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Assessing carnivore diet by faecal samples and stomach contents: a case study with Alpine red foxes

Research Article

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Abstract: Research on the feeding habits of mammalian carnivores relies mainly on the analysis of stomach contents and faecal samples, but the outcomes of these two methods have only been compared in a few studies, with contrasting conclusions. In an Alpine area of NW Italy, we analysed both fox faeces collected along standardised transects, and the stomach contents of road-killed individuals. Faecal analysis involved the identification of macroscopic fragments, the identification of earthworm *chaetae*, and the assessment of relative volumes using Kruuk and Parish's technique. Use of both methods indicated that the diet of the red fox included mainly fruit and mammals, but quantitative differences emerged. Garbage, birds, and cultivated fruit were over-represented in the stomach contents, while earthworms, mammals, and wild fruit prevailed in the faecal samples. Logistic Regression Analysis suggested that the method of analysis was the main factor in determining the occurrence of food items in fox diet. Nonetheless, evidence suggests that road-killed foxes may include a disproportionately high percentage of synanthropic individuals and therefore be biased towards anthropogenic food. Results suggest that by using Kruuk and Parish's technique, the main limitation of faecal analysis, *i.e.* the inaccurate estimation of the relative volume of each food item, can be overcome.

Keywords: *Food habits • Frequency of occurrence • Percent volume • North-West Italy*

1. Introduction

Diet analysis is a major issue for research in the ecology of mammalian predators, given that food availability is considered to influence their population size [1], social organization [2] and inter-specific relationships [3], as well as the spreading of zoonoses [4]. Thus, information on carnivore food habits is of paramount importance with regard to both conservation and public health.

Research on mammalian diets relies mainly on the analysis of stomach contents and faecal samples. The first method has the advantage of analysing only partially digested food, allowing for easier identification of the remains to the species-level, and also provides a more accurate measurement of the relative volume of each item [5,6]. Conversely, faeces are generally easy to find in the field, allowing for the homogeneous sampling of the different habitats included in any given study area, and their collection does not involve the death of animals (see [7] about ethical considerations).

Although the correct interpretation of the results requires that the limits of each method are disclosed and accounted for, multiple techniques have been applied and compared in only a few studies, yielding contrasting conclusions: no method-related differences in diet composition have been found comparing stomach and intestine contents of martens *Martes americana* and *M. pennanti* [8,9], while differences have been reported for prairie dog *Cynomys ludovicianus* [10] and red fox *Vulpes vulpes* [11,12].

The diet of the red fox includes a wide variety of food resources [13-16], generally as a consequence of its broad geographic range which covers almost the whole northern hemisphere and Australia [17]. The ability of the fox to adjust its feeding behaviour in response to the variation of food resources enables the

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species to be placed at any point along the specialist – generalist continuum [18,19], justifying the need for the investigation of fox diet in several environmental conditions.

The aim of our study was to compare fox diets using analysis of stomach contents and faecal samples in the western Italian Alps, where the red fox has been reported to rely mainly on rodents, wild fruit, and ungulate carrion [20-22].

We applied the most widely used method for faecal analysis, involving the identification of macroscopic fragments and the sampling of the micro-fraction for earthworm *chaetae* ("method A" in [11]). Although it may be preferable to estimate the original biomass of prey represented by faecal remains [23], we assessed the relative volume of each food item by Kruuk and Parish's technique [24], which has been widely applied in the study of carnivore diets [21,25-27]. Considering both the food habits of Alpine foxes and the limits of each method, we hypothesised that discrepancies between faecal and stomach samples would have occurred mainly with regard to the volume of medium- and large-sized mammals, which, by scat analysis, is more difficult to assess with respect to that of small prey items [24].

2. Experimental Procedures

Between June 2002 and December 2004, the stomach contents of road-killed foxes were extracted and preserved at –40°C (N=121) upon collection of each animal, with both the sex and height above sea level (m a.s.l.) being recorded. The age (adults *vs*. <1 year old individuals) was determined according to the degree of ossification of limb bones and skull sutures [28]. During the same period, faeces were collected at monthly intervals along 20 transects (mean length=800 m, SD=344) ranging from 700 to 2,000 m a.s.l. and uniformly distributed throughout the main habitats of the study area. All faecal samples (N=117) were stored in polythene bags and refrigerated until processing.

