VARIATION IN THE DIET OF THE RED FOX
IN A MEDITERRANEAN AREA

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INTRODUCTION

The red fox *Vulpes vulpes* has one of the largest geographic range of all land mammals (excluding man and its commensals) ; its diet has been studied in many areas, mainly in Europe and North America (see Artois, 1989, for a review). The emerging pattern is an extreme variability : main food items range from small mammals (e.g. Yoneda, 1982) to rabbits (e.g. Reynolds, 1979), to fruits and insects (e.g. Ciampalini & Lovari, 1985), to earthworms (Macdonald, 1980), to garbage (e.g. Saunders *et al.*, 1993). Opportunism and ability to track variation in food availability are characteristic of this species (Cavallini & Lovari, 1991). It is unclear, however, whether this variability derives from differences among classes of individuals (e.g. males having different diet from females, as it has been hypothesized for mustelids ; Giuliano *et al.*, 1989 ; King, 1989, or larger individuals selecting larger prey) or from changes in the feeding behaviour of the whole population.

Not all the possible sources of variability in fox diet have received the same attention by researchers : whereas seasonal variation has been quantified since the first studies (Errington, 1935 ; Hamilton, 1935 ; Scott, 1943), local variation has more rarely been addressed, though studies in neighbouring areas have shown that it may be large (e.g. Cavallini & Lovari, 1991 ; Lovari *et al.*, 1994). The difference in diet between sexes, ages and individuals of different body size or body condition been have been tested even more rarely.

Aims of this paper are therefore : (1) to describe the diet of the red fox in a Mediterranean area ; (2) to evaluate statistically the importance of several possible sources of variation in diet (seasonal, local, sexual, and related to age, body condition, and body size) ; a corollary aim of this study is (3) to understand the role of grass and other vegetable matter (often classified as non-food items) ; it has been hypothesized that grass is ingested either for medicinal purposes (anti-parasite) or accidentally, during the hunting or harvesting of other items (e.g. Fairley, 1970).

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STUDY AREA

The Pisa province, in Central Italy, (43° N, 10-11° E ; 52 km E-W by 75 km N-S ; 2448 km^2) is mostly flat and intensively cultivated (mainly cereals) in the North, becoming increasingly hilly (up to 800 m a.s.l.) and wooded towards the South. Main cultivated fruits in the area are olives and grapes ; isolated cherry and peach trees are present throughout the area, but small plantations are common in the internal valleys. The climate is Mediterranean, with mild winters and dry, hot summers. In 1992, minimum temperatures (monthly average) ranged from 3.4 °C to 19 °C, and maximum temperatures from 12 °C to 31 °C. Monthly means were below 10 °C for 3 months, and above 20 °C for 4 months. Rainfall is heavier in autumn (35.9 % of total rainfall), in winter (28.9 %) and in spring (23.7 %), whereas only 11.5 % of total rain occurs during summer. Interannual variation is large : in 1992, the least rainy months (less than 20 mm of rain per month) were January, February, March, August, and May (in increasing order ; Cavallini, 1994b). Based on the overall similarity among smaller administrative units (communes), the study area was subdivided in 4 sections (Cavallini, 1994b ; in north to south order) : (1) a coastal belt (500 km^2), flat, with very high human population (> 400 km^{-2}), scarce woodlands (20 % of total area) and large cultivated areas (> 50 %) ; (2) internal valleys (713 km^2), mostly flat, with high human population (> 200 km^{-2}), scarce woodlands (22 %) and large cultivated areas (> 50 %) ; (3) coastal hills (412 km^2 ; up to 400 m a.s.l.) with low population (36 km^{-2}), more even percentages of woodlands (38 %) and cultivated fields (45 %) ; (4) southern hills (823 km^2), higher (up to 800 m a.s.l.), with the lowest population density (33 km^{-2}), the highest proportion of wooded areas (51 %) and least cultivated fields (33 %). Isolated high hills (Monti Pisani ; up to 980 m a.s.l.) were present in the North of the area. For some analyses, I aggregated sections 1 and 2 (hereafter « north »), and sections 3 and 4 (hereafter « south »). The areas selected for faeces collection were : two on the coastal belt (Vecchiano and Coltano) ; one on the Monti Pisani ; two on the internal valleys (Lucagnano and Collebrunacchi) ; two on the coastal hills (S. Luce and Laiatico) ; and two on the southern hills (Berignone and Rio-Arbiaia). Foxes were hunted (up to 1 fox per km^2) in all areas except Berignone (a protected reserve) and Monti Pisani (where they were shot only occasionally ; Cavallini, 1994b). Fox density was highest in these two areas (Cavallini, 1994a). Most areas (6 of 9) were dominated by grassland (mainly cultivated), whereas Berignone, Monti Pisani and Lucagnano were more wooded (for the location and the habitat composition of the areas, see Cavallini, 1994a).

MATERIAL AND METHODS

We analysed both gut contents and faecal material, because the two methods are not entirely comparable (Cavallini & Volpi, 1995). Hunters collected foxes in the whole province from January to the beginning of May 1992, during the main fox hunting season. We collected foxes from hunters within 6 hours of death and stored them in plastic bags in a refrigerator cell (48 hours, -2 °C) until dissection (within 2 days from refrigeration). We removed the entire gut (from oesophagus to rectum) and stored it in a deep-freeze (-20 °C) until processing. We analysed separately stomachs and intestines. We collected faeces monthly for one year in 9

