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Original investigation

Feeding habits and overlap among red fox (*Vulpes vulpes*) and stone marten (*Martes foina*) in two Mediterranean mountain habitats

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Abstract

The feeding habits of two carnivorous opportunists, red fox (*Vulpes vulpes*) and stone marten (*Martes foina*), have been compared in two Mediterranean mountain habitats (mesic and xeric), located in the Sierra Nevada National Park (SE Spain), between April 1997 and March 1998. The analysis of scats revealed a very important interspecific trophic niche overlap in the mesic habitat. In the xeric habitat the differences were significant and the overlap moderate. Seasonal variations existed in the degree of overlap, which reached its highest level in winter in the mesic habitat and in spring in the xeric habitat. The results indicated that the availability of food in each habitat was important in determining the divergence of the diets. Thus, in the mesic habitat, competition could be possible, although it was not important enough to cause a habitat segregation. Martens seemed to be more adaptive than foxes, probably due to their smaller size and arboreal life, allowing them to exploit fruit which is not as profitable for the fox. Foxes based their diet on small mammals, carrion and cultivated fruit in both habitats. Rabbits were also seasonally important in the xeric habitat. The trophic niche breadth of foxes was higher in the mesic habitat. The inter-habitat comparison showed significant differences in the diet of martens. In the xeric habitat, martens centred their diet on small mammals and fruit of *Juniperus phoenicea*, *Morus ulmifolius* and *Amelanchier ovalis*, while in the mesic habitat their diet was very similar to that of foxes. The trophic niche breadth was higher in the xeric habitat than in the mesic. The habitat conditions particulary influenced the overlap of the diets and these variations were fundamentally caused by the different availability of small fruit.

Key words: *Martes foina*, *Vulpes vulpes*, trophic overlap, Spain

Introduction

Interaction between species is important within carnivorous mammal communities because competitive phenomena generally appear which may determine the qualitative and quantitative community composition (DELIBES 1983; HESTEINSSON and MACDONALD 1992; WHITE et al. 1994). In comparison with the rest of Europe the Iberian peninsula has a great richness of carnivorous mammals, with a total of six-

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teen species that appear frequently in sympatric situations. However, there are only a few studies on co-existence between sympatric species (AYMERICH 1982; PALOMARES 1996; GIL-SÁNCHEZ 1998). The Sierra Nevada is a high mountain range in the Mediterranean region where two generalist carnivorous co-exist, the red fox V*ulpes vulpes* and the stone marten *Martes foina*.

The aim of this study was to investigate the diet of red foxes and stone martens in two Mediterranean mountain habitats and to evaluate the degree of differences and overlap in the diet.

Material and methods

Two different habitats, "mesic" and "xeric", were studied in the Sierra Nevada National Park, an area with the highest diversity of botanical endemism on the Iberian Peninsula (MORILLO and GÓMEZ-CAMPO 2000). Both areas are fluvial valleys separated by sixteen kilometres and belong to the Guadalquivir river basin.

The sampling region "mesic habitat" is located in the valley of the Genil river, a semi-humid supramediterranean habitat with acid soils, where the dominant trees are: *Quercus pyrenaica*, *Sorbus aria*, *S. torminalis*, *Castanea sativa*, *Cotoneaster granatensis*, *Quercus rotundifolia*, and *Pistacea terebinthus*. The climate is characterized by an average annual temperature of 11 °C and average annual precipitations of 800 mm (ANDALUCÍA 1992). This area possesses remains of humid forests that dominated the Iberian Peninsula during glacial periods. Our study area was situated between 1 200 and 1 400 m asl (37° 08′ N and 3° 23′ E). The area is well conserved although the impact of cattle grazing is evident. Currently game activities are forbidden.

The sampling region "xeric habitat" is located in the valley of the Dilar river (at 1 000–1 400 m asl; N41° 03′ and E4° 53′), a xeric supramediterranean habitat with calcareous soil. The dominant vegetation is woodland with *Pinus pinaster*, *Pinus halepensis*, *Pinus silvestris nevadensis*, *Juniperus phoenicea*, and *Amelanchier ovalis*. The average annual temperature is 14 °C and the average annual precipitation is 600 mm (ANDALUCÍA 1992). This area suffered a fire some years ago affecting its repopulated forests of *P. pinaster*.

The diet of foxes and martens was studied through scat analysis (PUTMAN 1984). A certain track was selected in each habitat and scats were collected monthly between April 1997 and March 1998, by two or three people. The tracks were previously cleared of scats in March 1997. The scats were always collected in the first week of every month, the aim being to obtain a signficant sample from the previous month. In total 856 scats were obtained: 178 in the mesic habitat and 678 in the xeric habitat (Tab. 1).