Both faecal and stomach samples were collected in the same eight river valleys (respectively, Lys: N=6, 8; Evançon: N=3, 4; Marmore: N=55, 31; Ayasse: N=10, 4; Buthier: N=1, 3; Grand Eyvia: N= 1, 9; Dora of Rhême: N=4, 4; Dora Baltea: N=27, 56; Figure 1) of Aosta Valley region, North-West Italy (3,264 km^2 in size, with altitude ranging from 310 to 4,810 m a.s.l.). Sampling for faeces was conducted to match the seasonal and altitudinal distribution of stomach samples. Although faeces prevailed slightly in winter and above 1500 m a.s.l. (Figure 2), we assumed that faeces and stomach contents sampled the same population.

Faecal samples were washed through three sieves of 1.5, 0.3 and 0.1 mm mesh and food remains inspected to count or estimate the total numbers of each kind of food present.

Undigested remains were identified by reference keys [29-32] and personal collections of hair photos and seeds. The micro-fraction remaining in the sieve with the smallest meshes was observed under a 40x binocular microscope in order to assess the mean number of earthworms eaten (following a standardised procedure [33]). Food remains of human origin, generally including packing paper, tin-foil, string, *etc*., were recorded as "garbage".

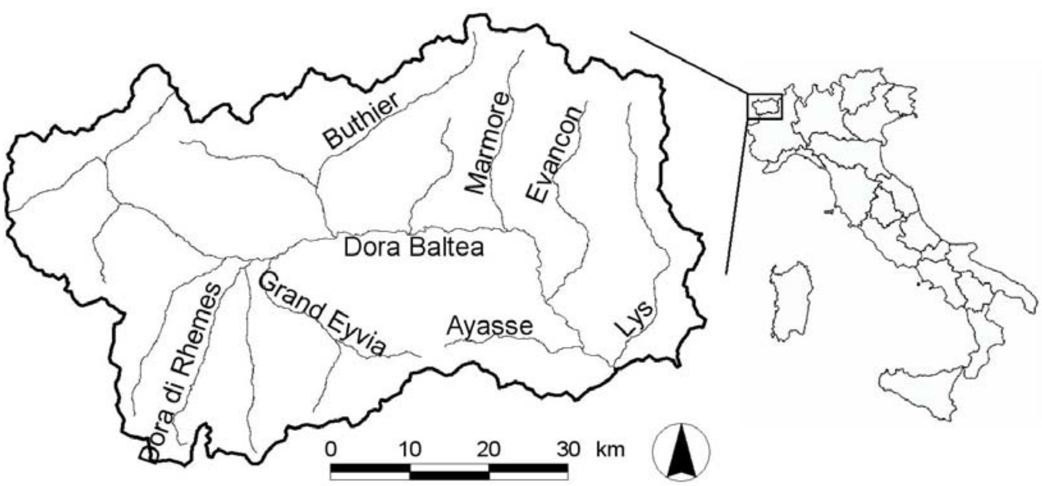

Figure 1. Study area, with the eight river valleys where both faecal and stomach samples were collected.

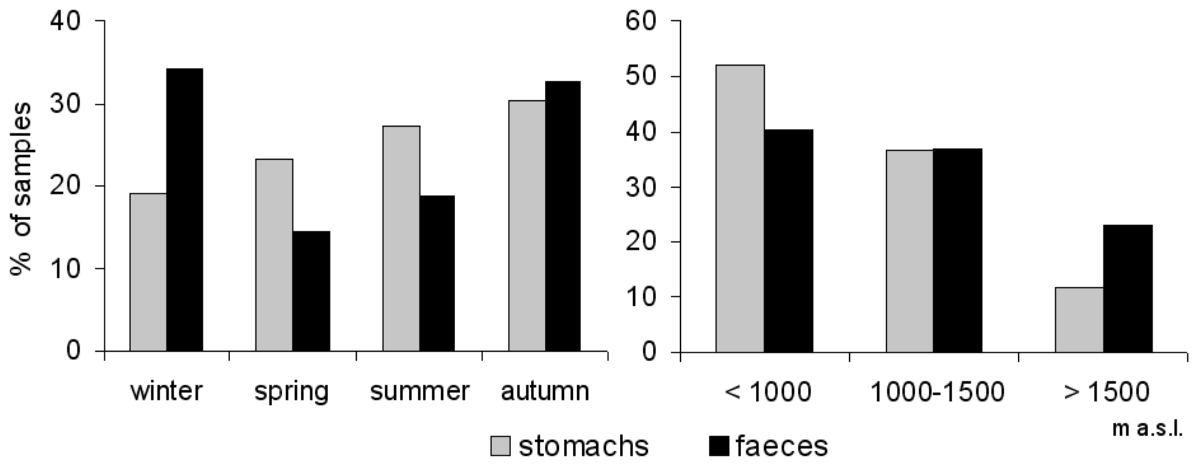

Figure 2. Seasonal and altitudinal distribution of both stomach and faecal samples.