areas uniformly distributed in the study area (see « Study area ») and stored them in a deep-freeze until processing. Gut contents and faeces were filtered with a 1 mm sieve and macroscopically sorted out into categories. We examined the sediment for earthworm chetae (Kruuk & Parish, 1981). Gut contents were also weighed. Parasites (mainly Cestoda worms) abundance in the intestines was recorded on a 0-2 scale (absent, 1 - 10, > 10 worms). We microscopically analysed hairs and feathers (Day, 1966 ; Debrot *et al.*, 1981), and classified other items to lowest taxonomic level possible by comparison with reference material (Museum of Natural History of Livorno and samples collected by us). Food items were later aggregated in the following categories : small mammals, large wild mammals, domestic mammals, wild birds, domestic birds, eggs, other vertebrates (including reptiles, amphibians, and fishes), Coleoptera, Orthoptera, other insects, other arthropods, other invertebrates, wild fruits, cultivated fruits, other plant matter (grass and leaves), refuse. We aggregated several categories in some higher-level groups : vertebrates (including all mammals, all birds, eggs, and other vertebrates), mammals, birds (including eggs), invertebrates (including Coleoptera, Orthoptera, other insects, other arthropods, and other invertebrates), plants (wild fruits, cultivated fruits, other plant matter), anthropogenic matter (domestic mammals, domestic birds, cultivated fruits, and refuse). Several categories presented problems of identification : the distinction between wild and domestic mammals (mainly based on colour of remains) was sometimes unclear ; domestic mammals and birds were classified as refuse if they obviously came from garbage (e. g. large pieces of pig fat, or the skin of a domestic rabbit), but in faeces such distinction was often difficult. We included amorphous matter (deriving from fully digested material such as meat or fat) in refuse when no hair of large mammals was present. Lagomorphs have been discriminated in rabbits and hares by examining the hair scale pattern (Reynolds & Aebischer, 1991). In our area, such distinction was not always reliable (pers. obs.). We therefore pooled the two species in a single category.

To allow direct comparison with past and future studies, results of the analyses are presented in four different ways. Absolute frequency was calculated as the percentage of samples in which a given food item was present. Because some faeces contained more than one food item, the sum of percentages exceeded 100. Relative frequency is the percentage of each food item out of the total sample items. Relative frequency depends on the taxonomic level employed. We therefore report it only for lower-level categories. To estimate percentage volume, the total number of each prey before ingestion (known by reference material), and the proportion of total bulk for each food category was estimated ; the average proportion across samples is therefore an estimate of the volume of ingested food (Kruuk & Parish, 1981 ; Cavallini & Nel, 1990). To reduce inter-observer variability of the estimate, two or three obervers replicated estimates whenever possible (> 15 % of samples). For stomach and intestine analyses the volume estimate was also corrected for total mass of contents (hereafter « percentage mass »), to reduce the importance of guts that were almost empty. The use of published factors for many categories, and of the high variability between estimates of different studies (Lockie, 1959 ; Liberg, 1982 ; Palomares & Delibes, 1990 ; Roger *et al.*, 1990 ; Stahl, 1990 ; Reynolds & Aebischer, 1991). Age of sampled foxes was determined by counting incremental annuli in canine teeth and measuring the width of canine teeth pulpar cavity and the mass of eye lens (Cavallini & Santini, 1995a). Owing to the small number of older foxes, the

sample was pooled in two age classes : yearlings (< 1 year old at the time of sampling) and adults (> 2 years old). Body condition was estimated by the logarithm of kidney fat index (LaJeunesse & Peterson, 1993 ; Cavallini, 1994b), and head plus body length was measured (from the tip of the nose to the base of the tail ; Cavallini, 1995).

Because of non-normality of data, we used non-parametric statistics for all analyses (Kruskal-Wallis one-way ANOVA : H ; Mann-Whitney test : U ; Spearman rank correlation : r_s ; Siegel & Castellan, 1988). Because of the large number of tests, we conservatively used an α-level of 0.01 instead of the conventional 0.05 when analysing several tests involving the same variables (Rice, 1989). All tests were two-tailed. Cluster analysis was conducted on correlations rather than on distances because we wish to measure similarity in patterns of variation rather than in absolute magnitude (Wilkinson, 1990).

RESULTS

GUT CONTENTS

We collected 330 foxes (125 females and 205 males), but due to damage during hunting we could analyse 320 guts. Of those, 10 intestines and 54 stomachs did not contain measurable quantities of food (< 6 g). Average mass of content was 90 ± 71 g for stomachs, 58 ± 23 g for intestines. From January to the beginning of May, diet was dominated by vertebrates (78 % by volume in stomachs, 66 % in intestines), especially mammals (57 and 54 %) and birds (21 and 12 %). Vertebrates were present in almost all guts (stomachs : 94 % ; intestines : 88 %). Most of mammals were domestic (29 and 26 %) and small rodents and insectivores (19 % both in stomachs and in intestines). Proportions of domestic and wild birds were more even (wild : 10 and 5 % ; domestic : 11 and 7 %). Invertebrates (mostly insects) were less common (7 % both in stomachs and in intestines). Plants were a secondary food item (11 and 16 %), mostly fruits (cultivated : 4 and 8 % ; wild : 1 and 2 %). Refuse was also scarce (6 and 11 %), but part of domestic mammals and birds may have been consumed as garbage. Birds, invertebrates and plants were almost equally frequent in guts (from 33 to 47 % of stomachs or intestines). Food deriving (directly or indirectly) from human activities was about half of the diet (50 and 52 % ; Tab. I). Among small mammals, muroid rodents (*Apodemus* sp., *Mus* sp., *Rattus* sp.) and voles (especially *Pitymys* sp.) were most abundant, whereas insectivores were less common. Among large wild mammals, most frequent were lagomorphs (rabbits, *Oryctolagus cuniculus* and hares, *Lepus europaeus*), followed by wild boars *Sus scrofa*. Other mammals (porcupines *Hystrix cristata*, coypus *Myocastor coypus*, roe deer, *Capreolus capreolus*) were occasionally eaten, probably as carrion. Domestic mammals were mainly rabbits and sheep *Ovis ammon* and domestic birds were mainly hens *Gallus gallus*, rarely ducks (Anatidae). Wild birds were mainly Passeriformes (especially blackbirds *Turdus merula*) and Galliformes (*Phasianus colchicus*). The percentage of grass and other vegetable matter (of dubious trophic value) was positively correlated only with the percentage of invertebrates in stomachs ($r_s = 0.178$, p <0.001, N = 266), but not in intestines ($r_s = 0.038$, p >0.05, N = 310). It was not different

in guts with different levels of worm infestation (mainly Cestoda ; stomachs : $H = 1.36$, $p = 0.5$; intestines : $H = 0.15$, $p = 0.9$). The percentage of occurrence overestimated the importance of food items eaten in small quantities per meal (especially all invertebrates), whereas it underestimates large food items eaten in large quantities per meal (especially large wild & domestic mammals). The percentage volume of vertebrates and of food of anthropogenic origin in stomachs were positively correlated with total content mass in the stomach ($r_s = 0.232$, $p < 0.001$ and $r_s = 0.184$, $p = 0.002$, respectively, $N = 266$), whereas the volume of invertebrates and vegetables was negatively correlated with stomach content mass ($r_s = -0.192$, $p = 0.002$ and $r_s = -0.236$, $p < 0.001$, respectively, $N = 310$). However the differences between percentages of volume and mass were small ($- 5 \%$), smaller than the difference between stomachs and intestines (Tab. I).

