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Seasonal variation in diet and trophic niche of the Red fox in an Alpine habitat

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Abstract

The diet and trophic niche breadth of the fox (*Vulpes vulpes*) were studied in a high-elevation Alpine ecosystem to determine their monthly variations. The analysis of 270 faeces showed that the fox used all the potential resources present in its habitat: of total diet, small mammals were the most frequent food category, but Orthoptera and marmots were also very important. Correlations between diet and weather variables suggested a seasonal shift in diet. From June to November foxes preyed mainly on insects and marmots, whereas ungulates, Lagomorpha, garbage and earthworms were eaten more often from December to May. These changes appeared related both to seasonal differences in food availability and to the presence of alternative preferred foods. Trophic niche was wide during the entire year, with a moderate increase in winter–spring when the absence of some main prey types forced the fox to exploit a larger range of items.

Introduction

The adaptable behaviour of the red fox has enabled it to colonize a variety of habitats, including those typically montane (Macdonald 1987). Although the fox is probably the most common carnivore in the Alps, only two recent studies (Cantini 1991; Storch and Kleine 1991) have dealt with the diet of the fox in the Alpine region, and both were carried out at elevations between 300 and 1700 m. The diet of the fox in the highest part of its altitudinal distribution in Europe has been locally investigated only by Leinati et al. (1960).

Montane ecosystems are strongly seasonal in terms of climate and productivity. Given the opportunistic feeding habits of the fox (e. g. Englund 1965; Goszczynski 1986; Calisti et al. 1990), it can be expected that its diet in the Alps would largely reflect the seasonal changes in food availability.

Our study area, in the Italian Western Alps, is frequented by at least 370 Alpine chamois (*Rupicapra rupicapra*) (minimum density: 10 individuals/km^2), about 20 Alpine ibex (*Capra ibex*), at least 25 roe deer (*Capreolus capreolus*) and 5–15 red deer (*Cervus elaphus*). Furthermore, although no estimates are available, the study area supports wild boars (*Sus scrofa*) and dense populations of Alpine marmot (*Marmota marmota*) and insects (mainly Orthoptera). The results of the research conducted in the Alps by Leinati et al. (1960) showed that ungulate carrion, especially in late winter, and marmots, in summer, are well represented in the fox diet in the Alps, but did not include Orthoptera among the most important food items. Nevertheless, since strong predation on Orthoptera has been reported in other habitats (Calisti et al. 1990 for a review), we expected that the local abundance of marmots and Orthoptera would largely influence the diet of the fox in the months when they are available. The densities of small mammals in the study area were not known, but they can also be a main component of the fox diet, as found in northern highly seasonal habitats (Lindström 1989).

The aim of this paper is to present a picture of the seasonal variation of the fox trophic niche in a typical Alpine ecosystem. We were particularly interested in determining the extent of fox predation on marmot and Orthoptera and in documenting the use of ungulate carcasses.

Study area

The study area in the Western Italian Alps, about 80 km west of Torino, comprises the Val Troncea Natural Park (3280 ha) and the small part of the homonymous valley at lower altitude outside the park boundaries. Elevation ranges from 1560 m to 3280 m a. s. l. Topography, vegetation and climate of the valley are typically Alpine. Precipitation peaks in spring and autumn, while winter is characterised by 4–6 months of permanent snow cover and low temperatures. Mean annual temperature is about 8 °C (Fig. 1). Larch (*Larix decidua*) forests and pastures cover the slopes to about 1900–2100 m, while Alpine meadows are prevalent at higher altitudes. At the end of the valley lies a small tourist village, inhabited mainly during summer and Christmas holidays. Many tourists visit the park from May to August.