The contribution of each food item in terms of volume was assessed according to Kruuk and Parish [24]. For each faecal sample, the method entails estimating by eye of the bulk of each item 'as ingested' by the fox, *i.e.* the overall volume of each entire prey item. The authors themselves declared that this estimate presents little difficulty for small prey, which are ingested in their entirety, while for larger prey, such as large ungulates, their estimated relative volume is computed as 100 minus the score given to other remains. To reduce the equating of occurrence bias [34,35], the undigested remains occurring in negligible proportions were not considered in the analysis.

Stomach contents were washed through a sieve of 1.5 mm mesh width and sorted by hand to assess the percent volume of each item as ingested. Whenever necessary, teeth, hairs, and feathers were observed by a microscope and compared with available keys and personal collections as for faeces.

The results of both stomach and faeces analyses were expressed as percent frequency of occurrence (%FO = number of samples containing a specific food item/total number of samples x 100), percent volume (%V = total estimated volume of each food item as ingested/number of samples containing that item) and percent mean volume (%mV = %FO´%V/100), which outlines the proportional contribution of each food item to the overall diet [24].

Data were grouped i) seasonally (winter: I-III; spring: IV-VI; summer: VII-IX; autumn: X-XII) in order to investigate time-related variations in fox diet and ii) according to three height classes (500-1000, 1001-1500 and 1501-2000 m a.s.l.), broadly corresponding to different degrees of urbanization (high, medium and low, respectively).

For exploratory analyses, data were grouped in eight main food categories (wild fruit, cultivated fruit, earthworms, insects, birds, rodents, other mammals, garbage), and their variation between collection methods, and among seasons and altitude classes was assessed by the chi-squared test (χ^2) for raw frequency data, and either Mann-Whitney's (U) or Kruskal-Wallis' tests for volumes respectively. Because of the use of repeated tests on related data, the level of significance was calculated by Bonferroni's sequential technique [36].

To assess the agreement between the overall fox diets obtained by the two methods, the relative importance of the main food items was ranked in ascending order according to each quantification index (%FO, %V, %mV), and ranks were compared by pairs using Spearman's test [35,37]. The relationship between the proportions of use (%mV) of the eight main food items as assessed by each method was also tested by Spearman's coefficient.

The relationship between the occurrence of each food item in the fox diet and three variables – method of analysis, season and height a.s.l. – was assessed by Logistic Regression Analysis (LRA). Backward stepwise regression was used, testing for the statistical significance of each coefficient in the model by Wald's test.

For stomach contents, the variation in the frequency of occurrence and percent volume of the main food categories between both sex and age classes was tested by the chi-squared test and Mann-Whitney's test respectively, applying Bonferroni's sequential technique to calculate the respective levels of significance [36].

3. Results

By both methods, the diet of the red fox included mainly fruit (%mV: 32.8 in stomachs and 31.3 in faeces), and mammals (%mV: 24.7 in stomachs and 42.3 in faeces). Garbage and birds represented 14.6% and 10.0% of the fox diet respectively, as assessed by the analysis of stomach contents, while their importance was negligible using analysis of faeces (Appendix 1; Figure 3).

Considering fruit eaten by foxes, stomach contents included eight cultivated species and 4 wild ones, while faeces included 9 wild fruit species and 5 cultivated ones. Only one bird family (Passeriformes) was found in the faecal samples *vs*. three (Passeriformes, Columbiformes and Galliformes) in the stomach contents. The dormouse (*Glis glis*) and the mountain hare (*Lepus timidus*) were exclusive to the faecal samples, while rats (*Rattus* sp.) were found only in fox stomachs.

The frequency of occurrence of wild fruit, earthworms, rodents and other mammals was higher in the faecal samples, while birds and garbage prevailed in fox stomachs (Table 1). No variation emerged when comparing the two methods in terms of percent volume.