TABLE I

Diet composition of the red fox Vulpes vulpes *in the province of Pisa, Central Italy, January to May 1992, based on 266 stomachs and 310 intestines with measurable ($\geq$ 6 g) contents. « volume » is the estimated percentage of volume, « mass » is the percentage of volume corrected for the mass of contents, « relative freq » is the percentage of occurrence on total occurrences, and « absolute freq » is the percentage of occurrences on total number of samples. The relative frequency of occurrence cannot be calculated unambiguously for larger categories, because it depends on the number of categories included.*

	Stomach				Intestine			
	volume	mass	relative freq	absolute freq	volume	mass	relative freq	absolute freq
Vertebrates	78	80	-	94	66	65	-	88
Mammals	57	59	-	82	54	55	-	76
Small mammals	19	20	15	44	19	21	15	37
Large wild mammals	9	8	4	12	9	9	5	13
Domestic mammals	29	32	12	35	26	25	12	32
Birds	21	20	-	45	12	10	-	33
Wild birds	10	8	7	19	5	4	5	13
Domestic birds	11	12	9	25	7	6	7	17
Eggs	0	0	1	2	0	0	1	2
Other vertebrates	0	0	1	4	0	0	1	1
Invertebrates	7	6	-	45	7	8	-	45
Coleoptera	2	2	10	30	4	5	14	35
Orthoptera	0	0	1	1	0	0	0	1
Other insects	4	3	11	30	2	2	8	20
Other arthropods	0	1	3	7	1	1	2	4
Other invertebrates	0	0	2	6	0	1	3	6
Plants	11	7	-	47	16	15	-	47
Wild fruits	1	0	2	5	1	2	2	5
Cultivated fruits	4	3	5	15	8	7	7	17
Other plant matter	6	4	11	31	7	7	12	30
Refuse	6	7	8	22	11	12	10	24
Anthropogenic matter	50	55	-	72	52	49	-	71

Sources of variation

The diet was partly different between sexes ; females ate more small mammals than males (stomach : 23.0 ± 31.1 % *vs* 16.8 ± 30.9 % ; U = 6308.5, p = 0.0008, N = 262 ; intestine : 24.4 ± 34.8 % *vs* 15.5 ± 31.3 % ; U = 8917, p = 0.002, N = 304) and more invertebrates (stomach : 9.1 ± 18.3 % *vs* 5.2 ± 14.9 % ; U = 6432.5, p = 0.002, N = 262 ; intestine : 10.0 ± 20.9 % *vs* 5.1 ± 12.4 % ; U = 9436, p = 0.03, N = 304). Other items were present in similar proportions. Yearlings had a diet similar to adults (all Us < 178, p > 0.05). The volume of no food item was correlated with either the kidney fat index ($r_s \leqslant 0.15$, p > 0.01) or body length ($r_s \leqslant 0.14$, p > 0.01). Local variation in diet were found only for domestic birds (stomachs : H = 15.4, p = 0.001 ; intestines : H = 24.8, p < 0.001), cultivated fruit (stomachs : H = 23.5, p < 0.001 ; intestines : H = 17.3, p < 0.001) and refuse (stomachs : H = 9.9, p = 0.019 ; intestines : H = 8.9, p = 0.03 ; Fig. 1). In particular, cultivated fruits were a larger proportion in the North of the study area than in the South (stomachs : U = 10194, p < 0.0001, N = 262 ; intestines : U = 13641.5, p < 0.0001, N = 304). The variation was not obviously related to any environmental or sociological variable, e.g. refuse were more abundant in the South, where human population density was lower (Fig. 1).
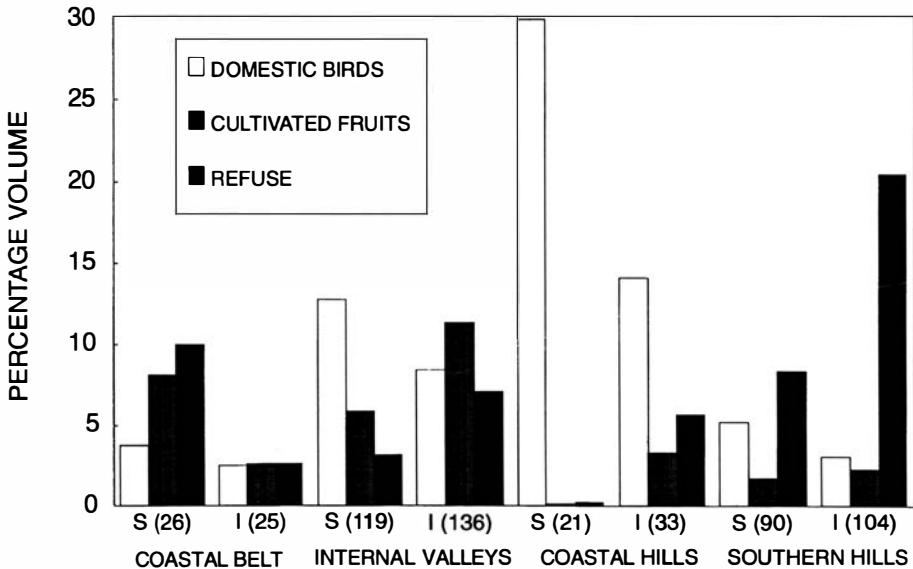

Figure 1. — Local variation in the consumption of domestic birds, cultivated fruits and refuse by the red fox in four contiguous sections of the Pisa province, Central Italy, January to May 1992. S = stomachs, I = intestines ; sample size between parentheses.