The analysis of the scats was carried out following the standard method of drying, washing and sifting (GIL-SÁNCHEZ 1996, 1998; REYNOLDS and AEFBISCHER 1991). The data are presented as frequency of occurrence (%F = number of scats containing a particular item/total scats × 100) and percentage of volume (%V = estimated volume of each item/total estimated volume × 100) (KAUHALA et al. 1998). For further analysis the 78 food items found are grouped into 14 categones (Tab. 2). The seasonal variation of the diet of both species was studied during the following periods: spring (March, April, May); summer (June, July, August); autumn (September, October, November); winter (December, January, February).

Table 1. Number of scats, trophic niche breadth and overlap, in different seasons and total, of stone marten (MF) and red fox (VV), in two Mediterranean mountain habitats in the southeastern Iberian Peninsula.

	Spring		Summer		Autumn		Winter		Total	
	MF	VV	MF	VV	MF	VV	MF	VV	MF	VV
					Mesic habitat					
N of scats	28	12	25	17	21	17	30	28	104	74
Levin's Indes B	4.58	2.56	6.11	3.60	5.51	3.90	2.23	2.37	5.02	3.80
Pianka's Index	0.72		0.62		0.63		0.99		0.92	
					Xeric habitat					
N of scats	75	40	156	45	139	16	176	31	546	132
Levin's Index B	4.52	3.45	2.63	8.27	3.77	4.08	2.97	3.79	6.03	5.76
Pianka's Index	0.54		0.42		0.25		0.49		0.47	

Table 2. Diet of stone marten and red fox in two Mediterranean mountain habitats ("xeric" and "mesic") in the southeastern Iberian Peninsula. %F-percentage of occurrence; %V-percentage of volume in scats.

	Martes foina				*Vulpes vulpes*			
	xeric		mesic		xeric		mesic	
	%F	%V	%F	%V	%F	%V	%F	%V
Small mammals	28.8	23.6	46.1	37.7	27.3	23.7	52.7	39.8
Arvicola sapidus	4.6	4.2	13.5	13.2	2.3	2.2	5.4	2.8
Microtus duodecimcostatus	0.6	0.5	1.0	0.3	1.5	1.4	6.8	5.8
Apodemus sylvaticus	8.4	7.7	3.9	3.6	5.3	4.6	13.5	12.4
Eliomys quercinus	–	–	1.0	0.5	–	–	–	–
Mus spretus	3.5	2.9	–	–	5.3	3.7	0.2	4.5
Rattus rattus	0.4	0.3	2.9	2.9	2.3	2.1	–	–
Crocidura russula	0.7	0.7	2.9	1.5	0.8	0.6	–	–
Suncus etruscus	–	–	1.9	1.3	–	–	–	–
Talpa occidentalis	–	–	1.0	0.9	–	–	–	–
Small mammals non identif.	10.6	7.2	18.3	13.4	12.1	9.0	17.6	14.3
Lagomorphes	3.3	3.2	1.9	1.9	24.2	21.8	–	–
Lepus granatensis	–	–	1.9	1.9	0.8	0.8	–	–
Oryctolagus cunniculus	3.3	3.2	–	–	23.5	21.1	–	–
Carrion	3.3	1.9	25.0	15.0	28.8	23.4	32.4	26.9
Capra aegagrus f. hircus	0.2	0.0	8.7	8.2	9.9	8.4	13.5	12.2
Capra pyrenaica	0.6	0.5	1.9	1.9	7.6	7.4	14.9	12.5
Ovis ammon f. aries	–	–	1.9	1.9	–	–	2.7	1.5
Sus scrofa	0.4	0.0	–	–	2.3	1.6	–	–
Sus scrofa f. domestica	–	–	–	–	–	–	1.4	0.7
Carrion non identif.	2.2	1.4	2.9	2.9	9.1	6.1	–	–
Birds	3.3	1.3	1.0	4.0	6.1	3.2	4.1	2.1
Alectoris rufa	0.4	0.3	–	–	3.0	1.9	1.4	0.1
Columba sp.	0.4	0.4	–	–	–	–	–	–
Otus scops	0.2	0.2	–	–	–	–	–	–
Turdus merula	–	–	1.0	1.0	–	–	–	–
Turdus sp.	0.2	0.0	–	–	–	–	–	–
Pyrrhocorax phyrrocorax	–	–	–	–	–	–	1.4	1.4
Birds non identif.	2.0	0.5	1.0	0.0	3.0	1.3	1.4	0.7
Reptils	0.0	0.9	3.9	0.6	4.6	1.0	1.4	0.1
Elaphe scalaris	0.4	0.0	1.0	0.0	–	–	1.4	0.1
Malpolon monspessulanus	–	–	1.0	0.0	0.8	0.2	–	–
Natrix maura	0.2	0.0	–	–	–	–	–	–
Timon lepida	1.1	0.7	–	–	–	–	–	–
Psamodrummus algirus	0.2	0.2	2.9	0.5	3.8	0.8	–	–
Reptiles non identif.	0.2	0.00	–	–	–	–	–	–
Arthropods	16.7	4.3	25.0	8.5	28.0	3.4	32.4	8.7
Coccinella sp.	–	–	–	–	0.8	0.0	–	–
Hiulus sp.	–	–	10	0.0	–	–	–	–
Melolonta melolonta	0.8	0.4	4.8	2.8	4.6	0.9	4.1	1.6
Rizotropus sp.	1.3	1.0	–	–	–	–	–	–
Blatta sp.	–	–	1.0	0.0	–	–	–	–
Carabidae spp.	–	–	–	–	0.8	0.0	2.7	1.1
Cerambicidae sp.	–	–	–	–	–	–	1.4	0.5
Scarabidae spp.	0.4	0.0	2.9	0.0	2.3	0.1	1.4	0.5
Coleptera non identif.	3.9	1.0	3.9	0.0	3.8	0.1	6.8	1.0
Apis melifera	0.2	0.1	–	–	–	–	–	–