Considering the faecal samples, seasonal variation of the main food items in the %FO occurred for earthworms (χ^2=18.9, P<0.01, 3 d.f) and insects (χ^2=17.0, P<0.01, 3 d.f), which were both less preyed upon in winter, and wild fruits (χ^2=11.8, P<0.05, 3 d.f.), which were mainly eaten in summer, while cultivated fruit prevailed in the stomach contents in autumn (χ^2=20.3, P<0.01, 3 d.f). In the faecal samples, the percent volume of earthworms was higher in spring ($\%V_{win}$=20.0, $\%V_{spr}$=26.5, $\%V_{sum}$=12.9, $\%V_{aut}$=8.7, χ^2=40.70, P<0.001, 3 d.f.), and that of insects was higher in summer ($\%V_{win}$=12.5, $\%V_{spr}$=10.6, $\%V_{sum}$=15.2, $\%V_{aut}$=2.1, χ^2=22.4, P<0.001, 3 d.f.), while no difference was found for stomach contents. By both methods, no altitudinal variation emerged for any main food item.

The consumption of cultivated fruit was inversely related to that of rodents for both faecal and stomach samples. For stomach contents, the presence of cultivated fruit was also inversely related to that of wild fruit, birds, and garbage. For faecal samples, the presence of “other mammals” was inversely related to that of rodents and cultivated fruit, while earthworm and insect consumption was positively correlated (Table 2).

When comparing the ranks of the main food items for the two methods of analysis, a significant correlation emerged only when expressing fox diet as percent volume (Table 3).

Among the three variables investigated, the method of analysis was the only (or main) variable included in the LRA model for garbage, earthworm, and mammal occurrence in fox diet, while the season mainly influenced the occurrence of insects and cultivated fruit, the latter varying also with altitude; bird occurrence was influenced by both the method and season (Table 4).

In terms of frequency, no difference was found between the stomach contents of either males (N=43) and females (N=31), or adults (N=49) and young foxes (N=33); in terms of volume, insects were consumed more by adults ($\%V_{Ad}$=55.5, $\%V_{Juv}$=9.17, U=1.5, P<0.05; Table 5).

4. Discussion

Both stomach and faecal collection methods depicted the red fox as a generalist predator, mainly relying on fruit and mammals. Also the seasonal trends were generally consistent with the expected food availability,

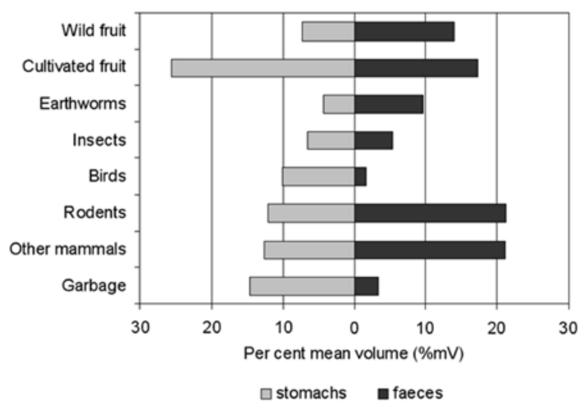

Figure 3. Percent mean volume of the main food items in fox diet as assessed by the analysis of stomach contents and faecal samples.

Food items	%FO faeces	%FO stomachs	χ^2	P
Wild fruit	25.6	13.2	5.88	<0.05
Cultivated fruit	28.2	36.4	1.81	n.s.
Earthworms	25.7	12.4	7.04	<0.05
Insects	13.8	19.8	1.97	n.s.
Birds	3.3	14.9	12.07	<0.01
Rodents	34.9	19.8	6.96	<0.05
Other mammals	30.9	16.5	7.03	<0.05
Garbage	4.6	20.7	17.28	<0.001

Table 1. Variation in the frequency of occurrence (%FO) of the main food items, as assessed by the analysis of stomach contents (N=121) and faecal samples (N=117).