FAECES

A total of 1261 faeces was analysed, with large differences in sample size among both months and sampling areas (monthly sample size ranged from 167 in

September to 37 in December, with an average of 105 ± 44 per month ; in winter fewer samples were collected, because rain washed away some faeces ; Cavallini, 1994a). Faeces from two areas (Berignone and Monti Pisani) were almost a half of total sample (337 and 247 faeces, respectively), whereas in one (Collebrunacchi) only 27 samples were collected. Average sample size per area was 140 ± 102. The heterogeneity of sample size prevented us from analysing simultaneously local and seasonal diet variation with a two-way ANOVA ; therefore local and seasonal variation were analysed separately.

As for guts, the diet was largely dominated by vertebrates (49 % of volume, especially mammals : 43 %). Among vertebrates, main food items were small mammals (26 %, mainly Arvicolidae and Muridae) and domestic mammals (11 % : rabbits, sheep and pigs), presumably often consumed as carrion or refuse. Fruits (both wild, 14 % and cultivated, 20 %) were also abundant. The volume of grass and other vegetable matter was positively correlated only to invertebrate volume ($r_s = 0.103$, $p < 0.01$). Invertebrates (9 %) and refuse (6 %) were minor items ; total matter of anthropogenic origin was 38 % of diet (Tab. II). The average of individual averages among areas (that avoid overestimating the importance of areas with larger sample sizes) reduced the volume estimate for small mammals

TABLE II

Diet composition of the red fox Vulpes vulpes *in 9 areas of the province of Pisa, Central Italy, 1992-1993, based on 1261 faeces collected. Abbreviations as in Table I, except « weighed volume » that is the average of percentage volumes in individual areas (to avoid the bias toward areas with larger samples)*

	volume	weighed volume	relative freq	absolute freq
Vertebrates	49	50	-	66
Mammals	43	43	-	58
Small mammals	26	23	20	39
Large wild mammals	6	6	5	9
Domestic mammals	11	13	7	14
Birds	6	7	-	17
Wild birds	3	4	6	11
Domestic birds	2	3	3	5
Eggs	0.2	0.2	1	2
Other vertebrates	0.1	0.1	0.2	0.4
Invertebrates	9	11	-	35
Coleoptera	8	9	15	28
Orthoptera	1	1	3	5
Other insects	1	1	3	6
Other arthropods	0.1	0.1	0.5	1
Other invertebrates	0.3	0.2	1	2
Plants	37	35	-	58
Wild fruits	14	8	11	22
Cultivated fruits	20	23	16	31
Other plant matter	3	4	5	10
Refuse	6	5	4	9
Anthropogenic matter	38	45	-	51

and wild fruits, whereas it increased the estimate for food items of anthropogenic origin (domestic mammals, domestic birds, cultivated fruits ; Tab. II, « weighed volume »).

Local variation

Vertebrates and plants were not uniformly abundant in the fox diet in all areas (H = 52.5, p < 0.0001, and H = 81.4, p < 0.0001, respectively, N = 1261), whereas invertebrates were consumed in even percentages (H = 10.5, p = 0.231 ; Fig. 2a). Among vertebrates, small mammals were much more consumed in Berignone than in other areas (H = 55.3, p < 0.0001). Also large wild and domestic mammals were not uniformly eaten across areas (H = 39.1, p < 0.0001, and H = 95.5, p < 0.0001 ; Fig. 2b). Birds were more important in some areas (H = 42.3, p < 0.0001). Such heterogeneity was mainly due to domestic birds, more eaten in some areas (Collebrunacchi, Coltano, Vecchiano) than in others (Berignone, Santa Luce ; H = 27.0, p = 0.0007), whereas wild birds (mainly small and medium Passeriformes and pheasants) were not much different among areas (H = 18.5, p = 0.018). Eggs and other vertebrates were equally represented in the diet in all areas (H = 18.8, p = 0.016, and H = 11.7, p = 0.167, respectively ; Fig. 2b). The consumption of fruit, both wild and cultivated, was highly variable among areas (H = 241.5 and H = 162.9, respectively, p < 0.0001 ; Fig. 2c). Also species of fruits eaten were different among areas (strawberry tree *Arbutus unedo* and juniper *Juniperus* spp. berries in Berignone, olives *Olea europaea* and chestnuts *Castanea sativa* on Monti Pisani). The consumption of wild fruits was positively correlated with the percentage of woodland in the area (r_s = 0.820, p < 0.02, N = 9). Other vegetable matter was also eaten in different quantities (H = 20.8, p = 0.008 ; Fig. 2c). Anthropogenic food was not eaten in significant quantities (< 7 %) in Berignone (the only area without resident human population), but was uniformly abundant (43-55 %) in all other areas (H = 270.8, p < 0.0001). A cluster analysis based on the volumetric percentages of different food items (Pearson correlation ; average clustering) revealed that the diet of red foxes in Berignone was very different from that in other areas, having many small mammals and little food of human origin. It was partly similar to that of Monti Pisani ; these were the only areas with limited human presence, and had the highest fox population density (Cavallini, 1994a). The diet of foxes in the remaining areas was rather homogeneous (Fig. 3).