Table 2. Continued.

	Martes foina				*Vulpes vulpes*			
	xeric		mesic		xeric		mesic	
	%F	%V	%F	%V	%F	%V	%F	%V
Xilocopa sp.	0.2	0.2	–	–	–	–	–	–
Polistes sp.	0.2	0.1	–	–	–	–	–	–
Mantis religiosa	0.2	0.0	–	–	–	–	–	–
Hymenoptera non identif.	0.4	0.0	1.0	0.0	–	–	1.4	0.0
Ortoptera non identif.	7.5	1.5	9.6	1.7	9.1	2.1	13.5	4.1
Anacridium sp.	0.4	0.2	–	–	–	–	–	–
Buthus occitanus	0.4	0.1	–	–	3.8	0.2	–	–
Scalopendra sp.	0.6	0.3	1.0	1.0	3.0	0.1	1.4	0.0
Arthropod non identif.	0.18	0.05	–	–	–	–	–	–
Juniper								
Juniperus phoenicea	28.0	26.3	–	–	0.8	0.0	–	–
Serviceberry								
Amelanchier ovalis	18.7	16.7	–	–	6.1	2.9	–	–
Blackberries								
Rubus sp.	6.4	5.0	19.2	11.4	3.0	1.2	9.5	2.9
Fig								
Ficus carica	8.6	5.5	7.7	4.4	8.3	2.3	–	–
Wild tree fruit	0.4	0.2	2.9	2.0	6.1	3.4	4.1	0.9
Celtis australis	0.2	0.2	–	–	–	–	–	–
Prunus sylvestris	0.2	0.0	1.9	1.1	6.1	3.4	4.1	0.9
Sorbus aria	–	–	1.0	1.0	–	–	–	–
Wild bush fruit	3.9	3.3	9.6	6.6	1.5	0.5	4.1	1.0
Crataegus monogyna	0.4	0.4	1.9	0.1	–	–	–	–
Juniperus oxycedrus	1.8	1.4	–	–	0.7	0.2	–	–
Rosa sp.	0.9	0.9	1.0	1.0	–	–	1.4	0.7
Rubia peregrina	0.7	0.5	–	–	–	–	–	–
Fruit non identif.	0.2	0.1	2.9	1.7	–	–	–	–
Seeds non identif.	–	–	4.8	3.8	0.8	0.3	2.7	0.3
Cultivated fruit	6.4	4.1	10.6	8.2	15.2	9.2	24.3	15.1
Malus domestica	2.2	1.6	3.9	3.0	3.0	0.5	12.2	4.2
Pyrus communis	0.6	0.5	–	–	1.5	1.5	–	–
Vitis vinifera	1.3	0.3	–	–	2.3	0.8	–	–
Cultivated plum	0.4	0.2	–	–	4.6	0.9	9.5	8.2
Cultivated cherry	2.0	1.5	6.7	5.1	6.1	4.8	2.7	2.7
Cultivated medlar	–	–	–	–	0.8	0.8	–	–
Others	5.5	3.7	13.5	2.9	10.6	4.0	9.5	2.5
Martes foina	0.6	0.4	–	–	3.0	1.7	2.7	2.4
Mustela nivalis	0.2	0.4	–	–	–	–	–	–
Egg	1.1	0.0	8.7	0.2	3.0	0.1	6.8	0.1
Honey	0.2	0.2	–	–	–	–	–	–
Grass	–	–	1.0	0.3	1.5	0.9	–	–
Plants non identif.	2.0	1.8	1.9	1.7	0.8	0.6	–	–
Rubish	0.6	0.4	–	–	2.3	0.7	–	–
Others non identif.	0.7	0.6	1.0	0.7	–	–	–	–