Material and methods

From May 1990 to June 1991, 3–4 monthly collections of faecal samples were made at elevations between 1560 and 2850 m. In a total of 46 excursions on foot or skis 270 faeces were collected (sample size: May: 4; Jun: 25; Jul: 16; Aug: 18; Sep: 44; Oct: 23; Nov: 31; Dec: 7; Jan–Feb: 16; Mar: 26; Apr: 15; May 1991: 22; Jun 1991: 23). On the two trails followed each month, all scats were collected; outside these trails, only obviously fresh samples were collected. Scats were stored in polythene bags and frozen at −20 °C, to be thawed later and analysed as described in Kruuk and Parish (1981), Ciampalini and Lovari (1985) and Calisti et al. (1990). To allow comparisons with other studies, results are reported as percentage of occurrence (number of occurrence of each food/total number of occurrences × 100) (Cavallini and Lovari 1991), percent frequency of occurrence (number of occurrence of each food/number of faeces × 100), and percentage of volume (estimated volume of each food/total estimated volume × 100) (Kruuk and Parish 1981). In February we only found two scats, therefore we pooled data for January and February. In winter, frequent snowfalls often prevented faecal collections, both by limiting the movements of the foxes and rapidly covering tracks and scats (Patalano and Lovari 1993). As a result, more faecal samples were found during summer–autumn. In the evaluation of the total yearly diet, scats collected in May 1990 and June 1991 were excluded so that each month would be represented only once. The total percentages of occurrence and volume were computed as means of monthly values.

A standardized index of trophic niche breadth (B_{sta}) (Colwell and Futuyma 1971) was calculated from both percentages of occurrence and percentages of volume. The index has the formula $B_{sta} = B-1/B_{max}-1$, where B is the Levins' index of niche breadth (Levins 1968) and B_{max} is the total number of food categories recognized. B_{sta} values can range between 0 (minimum niche breadth) and 1 (maximum niche breadth).

The availability of Orthoptera was estimated by direct counts of the number of individuals seen along two fixed transects (100 m each) (Cavallini and Lovari 1991). One transect was located in pastures at 1900 m, the other in Alpine meadows at 2200 m.

To identify seasonal variations in consumption of the main food categories, Spearman rank correlations (Siegel 1956) were performed between percentages of occurrence and volume and climatic variables (Calisti et al. 1990; Cavallini and Lovari 1991). Differences between summer–autumn and winter–spring diets were tested with a G-test of independence (Sokal and Rohlf 1981) on the occurrences (expressed as frequencies of scats where the category was found over the total number of scats) and with Mann-Whitney U-test (Sokal and Rohlf 1981) on volumes. Values of p less than 0.05 were considered significant.

Results

Diet

In the total diet, the most frequent and abundant prey remains were of small mammals (mainly Arvicolidae, followed by Muridae) (Tab. 1), with little seasonal variation (Fig. 2). Orthoptera, which were only available from June to November (Fig. 1) and consumed mainly from August to November (Fig. 2), were nevertheless the second most important

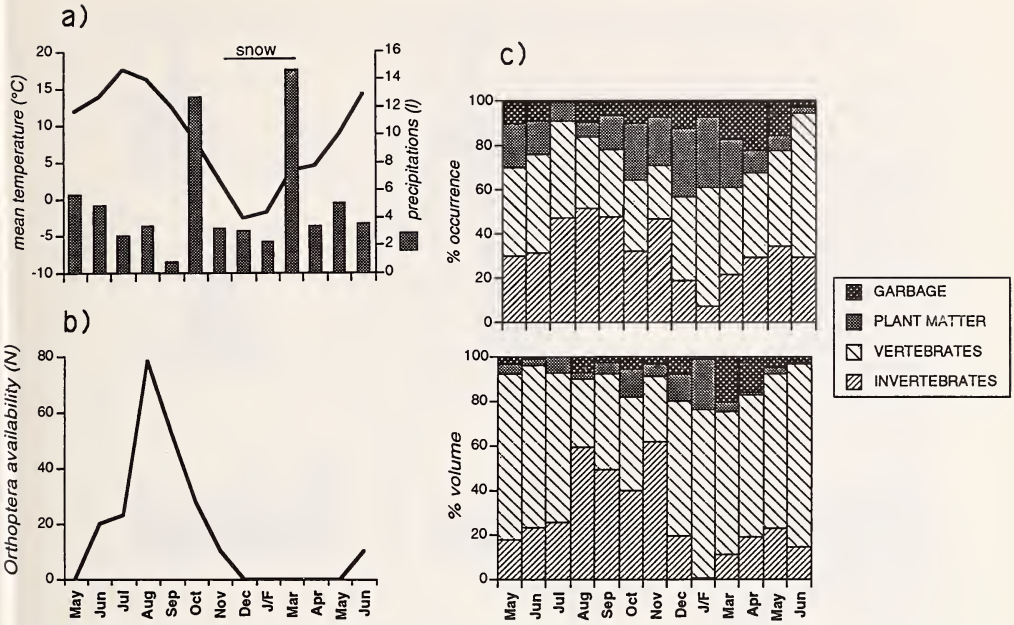

Fig. 1. Monthly changes of: a) Mean temperature and precipitation in the study area; b) Orthoptera availability in the study area; c) Percent occurrence and volume of the main groups of food categories in the diet of the red fox in Val Troncea