Seasonal variation

The diet was dominated by vertebrates in winter and spring, and by fruits in summer and autumn ; invertebrates were eaten mainly in summer (Fig. 4). Vertebrates were eaten most often between January and May (i. e. in the period of mating and births for most species, including the fox ; Cavallini & Santini, 1995b ; H = 253.4, p < 0.0001 ; Fig. 5), whereas they were < 40 % of volume in the rest of the year. Such variation was mainly due to variation in the consumption of mammals, which followed a similar trend (H = 235.9, p < 0.0001 ; Fig. 5). Small mammals were scarcely preyed from June to September, and were almost a half of the diet in March (H = 66.3, p < 0.0001 ; Fig. 5). Large wild mammals were eaten almost only from March to May (H = 53.4, p < 0.0001 ; Fig. 5). Domestic mammals followed a similar trend (H = 58.9, p < 0.0001 ; Fig. 5). Birds were eaten
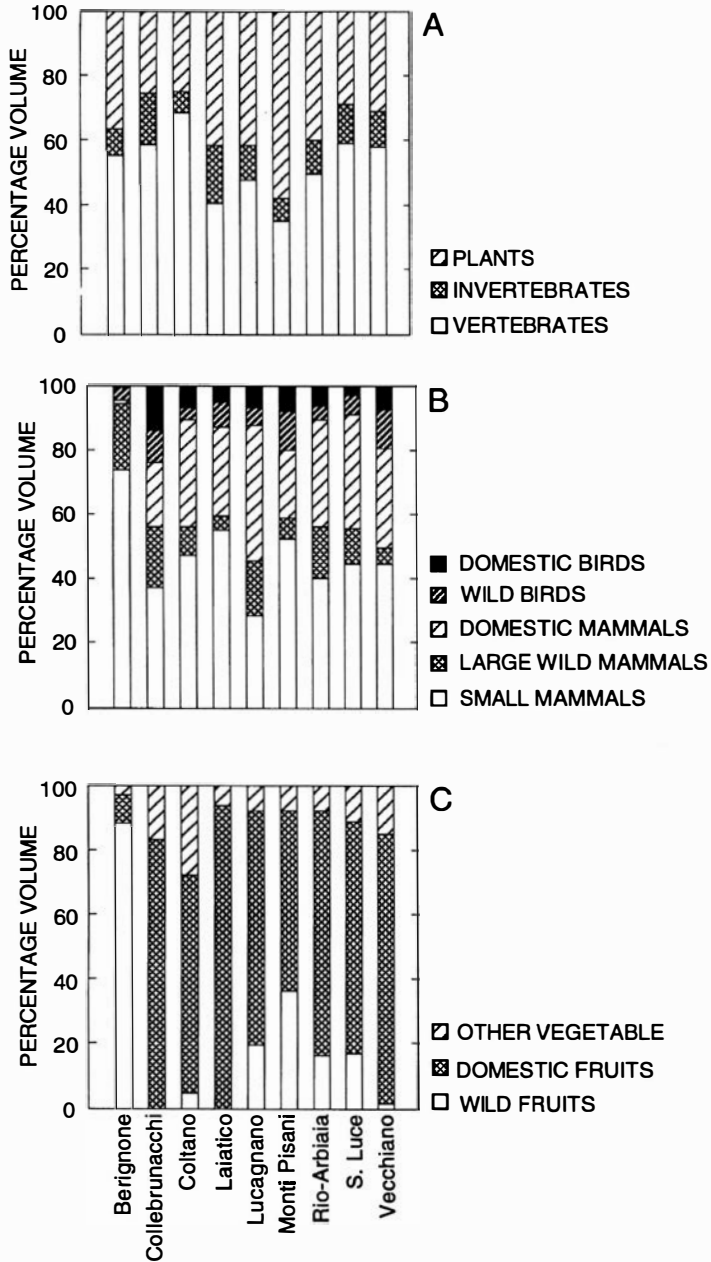
Figure 2. — Local variation of yearly diet of the red fox (faecal analysis ; percentage volume) in nine areas sampled in the province of Pisa, Central Italy. Sample sizes are : Berignone = 337 ; Collebrunacchi = 27 ; Coltano = 80 ; Laiatico = 57 ; Lucagnano = 61 ; Monti Pisani = 247 ; Rio-Arbiaia = 108 ; S. Luce = 172 ; Vecchiano = 172. A : main categories. B : percentages of lower-level categories within Vertebrates. C : percentages of lower-level categories within Plants.
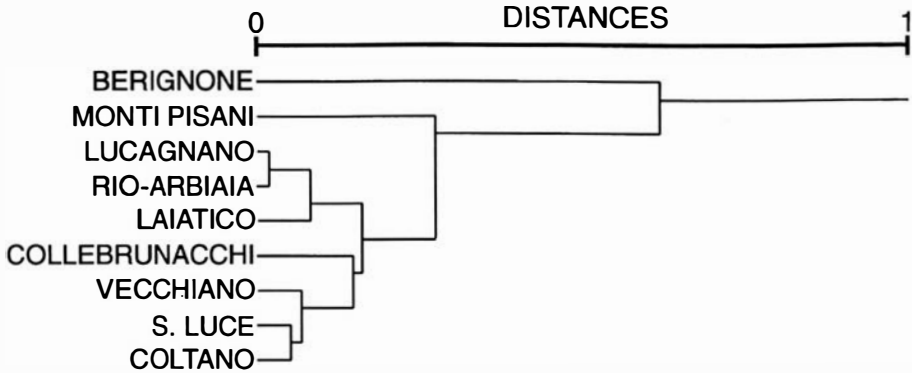
Figure 3. — Tree diagram (Cluster analysis ; Pearson correlation, average clustering based on the percentage volume of food items) showing global similarity of fox diets in the nine sampling areas.

more in spring and summer that in autumn and winter (total : H = 33.4, p = 0.0005 ; wild : H = 25.1, p = 0.009 ; domestic : H = 26.9, p = 0.005 ; Fig. 5). Eggs and other categories were evenly eaten during the year (H = 14.4, p = 0.212 and H = 7.9, p = 0.722, respectively). Invertebrates were rarely eaten between December and April, whereas they were more important in warmer months (H = 133.7, p < 0.0001 ; Fig. 6). A similar trend was followed by Coleoptera (H = 151.5, p < 0.0001), by Orthoptera (H = 51.4, p < 0.0001) and by other insects (H = 32.0, p = 0.0008), whereas there was no variation in the consumption of other