Diets were compared by χ^2 tests on contingency tables (Fedriani et al. 1999). The trophic niche breadth was calculated using the Levins' Index B (Levins 1968) and the trophic niche overlap using Pianka's Index (Pianka 1973), based on the %V of the prey categories (Kauhala et al. 1998).

Results

For the mesic habitat, the diet of both species was very similar ($\chi^2 = 22.14$; d. f. = 13; $p > 0.05$) and a high overall trophic niche overlap was observed (Tab. 1, 2). There were some seasonal variations but both species based their diets on small mammals, carrion, arthropods, cultivated fruit and berries (Fig. 1). In the xeric habitat the diet was statistically different ($\chi^2 = 80.92$; d. f. = 12; $p < 0.001$) between the two species and the overlap was annually moderate, and seasonally moderate to low (Tab. 1, 2). The marten based its diet mainly on small mammals, *J. phoenicea* and *Amelanchier ovalis*, but there was also a strong seasonal importance of *A. ovalis* in summer and *J. phoenicea* in winter. The fox based its diet on carrion, small mammals and lagomorphs (mainly rabbits). Seasonal variations are shown in figure 2.

Discussion

In the Sierra Nevada mammals (mainly small mammals and carrion) and fruit were the main food sources of both species in both habitats. The differences in the consumption of fruit in our study areas seems to be more related to availability than to other factors (but see Herrera 1989), as indicated by seasonal variations and differences between the habitats. When comparing the extent of the frugivory of these species both within Sierra Nevada habitats or between other regions in southern Spain a very marked variation is evident in the consumption of certain fruits (Amores 1975, 1980; Herrera 1989; Fedriani 1996; Gil-Sánchez 1996). This could possibly indicate that consumption is related to differences in the local availability of fruit plants.

In the mesic habitat the diet of both species was very similar, with a maximum overlap during winter. This was probably due to the extreme winter conditions when snow and frequent frost would diminish the availability of resources. This tendency to overlap in times of shortage of resources has been observed in other carnivores communities (Serafini and Lovari 1993; Sidorovich et al. 2000). However, this is not in accordance with the competition theory, which suggests that the convergence of the diets among sympatric species should be higher when the resources are abundant (Schoener 1982; Fedriani et al. 1999). Rosenzweig (1966) concluded that the coexistence of sympatric carnivores of different sizes is possible because differing corporal sizes allows for diet segregation. This agrees with our results in the xeric habitat. According to Pianka (1988), as a mechanism implied in coexistence, segregation of trophic niches should exist in order to diminish the competition for exploitation. In addition Polis et al. (1989) argued that the species segregate their niches as a mechanism to avoid an intraguild predation. However, our results in the mesic habitat, as well as those of Serafini and Lovari (1993) for the same species and studies of other carnivores, have found a high diet overlap among sympatric species with different morphology and ecology (Ciampalini and Lovari 1985; Reig and Jedrzejewski 1988; Gil-Sánchez 1998; Kauhala et al. 1998; Fedriani et al. 1999; Frafjord 2000; Sidorovich et al. 2000). Nevertheless, on some occasions a direct competition was indicated (Delibes 1983; Hersteinsson and Macdonald 1992; Withe et al. 1994; Lindström et al. 1995).