category in the annual diet (Tab. 1). Alpine marmots (often young individuals) and wild ungulates (mostly carcasses of Alpine chamois and roe deer, but also some young of roe deer and wild boar) were the only other items accounting for more than 10 % of total volume, but their occurrences were remarkably lower (Tab. 1). The presence of marmot in the diet showed a peak in June–July, whereas that of ungulates was higher in January–February than in the rest of the year (Fig. 2). Coleoptera remains were found in all months except December (Fig. 2). They were eaten very often but usually in small amounts (Tab. 1; Fig. 2). A similar discrepancy between occurrences and volumes was shown by Lepidoptera larvae and earthworms (Tab. 1). As a whole, fruits were found in almost 15 % of the scats and composed 4.5 % of the annual volume, but the main kind of fruits eaten by the fox (*Rosa* sp. fruits) did not reach 3 % of the volume (Tab. 1). More important was the role of garbage, which was present in 21 % of all the scats with a total volume of 6.6 % (Tab. 1). Birds (mainly Passeriformes) and Lagomorpha (mainly mountain hare, *Lepus timidus*) were seldomly consumed by foxes in the Troncea valley (Tab. 1).

Overall, vertebrates composed the bulk of the diet (38.2 % occurrence and 56.2 % volume; see also Fig. 1). The seasonal pattern of use of this food source was rather constant, with a moderate decrease during summer (Fig. 1). Invertebrates (33.3 % occurrence and 30 % volume) showed the opposite trend, decreasing markedly during winter (Fig. 1). Plant matter and garbage were taken mainly in winter and early spring, respectively (Fig. 1).

Correlations

In most cases, correlations between diet and main climatic variables confirmed the seasonality described above for some food categories (Tab. 2). Coleoptera consumption was inversely correlated to snow cover (percentage of days with snow-covered ground) and directly to mean temperature. The presence of marmot in diet showed the same kind of

Table 1. **Annual diet composition of the red fox in the Val Troncea Natural Park**
(n = 243 faecal samples)

Food items	% freq. occ.	% occ.	% vol.
Coleoptera	29.6	10.5	5.3
Orthoptera	42	12.9	16.7
Dermaptera	4.9	1.6	0.4
Coleoptera larvae	1.7	0.7	0.7
Lepidoptera larvae	15.6	4.8	2.6
Diptera larvae	3.7	1.1	0.7
Earthworms	18.5	7.3	3.7
Other invertebrates	0.8	0.2	0.1
Small mammals	44.4	17.1	21.6
Marmots	18.1	6.3	12.7
Lagomorpha	4.5	1.8	3.2
Ungulates	12.4	5.7	11.6
Other mammals	3.7	1.7	2.5
Birds	9.9	3.9	3.7
Reptiles	1.7	0.8	0.9
Amelanchier ovalis fruits	2.1	0.8	0.2
Rubus sp. fruits	2.1	0.8	1.0
Rosa sp. fruits	6.2	3.1	2.4
Other fruits	4.1	1.6	0.9
Other plant matter	24.3	9.1	2.8
Garbage	21.0	8.3	6.6
B_{sta}		0.50	0.37

B_{sta}: standardized trophic niche breadth index (see text).