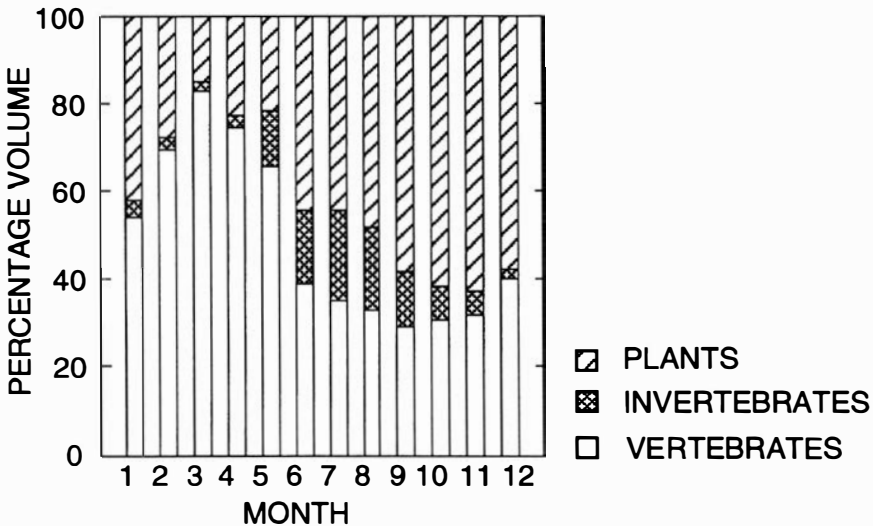Figure 4. — Seasonal variation of red fox diet in nine areas of Pisa province, Central Italy (main categories, average among areas ; N = 1261).
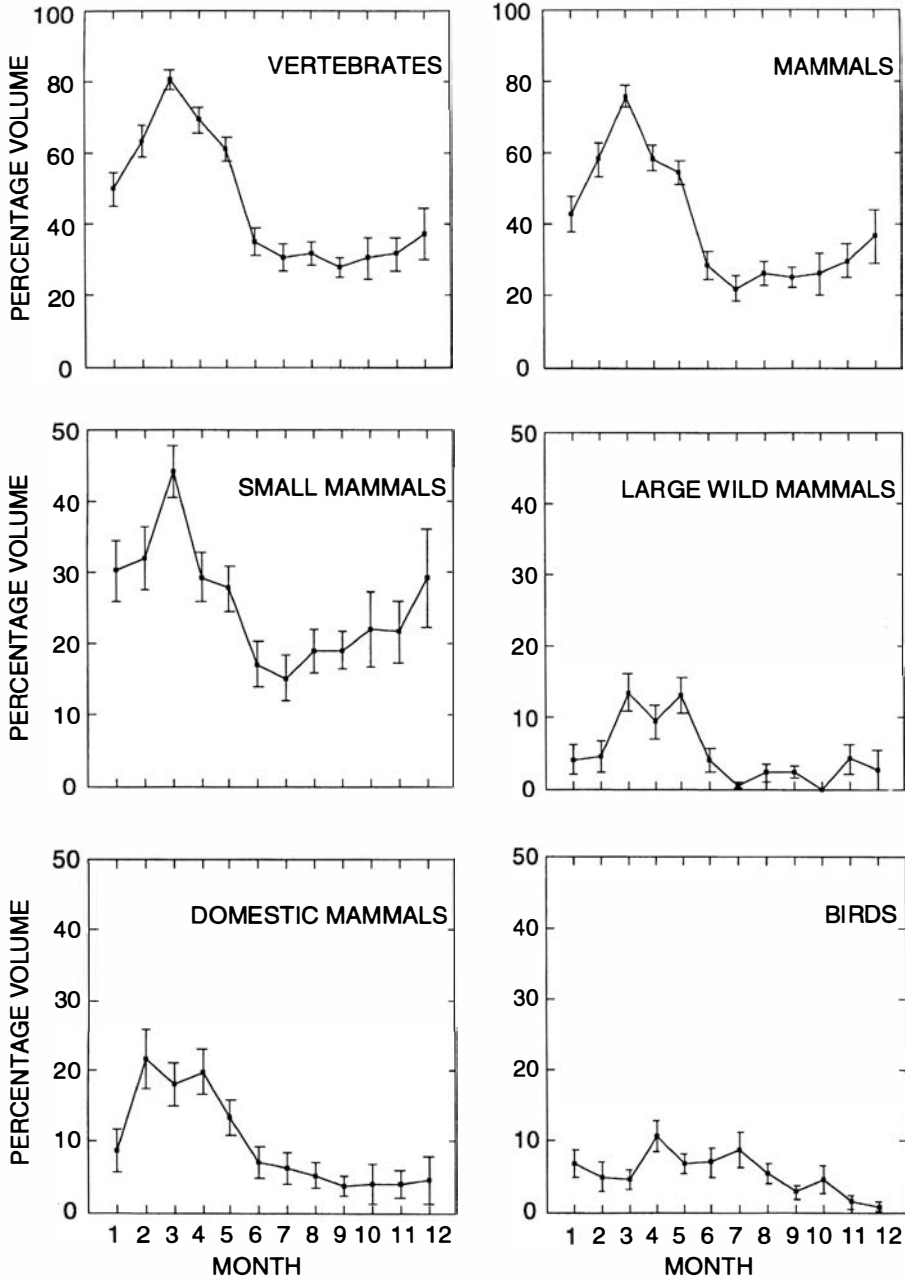
Figure 5. — Seasonal variation in the consumption of vertebrates by the red fox in nine areas of Pisa province, Central Italy (lower-level categories ; the average and standard error among areas are indicated ; N = 1261).
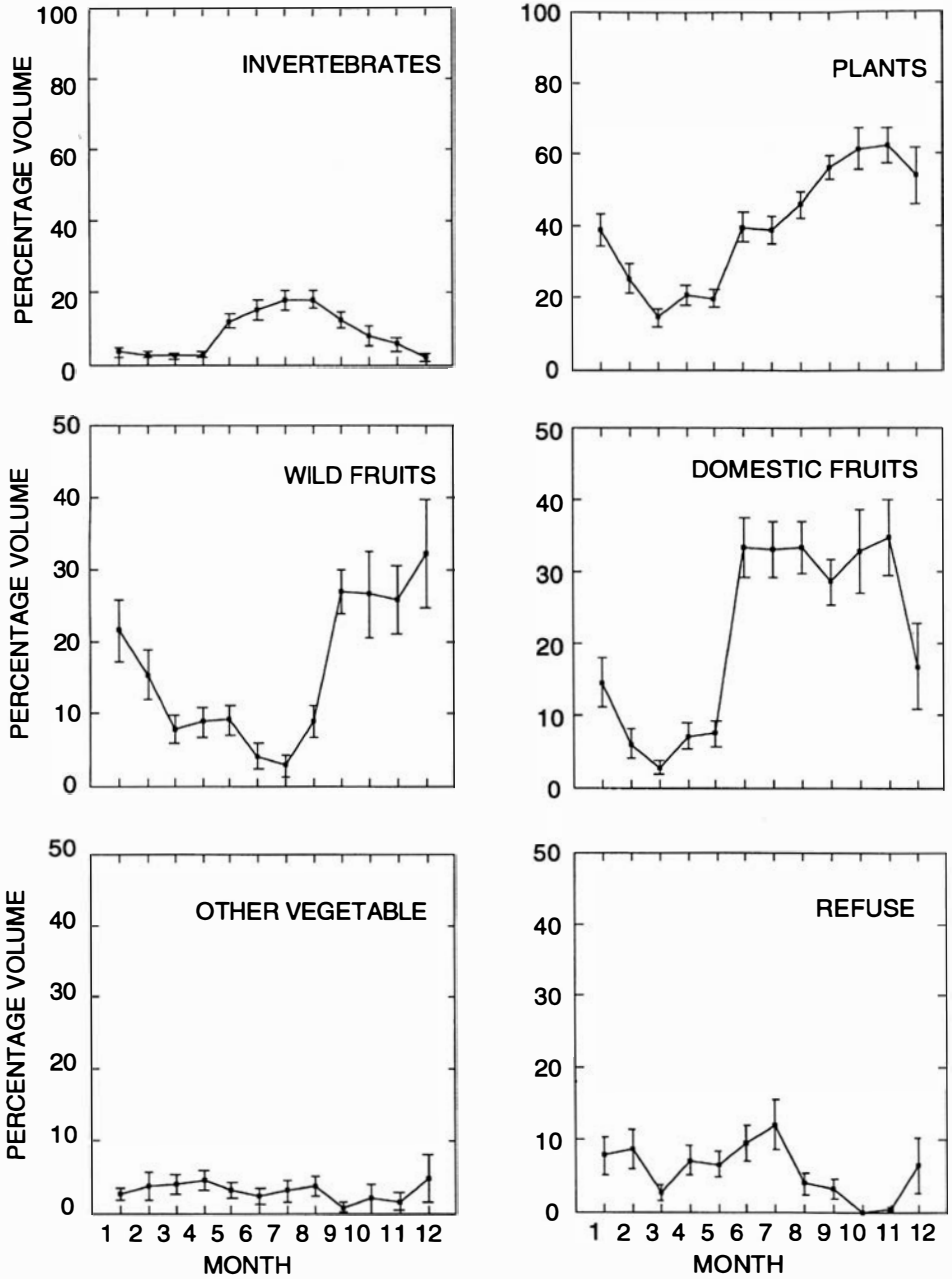
Figure 6. — Seasonal variation in the consumption of invertebrates, plants and refuse by the red fox in nine areas of Pisa province, Central Italy) lower-level categories ; the average and standard error among areas are indicated ; N = 1261).

