Fr, fruits. Predators (bold): Vv, *Vulpes vulpes*; Fs, *Felis silvestris*; Gg, *Genetta genetta*; Mf, *Martes foina*.

In relation to the distribution and abundance of *Microtus lusitanicus*, no significant differences were observed among the four landscape/vegetation formations (KW = 3.139, $P = 0.3707$) (Table 3).

Significant statistical differences among the four landscape/vegetation formations sampled were detected in relation to the relative densities of *Talpa occidentalis* (KW = 8.164, $P < 0.05$). This insectivore was more abundant in the pastures/agricultural fields. The significant pairwise comparisons detected by the Dunn test are presented in Table 3.

DISCUSSION

Diet patterns and niche breadth

This study was carried out in a short temporal scale and the sample size was not very large. As a consequence confidence limits for the various estimates were in general high. Nevertheless, some patterns could be easily distinguished and, therefore, a comparison with the Mediterranean biogeographic region of Iberia will be attempted.

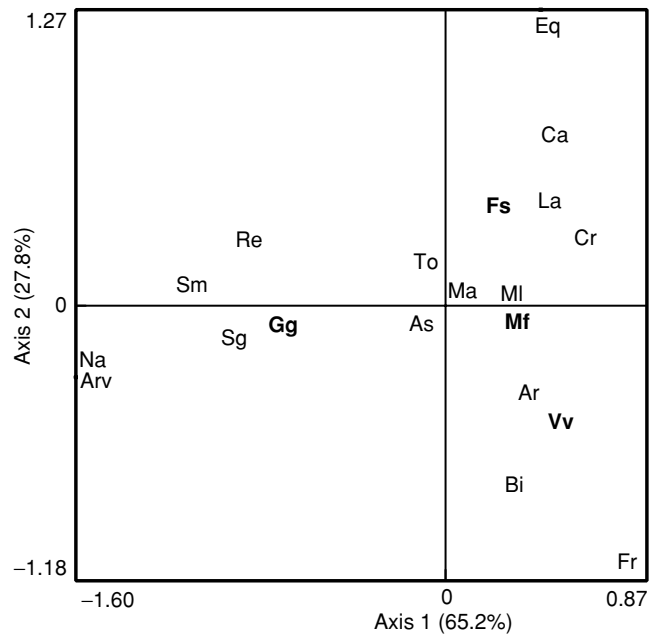


Fig. 4. Correspondence analysis ordination diagram (axes 1 and 2) obtained from the analysis of a predator–prey matrix, where values were the sample estimates of the frequency of occurrence for each prey type in the winter season. Prey: As, *Apodemus sylvaticus*; Ml, *Microtus lusitanicus*; Ma, *Microtus agrestis*; Eq, *Eliomys quercinus*; Cr, *Crocidura russula*; To, *Talpa occidentalis*; Sg, *Sorex granarius*; Sm, *Sorex minutus*; Na, *Neomys anomalus*; La, lagomorphs; Bi, birds; Re, reptiles; Ar, arthropods; Ca, carrion; Fr, fruits. Predators (bold): Vv, *Vulpes vulpes*; Fs, *Felis silvestris*; Gg, *Genetta genetta*; Mf, *Martes foina*.

As predicted, rodents were the major prey for this predator guild. The dependence of small and medium-sized carnivores on rodent populations was also documented in the ecosystems of the Eurosiberian region of north and central Europe (Goszczyński, 1986; Jedrzejewski *et al.*, 1989; Lodé, 1991; Jedrzejewska & Jedrzejewski, 1998; Lanszki *et al.*, 1999). This result differs from the Mediterranean ecosystems of Iberian Peninsula, where the consumption of rabbits by the medium-sized predators (red fox and wild cat) generally predominates (Amores, 1975; Fedriani, 1996; Gil-Sánchez *et al.*, 1999). This is particularly evident for the wild cat, which was pointed out as a species very close to a selective predator on rabbits in Mediterranean habitats (Gil-Sánchez *et al.*, 1999). However, our data suggest that there is some dietary plasticity in the consumption of lagomorphs by the wild cat, taking more wild rabbits when their availability was higher and changing to rodents when the lagomorphs became scarce (Stahl, 1986; Kozena, 1990; Sarmento, 1996).