Table 2. **Correlations, on a monthly basis, of food categories in diet with mean temperature (°C), precipitations (ml) and snow cover (% days with snow-covered ground)**
(n = 13 months)

Food items		Mean temp.		Precipitations		Snow cover	
		r_s	p	r_s	p	r_s	p
Coleoptera	freq. occ.	0.835	**	0.271	0.35	−0.621	*
	occ.	0.896	**	0.202	0.48	−0.615	*
	vol.	0.732	0.17	0.396	AS	−0.474	0.17
Marmots	freq. occ.	0.865	**	0.514	AS	−0.538	AS
	occ.	0.865	**	0.544	AS	−0.514	AS
	vol.	0.849	**	0.56	*	−0.514	AS
Ungulates	freq. occ.	−0.46	0.11	−0.235	0.42	0.452	0.12
	occ.	−0.42	0.15	−0.262	0.36	0.435	0.13
	vol.	−0.427	0.14	−0.161	0.58	0.386	0.18
Fruits	freq. occ.	−0.202	0.48	−0.312	0.28	0.556	*
	occ.	−0.521	AS	−0.284	0.32	0.689	*
	vol.	−0.606	*	−0.327	0.26	0.713	*

AS = almost significant ($0.10 > p > 0.05$); * = $p < 0.05$; ** = $p < 0.01$.

correlations as Coleoptera and a tendency to increase with precipitation. Fruits were eaten more frequently during cold and snowy months than during the rest of the year. This seemed also to be the case for ungulates, but significance was not reached. No trend was shown by Orthoptera, small mammals and garbage. Use of Orthoptera increased together with their estimated availability (occurrence: $r_s = 0.570$, $p < 0.05$; frequency of occurrence:

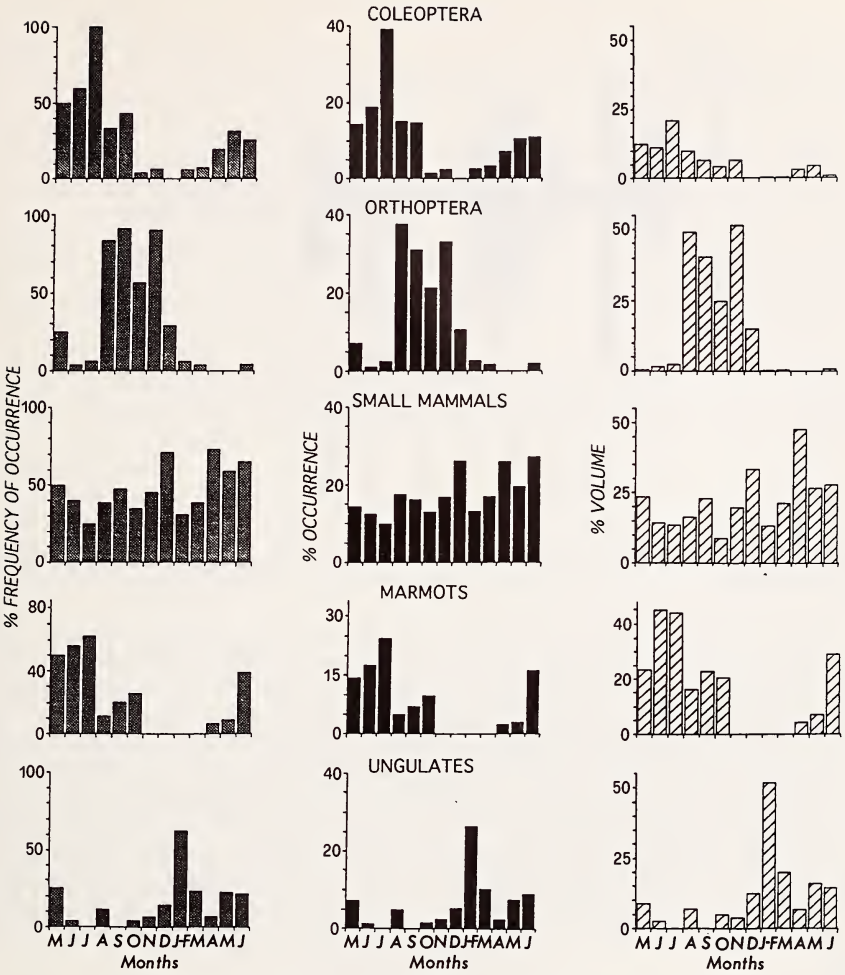

Fig. 2. Monthly variation of the main food categories in the red fox diet

$r_s = 0.587$, $p = 0.05$; volume: $r_s = 0.747$, $p = 0.01$; $n = 13$ months). No seasonal pattern was found for the variation of trophic niche breadth (B_{sta} values; in occurrences, May: 0.358; Jun: 0.374; Jul: 0.167; Aug: 0.19; Sep: 0.252; Oct: 0.433; Nov: 0.234; Dec: 0.267; Jan–Feb: 0.315; Mar: 0.369; Apr: 0.306; May 1991: 0.361; Jun 1991: 0.129; in volumes, May: 0.141; Jun: 0.153; Jul: 0.14; Aug: 0.122; Sep: 0.153; Oct: 0.323; Nov: 0.11; Dec: 0.228; Jan–Feb: 0.109; Mar: 0.256; Apr: 0.133; May 1991: 0.298: Jun 1991: 0.196) and no significant correlation between it and the monthly percentages of the main food categories or the number of scats collected each month.

Seasonality

Two main periods were distinguished in the diet of the fox in the study area on the basis of its monthly variation and the correlations shown by the main food categories (Fig. 3). From June to November foxes ate more insects (Orthoptera: occurrence G = 91, $p < 0.001$; volume Z = −2.37, $p < 0.05$; Coleoptera: occurrence G = 19.8, $p < 0.001$; volume Z

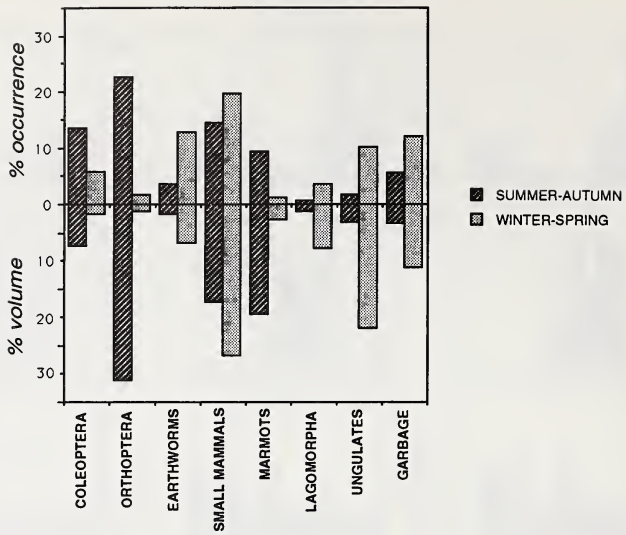

Fig. 3. Percent occurrence and volume of the main red fox food categories in summer–autumn and winter–spring diets

= −2.01, $p < 0.05$) and marmots (occurrence G = 23.4, $p < 0.001$; volume Z = −1.73, $p < 0.08$) than from December to May. Conversely, ungulates (occurrence G = 24.4, $p < 0.001$; volume Z = −2.56, $p < 0.05$), Lagomorpha (occurrence G = 6.6, $p = 0.001$; volume Z = −1.1, $p = 0.27$) garbage (occurrence G = 26.9, $p = 0.001$; volume Z = −1.46, $p = 0.14$) and earthworms (occurrence G = 19.4, $p < 0.001$; volume Z = −1.55, $p = 0.12$) appeared to be more frequent in winter–spring than in summer–autumn. Small mammals did not show significant seasonal differences (occurrence G = 2.4, $p = 0.06$; volume Z = −1.64, $p = 0.10$).

The winter–spring diet was dominated by mammals (62.8 % volume; see also Fig. 3). Nevertheless, the trophic niche appeared to be larger in this period (occurrence B_{sta} = 0.489; volume B_{sta} = 0.316) than in summer–autumn (occurrence B_{sta} = 0.372; volume B_{sta} = 0.234), although the difference did not reach significance (T-test: t = 5.7, $n = 2$, p = 0.055).

Discussion

Our data show that the fox can use all the potential sources of food present in its habitat. Small mammals, Orthoptera, marmots and ungulates supplied the fox with protein-rich food items. In particular, our results suggest that, as could be expected on the basis of their qualitative analysis (Cavani 1991), Orthoptera can be an important food resource not only in warm Mediterranean habitats (Calisti et al. 1990), but also in elevated Alpine regions (see also Patalano and Lovari 1993, for the Italian Apennines). In a similar area, Leinati et al. (1960) found a greater presence of vegetables and ungulate carrions and a lower existence of invertebrates in the fox diet. These differences are likely to be related to the local variation of food availability and also to the inclusion of lower-altitude ranges in the study area of Leinati et al.