arthropods (H = 8.7, p = 0.648) and other invertebrates (H = 10.5, p = 0.487). Plants were scarcely eaten in late winter and spring (February to May) and progressively more until November (H = 208.3, p < 0.0001 ; Fig. 6). Among plant matter, wild fruits were constantly important for four months (September to December), and insignificant outside this period (H = 109.6, p < 0.0001 ; Fig. 6). Domestic fruits were eaten in significant quantities for six months, starting earlier than for wild fruits (from June to November ; H = 166.7, p < 0.0001). Other plant matter showed seasonal variation (H = 56.9, p < 0.0001), but without clear seasonal trends (Fig. 6). Foods of anthropogenic origin were always important (25-55 % of the diet in every month), but were more abundant in June-July than in December-May (H = 49.1, p < 0.0001). Of this, refuse were not eaten in October-November, and most abundant in June-July (H = 36.3, p < 0.0002 ; Fig. 6).

DISCUSSION

The diet of the red fox in the Pisa province was varied, but clearly dominated by vertebrates and fruits. Whereas the importance of mammals and birds in the diet is a general phenomenon (see Artois, 1989 for a review), the high volume of fruits (both wild and cultivated) is a trait characteristic of Italian foxes (Leinati *et al.*, 1961 ; Ciampalini & Lovari, 1985 ; Calisti *et al.*, 1990 ; Cavallini & Lovari, 1991 ; Patalano & Lovari, 1993 ; Serafini & Lovari, 1993 ; Lovari *et al.*, 1994). This may be a general phenomenon for Central Mediterranean environments : also badgers *Meles meles* in Italy and small Indian mongooses *Herpestes auropunctatus* in the neighbouring Croatia ate more fruits than in the rest of their range (Kruuk & Kock, 1981 ; Ciampalini & Lovari, 1985 ; Cavallini & Serafini, 1995). Fruits were consumed in highly variable amounts in different sections of our study area and in different periods whereas mammals (and especially rodents) were more constant. Also in other areas foxes ate constant proportion of rodents in spite of large variation in rodent abundance (Artois & Stahl, 1991). The consumption of fruits was strongly related to availability (Cavallini & Lovari, 1991). The red fox is not very efficient in the digestion of fruits (Jaslow, 1987), whereas is very efficient in the predation (Henry, 1986) and digestion (Jaslow, 1987) of small vertebrates. In 29 studies reviewed, the relative percentage of occurrence of fruit ranged from 0 % (Coman, 1973) to 36 % (Ciampalini & Lovari, 1985), whereas mammals were never less than 16 % (Harris, 1981 ; up to 65 % : Fairley, 1970), with the only exception of one study in urban environment, where refuse was the largest part of food intake (Saunders *et al.*, 1993). These evidences together suggest that fruits are a supplementary food resource for the red fox, eaten when and where most abundant (Cavallini & Lovari, 1991), while mammals (and in particular small rodents) are a key resource (as proposed by Artois, 1989). The volume of grass and other vegetable matter seems consequent to accidental ingestion while eating invertebrates. The hypothesis of an antiparasite effect of grass ingestion (e.g. Fairley, 1970) was not supported by our data. We cannot however exclude that single plant species might be ingested for medicinal purposes. An analysis of the species of plants ingested should be conducted to clarify this point. The importance of foods of anthropogenic origin (especially fruits and domestic vertebrates) was very high in this study, comparable to urban areas (Doncaster *et al.*, 1990). This happens also in other areas of Central Italy (Pozio & Gradoni, 1981 ; Serafini & Lovari, 1993).