The importance of rodents in the four predators diets could be a result of food availability determined by:

- (1) high abundance of rodents, principally *Microtus lusitanicus* (the spatial distribution of this rodent indicated that the species was abundant in all the main landscape/vegetation formations);

- (2) low availability of other food categories, namely rabbits, in comparison with Mediterranean habitats (Carvalho & Gomes, in press).

Nevertheless, rodents were seldom an exclusive prey to any predator in each season. Predators were able to supplement their diets with one or two secondary prey types. In this context, rabbits and arthropods were important secondary prey for the larger carnivores (the red fox and the wild cat), whereas insectivores were most consumed by the smaller predators (genet and stone marten). The significant consumption of arthropods by the red fox has also been reported in Mediterranean habitats (Amores, 1975; Fedriani, 1996), but it is uncommon by the wild cat (Sarmiento, 1996; Gil-Sánchez *et al.*, 1999). This surprising result could be a consequence of local characteristics, especially the dryness of the plateau soil, covered by low matorral, which favours a high availability of this food resource.

The high consumption of insectivores by the genet and the stone marten stated in this study contrasts strongly with data obtained for these species in Mediterranean Iberia (Amores, 1980; Palomares & Delibes, 1991; Gil-Sánchez, 1996). These differences seem to be a consequence of the presence of a higher number of insectivore species in Eurosiberian Iberia, contrasting with the relative scarcity (in number of species and abundance) of insectivores in Mediterranean Iberia (Blanco, 1998a).

Birds, reptiles and fruits were taken with significance only during one or two seasons by each predator, not differing much from Mediterranean habitats.

Niche breadths of the four predators were in general high. Intra and inter-specific comparisons showed similar values throughout the year, although food resources were used differently by each predator in each season. This reflects some plasticity of this guild of carnivores, which were able to exploit a wide range of prey and switching to other food sources, according to their seasonal availability. This was most evident in the case of the red fox and the stone marten, which is in accordance with the reported opportunistic feeding behaviour of these predators (Amores, 1975; Delibes, 1978; Ruiz-Olmo & Palazon, 1993; Fedriani, 1996).

The most peculiar aspect was an apparent contraction of the niches of the red fox and the genet in autumn, contrasting with the other two carnivores. For the red fox this was a consequence of intense exploitation of a seasonally abundant food source (i.e. fruits). The consumption of fruits by the red fox in Mediterranean habitats is also very common (Amores, 1975; Serafini & Lovari, 1993). In the genet, the niche contraction was because of intense predation on its main prey, *Apodemus sylvaticus*, coinciding with the density peak of this rodent. In Mediterranean habitats, the diet of genets is more diverse and the preponderance of *Apodemus sylvaticus* is not so marked, being partially substituted by other prey types (arthropods, amphibians and reptiles) (Virgós *et al.*, 1999).

Therefore, our results contrast with Mediterranean predator-prey system features, where rabbits are the main support of carnivore communities (medium-

sized predators), rodents are secondary prey types and insectivores are almost irrelevant prey.

Structure of feeding resources partitioning

Our predictions of a high niche overlap between red fox/wild cat and genet/stone marten were only partially supported by our data. Indeed, our results indicate a more complex structure characterized by a dynamic niche differentiation and overlap, according to a seasonal pattern. The structure of resource partitioning was based on three distinct seasonal feeding patterns:

- (1) in spring/summer there was a convergence of trophic niches between the red fox and the wild cat, while the genet and stone marten occupied distinct trophic niches;
- (2) in autumn there was a clear separation of food niches among the red fox, the wild cat and the genet, while the stone marten was in an intermediate position;
- (3) in winter there was a convergence among all predators, less evident in the genet.

The considerable overlap between the red fox and the wild cat does not necessarily mean high competitive interaction. Indeed, the reverse may be true, since competition involves a resource in short supply (Abrams, 1980). In spring/summer, the overlapping niches of the red fox and the wild cat were associated to the higher availability of rabbits during this period (juvenile rabbits in spring and dead or moribund rabbits as a consequence of myxomatosis in summer). This is in accordance with predation theory, which predicts a convergence of diets when resources are more abundant (e.g. Schoener, 1982). The same phenomenon was observed between the red fox and another felid, the Iberian lynx *Lynx pardinus* in a Mediterranean habitat (Fedriani *et al.*, 1999). Therefore, it is more likely that the extensive overlap between the two species would be a reflex of the abundance of resources and that modest competition exists.