In our study area, the diet of the fox reflected the alternation of two main seasons typical of the montane ecosystems (Patalano and Lovari 1993). As shown for Orthoptera (see the correlations between availability and consumption), the temporal variation in feeding habits was likely to be mainly determined by the availability of different food

resources (Doncaster et al. 1990; Cavallini and Lovari 1991). For example, insects and marmots are unavailable in winter, and were present almost exclusively in the summer–autumn diet. As could be expected, the winter peak in mountain ungulate mortality (e. g. Geist 1971; Festa-Bianchet 1989) was reflected by an increase of this item in winter diet. The higher percentage of earthworms in the cold season may appear surprising. Actually, the use of this food was concentrated in the months between March and May, the only months when soil temperature and humidity were probably high enough to permit frequent earthworm activity on the ground (Kruuk and Parish 1985; Lambert 1990). Therefore, the variation in the consumption of this invertebrate may also be explained by that of its availability. On the other hand, the increased use of certain food categories in winter–spring would confirm the influence of the availability of alternative food resources on the feeding behaviour of an opportunistic carnivore, as suggested by Weckwerth and Hawley (1962). In our study area, garbage is mostly available during the summer months, when tourists are numerous. Nevertheless, rubbish remains were found in the scats mainly in winter. During this season important food items (i. e. insects and marmots) were absent and the fox exploited other resources, less preferred (i. e. garbage) or difficult to obtain (i. e. Lagomorpha).

The seasonality of the diet was not clearly reflected by the trophic niche size, as found in other areas (Calisti et al. 1990). If the number of scats collected each month is not large enough to be representative of the diet, the monthly value of niche breadth index might be influenced by sample size. No evidence of such a relation was found (correlations between B_{sta} values and monthly number of scats collected were far from significant) (Iriarte et al. 1990). Prigioni (1991) reviewed studies of fox diet in Italy and calculated for them an index of trophic niche breadth on a reduced number of main categories. The application of the same method shows that, in our study area, the fox has a very wide trophic niche. These findings could suggest that the lack of correlation between trophic niche breadth and climatic variables in our study might have been more correctly related to its large breadth (cf. Calisti et al. 1990) than to uncorrect sampling. In the Troncea Valley, the fox had a varied diet in each period of the year, with a moderate widening of the trophic niche during winter–spring. This variation was likely due to the increased presence in the diet of "secondary" items (e. g. garbage, fruits, Lagomorpha) in cold months, when some main food categories are absent and the fox is forced to exploit a larger array of items to meet its nutritional requirements.

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Zusammenfassung

Saisonale Variabilität von Nahrung und trophischer Nische beim Fuchs in alpinem Habitat

Mit dem Ziel, die monatliche Variabilität zu bestimmen, untersuchten wir die Nahrungswahl und die trophische Nische des Fuchses (*Vulpes vulpes*) in höheren alpinen Stufen. Die Analyse von 270 Exkrementen zeigte, daß sämtliche in diesem Habitat vorhandenen Nahrungsquellen genutzt wurden. In der gesamten Nahrung waren Kleinsäuger die am häufigsten gefundene Nahrungskategorie, gefolgt von Orthopteren und Murmeltieren. Korrelationen zwischen Nahrung und Klimavariablen wiesen auf einen saisonbedingten Wechsel in der Nahrungswahl hin. Von Juni bis November erbeuteten die Füchse hauptsächlich Insekten und Murmeltiere, während von Dezember bis Mai häufiger Ungulaten, Lagomorphen, Abfälle und Regenwürmer gefressen wurden. Dieser Wechsel scheint sowohl mit saisonalen Unterschieden in der Verfügbarkeit von Futter als auch mit dem Angebot an bevorzugter Alternativnahrung zusammenzuhängen. Die trophische Nische war während des ganzen Jahres breit und zeigte eine leichte Ausweitung im Winter und Frühjahr, wenn das Fehlen einiger Hauptbeuten die Füchse veranlaßte, ein breiteres Nahrungsangebot zu nutzen.

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