In most of the case studies different mechanisms to avoid competition when a trophic niche overlap existed were discussed: the space use-temporal segregation (Serafini and Lovari 1993; Fedriani et al. 1999); the micro- and macrohabitat segregation (Serafini and Lovari 1993; Gil-Sánchez 1998; Frafjord 2000); and also mechanisms dormant during winter (Kauhala et al. 1998). In the mesic habitat during spring, summer and autumn (when the availability of re-

sources was higher), the marten exploited small arboreal berries. Their more arboreal habits and smaller size could help the mustelid to climb bushes. This has been suggested as a possible adaptation of space segregation in order to avoid competition between the fox and the marten and also for other carnivores in areas of diet overlap (ROSENZWEIG 1966; SERAFINI and LOVARI 1993; GIL-SÁNCHEZ 1998).

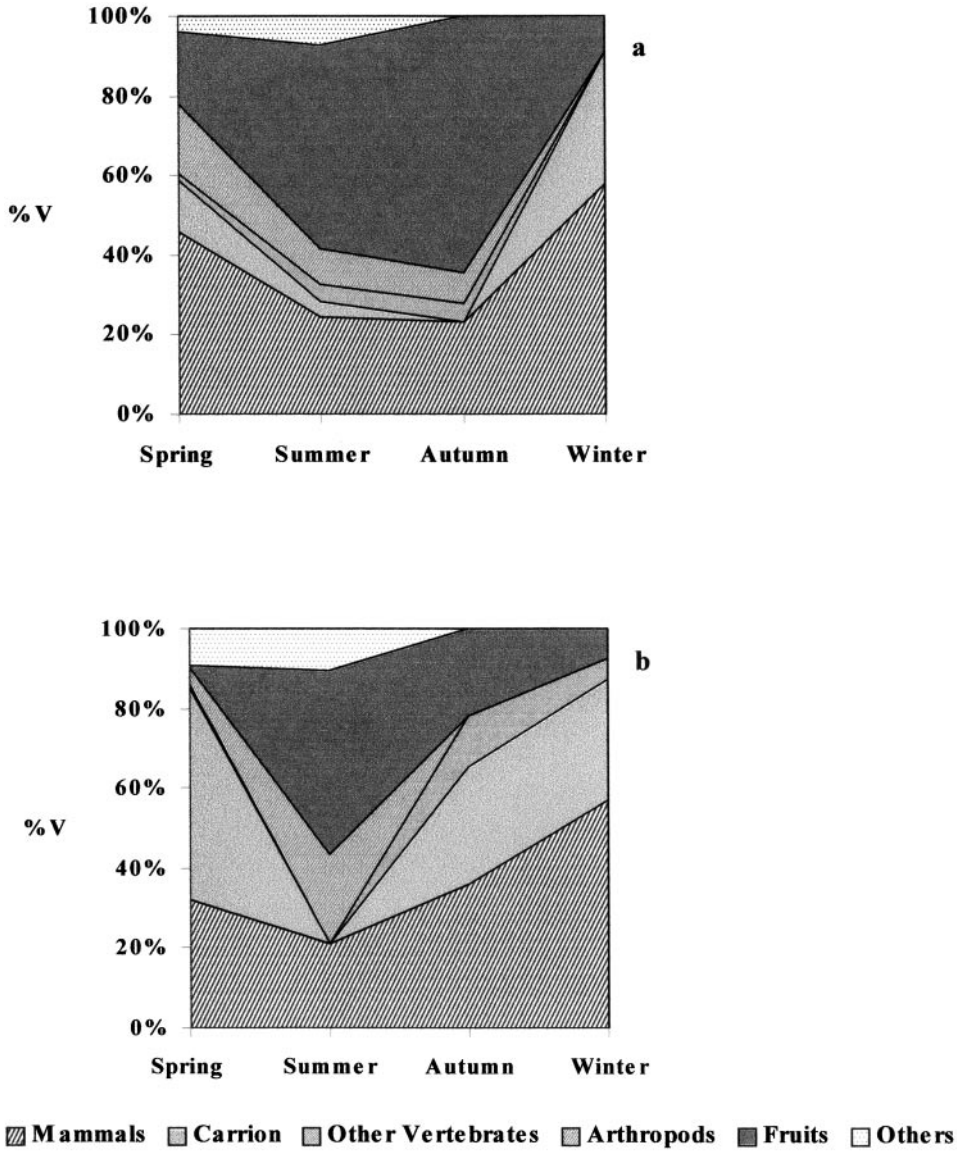

Fig. 1. a) Percentage of stimate volume (%V) in the scats of stone marten (*Martes foina*) for different prey categories and seasons in a mesic mountain habitat; b) percentage of stimate volume (%V) in the scats of red fox (*Vulpes vulpes*) for different prey categories and seasons in a mesic mountain habitat.