In autumn, when rabbits were scarce, the generalist condition of the red fox was advantageous, since it allowed this carnivore to shift to other feeding resources that were seasonally abundant (i.e. fruits), whereas the wild cat continued to prey on rabbits. This could be interpreted as a mechanism to reduce the possibility of competition for feeding resources when an important prey becomes scarce.

The food niche of the stone marten overlapped considerably with the other carnivores and, hence, seemed to be the least differentiated, especially during autumn and winter. This could be a consequence of the generalist behaviour of this predator (Delibes, 1978; Amores, 1980; Gil-Sánchez, 1996) that favours the exploitation of a wide range of prey shared by other carnivores, as predicted by Pianka (1973).

It seems clear that from the four predators, the genet presented the most differentiated food niche. In the PGNP, a high consumption of *Apodemus sylvaticus* was observed year-round by the genet. Other studies conducted in the region suggested that this could be a consequence of

a spatial coincidence of predator and prey, since both have the tendency to explore forest patches (Gomes, 1998). The data obtained on the spatial distribution of *Apodemus sylvaticus*, in this study, are in agreement with this interpretation. The association of the genet to riparian zones, observed in this study, explains the consumption of prey species with aquatic or semi-aquatic habits, such as *Neomys anomalus* and *Arvicola sapidus*, which were less available to the other predators and, consequently, allowed the differentiation of the genet's food niche.

The convergence of food niches in the winter season was obviously associated with the high consumption of rodents by the four predators, as a consequence of the low availability of secondary resources. Therefore, it is probable that some degree of competition existed during this season. However, our data are not adequate to establish whether or not competition really occurred.

To explain the feeding resource partitioning patterns, two possible explanations are suggested. First, predators have different body sizes, the red fox and the wild cat being much heavier than the genet and the stone marten. This could have important consequences on the ability of the predators to catch larger prey, such as adult lagomorphs. The size of predators has been pointed out as an important aspect in determining resource partitioning in other areas (Jedrzejewska & Jedrzejewski, 1998). However, this hypothesis alone does not entirely explain this question, because the genet and the stone marten could easily prey on juvenile rabbits or moribund individuals. Therefore, it is proposed that the use of space could be a better explanation. Rabbits are more abundant in the plateau dominated by a low matorral scattered with rocks and patches of tall scrub, as opposed to the agricultural/forest mosaic, where they are practically absent (Carvalho, 2001; Carvalho & Gomes, in press). Several studies on the spatial ecology of red fox and wild cat, conducted in the PGNP, reported that both predators explore larger areas, including the agricultural/forest mosaic and also open areas like the matorral in the plateau (Soares, 2000; L. Macedo, pers. comm.). Similar findings have been described elsewhere (Artois, 1985). Contrary to the red fox and the wild cat, the genet is more restricted to the agricultural/forest mosaic (Gomes, 1989, 1998). The distribution of genet latrines in the region supports this interpretation. Ten regularly used latrines were found during fieldwork, distributed in the agricultural/forest mosaic, generally near rivers and small streams. There are no data on the spatial ecology of the stone marten in PGNP. However, several studies reported from other regions indicated that heterogeneous mosaics of forest patches, agricultural fields and edges constituted the most suitable habitat for this mustelid (Leger, 1996; Vadillo, Reija & Vilá, 1997). The high consumption of *Talpa occidentalis*, which is more abundant in the agricultural fields, suggests that this tendency is also true in the PGNP.

In conclusion, our results allow us to identify the basic feeding strategies of a carnivore guild, in a locality within the Eurosiberian Iberia, and the establishment of relationships with the spatial distribution of their main prey. None the less, the pattern of resource sharing

among sympatric predators is only a small part of the information needed to explain their coexistence, and long-term research is required on the spatial-temporal dynamics of predators and their prey, to fully evaluate this matter.

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