The diet was rather homogeneous within the study area, with the exception of some secondary resources of human origin (Fig. 1) and of few wooded areas with little or no human population, where foxes were rarely hunted (Figs. 2-3). Such homogeneity is surprising given the large environmental variation within the area. Both aspects reveal the importance of man as the main factor shaping fox diet.

Seasonal variation was very large for all categories, as found in most other studies on fox diet (Artois, 1989). The pattern of variation in the consumption of several food items can be explained by the availability of resources : birds were eaten more in spring and summer, when young birds learn to fly and are more vulnerable ; invertebrates were eaten more in the warmer months, when they are more active and abundant (e.g. Cavallini & Lovari, 1991) ; the fruits were consumed more in the season when they become available. The low consumption of small mammals in summer is unexpected, because rodent abundance increases from spring until autumn, due to reproduction (Santini, 1983). The availability of alternative resources (invertebrates, fruits), easier to capture especially for cubs (a large part of fox population in summer ; Cavallini, 1994b) may explain this pattern.

The morphology of 1-year old foxes is not significantly different from that of adults (Storm *et al.*, 1976 ; Cavallini, 1994b). The lack of differences between diets of yearlings and adults found in this study is therefore predictable, and was previously reported (Catling, 1988). Younger foxes could have different diets. More surprising is the difference between the diet of males and females, especially considering the small sexual size dimorphism (e.g. Kolb & Hewson, 1974 ; Storm *et al.*, 1976). Such differences were not previously reported (Korschgen, 1959 ; Englund, 1965 ; Fairley, 1970). The higher consumption of small mammals and invertebrates (highly proteinic items ; e.g. Redford & Dorea, 1984) by females during late winter and spring (reproductive period of the fox in this area ; Cavallini & Santini, 1995b) may explain the good physical condition of females until parturition (Cavallini, 1994b). These results should be verified in a sample of foxes collected during an entire year.

Foxes ate more fruits when and where fox population density was higher (see also Cavallini, 1994a). This may be caused either by (1) foxes eating less proteinic resources when living at higher densities (e.g. because of lower hunting pressure), or by (2) higher availability of fruits supporting denser population of foxes. This question cannot be resolved without an experimental approach (manipulating fox density and fruit availability). The large and varied food base of foxes in this area makes however the second hypothesis less likely.

SUMMARY

The diet of the red fox *Vulpes vulpes* was studied in the province of Pisa, Central Italy, analysing both faeces (N = 1261 ; collected monthly for one year in nine areas) and gut contents (N = 330 ; collected between January and May in the whole province). Diet was very varied, and was dominated by vertebrates, especially mammals, and plants (especially fruit) whereas invertebrates were less abundant. Food of human origin was approximately a half of the diet. In late winter and spring, females ate more small mammals and invertebrates than males, whereas yearlings had diets similar to adults. The body fat and size were not related to the volume of any food item. Seasonal variation was large for most categories, vertebrates being eaten mainly in winter and spring, and fruits in summer and autumn. Invertebrates were eaten mainly in summer. Several of these trends could be explained by the availability of food, but small mammals were eaten less when they were presumably more abundant. Globally, the diet in rural areas was homogeneous, and very different from that in areas with little human intervention. Over the whole province, differences were limited to three secondary items of human origin. Grass and other vegetable matter in stomachs and in intestines were significantly related to the consumption of invertebrates, not to the presence of parasite worms in the intestines. The high consumption of fruits and of resources of human origin is a characteristic trait of the fox diet in this and other areas of Italy. Fruits may be a supplementary food item, whereas small mammals may be a key resource. Foxes ate more fruits when and where fox population density was higher. Reasons for these trends are discussed.

RÉSUMÉ

Le régime alimentaire du Renard *Vulpes vulpes* a été étudié dans la province de Pise, en Italie centrale, par l'analyse de fèces (N = 1261 ; recueillies chaque mois pendant un an dans neuf zones) et de contenus du tube digestif (N = 330 ; collectés de janvier à mai dans toute la province). Ce régime est très varié, dominé par les vertébrés (notamment les mammifères) et les végétaux (en particulier les fruits), les invertébrés n'étant que peu abondants. Les aliments d'origine anthropique comptent pour à peu près la moitié du régime. En fin d'hiver et au printemps, les femelles consomment plus de petits mammifères et d'invertébrés que les mâles, les jeunes ayant un régime semblable à celui des adultes. Aucune relation n'a été trouvée entre l'adiposité et la taille corporelle des individus et le volume d'un quelconque item alimentaire. La variation saisonnière est importante pour la plupart des catégories d'aliments, les vertébrés tendant à être principalement consommés en hiver et au printemps, les fruits en été et en automne et les invertébrés surtout en été. Plusieurs de ces tendances s'expliquent par les disponibilités alimentaires mais les petits mammifères apparaissent moins consommés quand ils sont apparemment le plus abondants. Globalement, le régime est homogène dans les zones rurales et s'avère fort différent de celui observé dans les zones soumises à faible emprise humaine. Sur l'ensemble de la province, les différences se limitent à trois items d'origine humaine. Les herbes et autres végétaux contenus dans les estomacs et les intestins sont de manière significative associés à la consommation d'invertébrés mais pas à la présence de vers parasites dans les intestins. La forte consommation de fruits et d'aliments d'origine anthropique est un trait caractéristique du régime du renard dans cette

région, et dans d'autres, de l'Italie. Les fruits pourraient être des aliments de complément alors que les petits mammifères seraient des aliments-clés. Les renards mangent plus de fruits quand et où leur densité de population est la plus forte. Les raisons de ces tendances sont discutées.

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