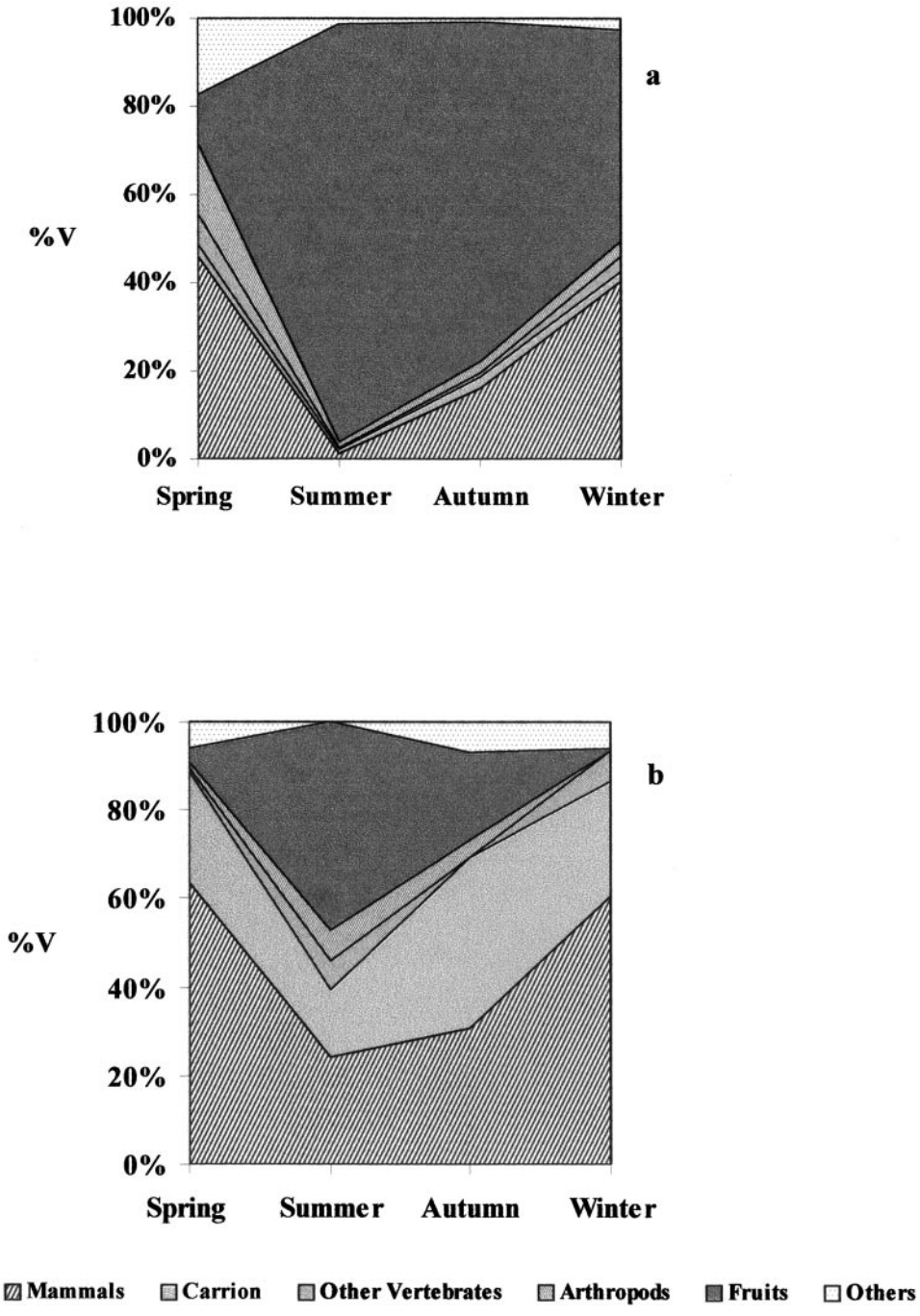

Fig. 2. a) Percentage of stimate volume (%V) in the scats of stone marten (*Martes foina*) for different prey categories and seasons in a xeric mountain habitat; b) percentage of stimate volume (%V) in the scats of red fox (*Vulpes vulpes*) for different prey categories and seasons in a xeric mountain habitat.

During this study, marten remains were detected in the fox scats on six occasions (two in the mesic and four in the xeric habitat). All were found in spring or summer and could be cases of asymmetric intraguild predation (PALOMARES and CARO 1999). The fox can be an important limiting factor for small mustelid populations (MULDER 1990), and this also seems to occur with the pine marten (LINDSTRÖM et al. 1995).

Regarding the trophic niche overlap and the possible competition between the fox and the marten we can conclude that: (1) the habitat conditions notably influenced the diet overlap; (2) these variations could be caused by the seasonal availability of small fruit (mainly berries), more profitable for the marten than for the fox; (3) the competition between both species could be possible although it would not be a decisive factor in the distribution of these two species.

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Zusammenfassung

Ernährungsgewohnheiten und Überlappungen bei Rotfuchs (*Vulpes vulpes*) und Steinmarder (*Martes foina*) in zwei mediterranen Gebirgslebensräumen

Die Nahrungsgewohnheiten von Rotfuchs und Steinmarder, zwei opportunistische Carnivoren, sind in zwei mediterranen Gebirgslebensräumen (mesisch und xerisch) in einer Studie verglichen worden, die von April 1997 bis März 1998 im Sierra-Nevada-Nationalpark (im SO von Spanien) ausgeführt wurde. Die Analyse von Exkrementen hat eine sehr hohe interspezifische Nahrungsüberlappung für den mesischen Lebensraum ergeben. Im xerischen Lebensraum waren die Unterschiede größer und die Überlappung schwächer. Jahreszeitlich bedingte Variationen existierten im Grad der Überlappung und erreichten im Winter ihr höchstes Niveau im mesischen Lebensraum und im Frühling im xerischen Lebensraum. Die Ergebnisse zeigten, daß die Verfügbarkeit von Nahrung in jedem Lebensraum eine wichtige Größe in der Entstehung der Divergenz in der jeweiligen Nahrungszusammensetzung war, so daß im mesischen Lebensraum Konkurrenz möglich aber nicht wichtig genug war, um eine Lebensraumtrennung zu verursachen. Der Marder schien die anpassungsfähigere Spezies zu sein, wahrscheinlich wegen seiner geringeren Größe und der Gewohnheit, in Bäumen zu klettern, die es ihm erlaubt, Früchte zu nutzen, die für den Fuchs nicht sehr profitabel wären. Die Nahrung des Fuchses setzte sich in beiden Lebensräumen aus kleinen Säugetieren, Aas und Früchten zusammen (Kaninchen waren auch im xerischen Lebensraum jahreszeitlich bedingt). Die Breite der Nahrungsnische des Fuchses war im mesischen Lebensraum höher. Der Vergleich zwischen den Lebensräumen wies große Unterschiede in der Nahrung des Marders auf. Im xerischen Lebensraum bestand die Nahrung des Marders aus kleinen Säugetieren und Früchten von *Juniperus phoenicea*, *Morus ulmifolius* und *Amelanchier ovalis*, während sie im mesischen Lebensraum der des Fuchses sehr ähnlich war. Die Breite der Nahrungsnische war im xerischen Lebensraum höher als im mesischen. Die Lebensraumbedingungen beeinflußten die Nahrungsüberschneidung auffallend, wobei die Unterschiede vor allem aus der unterschiedlichen Verfügbarkeit kleiner Früchte resultierte.

References

Amores, F. (1975): Diet of the red fox (*Vulpes vulpes*) in the western Sierra Morena (South Spain). Doñana, Acta Vert. **2**, 221–239.

Amores, F. (1980): Feeding habits of the stone marten, *Martes foina* (Erxleben, 1777), in Southwestern Spain. Säugetierkundl. Mitt. **28**, 316–322.

Andalucía, E. D. (1992): Atlas básico de Andalucía. Granada: Ed. Andalucía.

Aymerich, M. (1982). Etude comarative de régimenés alimentaires du lynx pardelle (*Lynx pardina* Temmick, 1824) et du chat forestier (*Fells silvestris* Schreber, 1777) au centre de la péninsule Ibérique. Mammalia **46**, 515–521.

Ciampalini, B.; Lovari, S. (1985): Food habits and trophic niche overlap of the badger (*Meles meles* L.) and the red fox (*Vulpes vulpes* L.) in a Mediterranean coastal area. Z. Säugetierkunde **50**, 226–234.

Delibes, M. (1978): Feeding habits of the stone marten, *Martes foina* (Erxleben, 1777), in northern Burgos, Spain. Z. Säugetierkunde **43**, 282–289.

Delibes, M. (1983): Interspecific competition and the habitat of the stone marten (*Martes foina* Erxleben, 1777) in Europe. Acta Zool. Fennica **74**, 229–231.

Fedriani, J. M. (1996): Dieta anual del zorro, *Vulpes vulpes*, en dos hábitats del Parque Nacional de Doñana. Doñana Acta Vert. **23**, 143–152.

Fedriani, J. M.; Palomares, F.; Delibes, M. (1999): Niche relations among three sympatric Mediterranean carnivores. Oecologia **121**, 138–148.

Frafjord, K. (2000): Do artic and red foxes compete for food? Z. Säugetierkunde **65**, 350–359.

Gil-Sánchez, J. M. (1996): Dieta de la garduña (*Martes foina* Erxleben, 1777) en una localidad de las Sierras Subbéticas de Granada (Sureste de España). Doñana Acta Vert. **23**, 83–90.

Gil-Sánchez, J. M. (1998): Dieta comparada del gato montés (*Felis silvestris*) y la jineta (*Genetta genetta*) en un área de simpatría de las Sierras Subbéticas (SE España). Misc. Zool. **21**, 57–64.

Herrera, C. M. (1989): Frugivory and seed dispersal by carnivorous mammals and associated fruit characteristics, in undisturbed Mediterranean habitats. Oikos **55**, 250–269.

Hersteinsson, P.; Macdonald, D. W. (1992): Interspecific competition and the geographical distribution of red and artic foxes *Vulpes vulpes* and *Alopex lagopus*. Oikos **64**, 505–515.

Kauhala, K.; Laukkanen, P.; Von Rége, I. (1998): Summer food composition and food niche overlap of the raccon dog, red fox and badger in Finland. Ecography **21**, 457–463.

Levins, R. (1968): Evolution in Changing Habitats. Princeton: Princeton Univ. Press.

Lindström, E. R.; Brainerd, S. M.; Helldin, J. O.; Overskaug, K. (1995): Pine marten – red fox interactions: a case of intraguild predation? Ann. Zool. Fennici **32**, 123–130.

Morillo, C.; Gómez-Campo, C. (2000): Conservation in Spain 1980–2000. Biol. Conserv. **95**, 165–174.

Mulder, J. L. (1990): The stoat *Mustela erminea* in the Duch dune region, its local extintion, and possible cause: the arrival of the red fox *Vulpes vulpes*. Lutra **33**, 1–21.

Palomares, F.; Ferreras, P.; Delibes, M.; Fedriani, J. M. (1996): Spatial relationships between iberian lynx and other carnivores in an area of southwestern Spain. J. Appl. Ecol. **33**, 5–13.

Palomares, F.; Caro, T. M. (1999): Interspecific killing among mammalian carnivores. Am. Nat. **153**, 492–508.

Pianka, E. R. (1973): The structure of lizard communities. Ann. Rev. Ecol. Syst. **4**, 53–74.

Pianka, E. R. (1988): Evolutionary Ecology. New York: Harper and Row.

Polis, G. A.; Myers, C. A.; Holt, R. D. (1989): The ecology and evolution of intraguild predation: potential competitors that eat each other. Annu. Rev. Ecol. Syst. **20**, 297–230.

Putman, R. J. (1984): Facts from faeces. Mammal Rev. **14**, 79–97.

Reig, S. (1992): Geographic variation in pine marten (*Martes martes*) and beech marten (*Martes foina*) in Europe. J. Mammalogy **73**, 744–769.

Reig, S.; Jedrzejewski, W. (1988): Winter and early spring food of some carnivores in the Bialowieza National Park, Eastern Poland. Acta Theriol. **33**, 57–65.

Reynolds, J. C; Aefbischer, N. J. (1991): Comparison and qualification of carnivores diet by faecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. Mammal Rev. **21**, 97–122.

Rosenzweig, M. L. (1966): Community structure in sympatric carnivora. J. Mammalogy **47**, 602–612.

Schoener, T. W. (1982): The controversy over interespecific competition. Am. Sci. **70**, 586–595.

SERAFINI, P.; LOVARI, S. (1993): Food habits and trophic niche overlap of the red fox and the stone marten in a Mediterranean rural area. Acta Theriol. **38**, 233–244.

SIDOROVICH, V. E.; POLOZOV, A. G.; LAUZHEL, G. O.; KRASKO, D. A. (2000): Dietary overlap among generalist carnivores in relation to the impact of the introduced raccon dog *Nyctereutes procyonides* on native predators in northern Belarus. Z. Säugetierkunde **65**, 271–285.

WHITE, P. J.; RALLS, K.; GARROTT, R. A. (1994): Coyote-kit fox interactions as revealed by telemetry. Can. J. Zool. **72**, 1831–1836.

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