		Wild fruit	Cultivated fruit	Earthworms	Insects	Birds	Rodents	Other mammals
Cultivated fruit	s. c.	-0.24**						
	f. s.	-0.08						
Earthworms	s. c.	-0.08	-0.001					
	f. s.	-0.06	0.02					
Insects	s. c.	-0.03	0.09	-0.05				
	f. s.	-0.05	-0.07	0.40***				
Birds	s. c.	0.08	-0.18*	-0.09	-0.10			
	f. s.	-0.004	-0.03	0.09	0.17			
Rodents	s. c.	-0.08	-0.22*	-0.06	0.02	-0.10		
	f. s.	-0.03	-0.19*	0.05	-0.12	-0.13		
Other mammals	s. c.	-0.11	-0.14	-0.12	-0.13	-0.19*	-0.01	
	f. s.	-0.17	-0.26**	-0.11	-0.13	-0.12	-0.27**	
Garbage	s. c.	-0.14	-0.19*	-0.07	-0.08	-0.16	-0.16	-0.14
	f. s.	-0.05	-0.06	-0.15	-0.10	-0.04	-0.16	-0.001

Table 2. Relationship between the proportion of use (%mV) of eight main food items, as assessed by Spearman's correlation coefficient for stomach contents (s.c., N=121) and faecal samples (f.s., N=117) (* $P<0.05$; ** $P<0.01$; *** $P<0.001$).

		Faecal samples		
		%FO	%V	%mV
Stomach contents	%FO	-0.14	0.28	0.07
	%V	-0.11	0.80**	0.17
	%mV	-0.04	0.74*	0.26

Table 3. Relationship (Spearmans' correlation coefficient) between the relative importance of the eight main food items as expressed by ascending ranks for each quantification method (* $P<0.05$; ** $P<0.01$).

	Variable	B	S.E.	Wald	df	P	Exp(B)
Wild fruit	Method	-0.658	0.351	3.509	1	0.061	0.518
Cultivated fruit	Season	0.512	0.138	13.86	1	0.000	1.67
	Altitude	-0.001	0.000	10.205	1	0.001	0.999
Earthworms	Method	-1.157	0.365	10.07	1	0.002	0.314
	Season	0.335	0.144	5.456	1	0.020	1.398
Insects	Season	0.350	0.16	4.8	1	0.028	1.419
Birds	Season	-0.774	0.25	9.62	1	0.002	0.461
	Method	1.877	0.632	8.83	1	0.003	6.535
	Altitude	-0.002	0.001	5.09	1	0.024	0.998
Rodents	Method	-0.967	0.341	8.049	1	0.005	0.38
	Season	0.236	0.136	3.02	1	0.082	1.266
Other mammals	Method	-0.824	0.357	5.31	1	0.021	0.439
	Season	-0.271	0.141	3.69	1	0.055	0.763
Garbage	Method	1.665	0.484	11.84	1	0.001	5.28

Table 4. Backward stepwise logistic regression model relating the occurrence of each food item in fox diet to three variables (method of analysis, season, altitude a.s.l.). The statistical significance of each coefficient in the model was tested by Wald's test.

Food items	Males		Females		Adults		Juveniles	
	%FO	%V	%FO	%V	%FO	%V	%FO	%V
Wild fruit	18.60	63.75	16.13	54.40	14.29	55.71	18.18	65.33
Cultivated fruit	30.23	68.08	35.48	68.64	30.61	63.67	45.45	79.33
Earthworms	9.30	36.25	12.90	41.25	14.29	34.29	6.06	37.50
Insects	18.60	31.88	25.81	44.38	20.41	55.50	18.18	9.17
Birds	18.60	71.25	9.68	60.00	12.24	65.00	18.18	76.67
Rodents	20.93	55.56	12.90	65.00	14.29	72.14	21.21	49.29
Other mammals	16.28	67.14	12.90	65.00	18.37	70.00	9.09	66.67
Garbage	25.58	76.82	25.81	73.75	22.45	79.55	24.24	68.75

Table 5. Main food items in the diet of different sexes and age classes.

with the slight altitudinal variation probably depended on the ranging behaviour of mountain foxes, whose home ranges usually include both Alpine prairies and valley bottoms [38]. Nonetheless, in determining the importance of the main food items in detail, some considerable differences emerged, outlining that each method can lead to the underestimation of the relative importance of some prey.

Unexpectedly, the best correspondence between the two methods was found when the importance of the different foods was compared by the percent volume, while the main source of variation occurred in the frequencies of occurrence. This result suggests that the method of quantification proposed by Kruuk and Parish [24], although being based on the estimate by eye of the bulk of each prey in faecal samples, can provide volume estimates as accurate as those obtained by the analysis of stomach contents. Although the use of estimated weights of remains [39] or biomass models [40,41] may be useful to assess the energy intake yielded by each food item [42], we suggest that Kruuk and Parish's method, also considering the ease and rapidity of volume assessment, represents an effective method to analyse faecal samples.

The underestimation of bird occurrence in fox diet through the analysis of faecal samples has been reported to be a general outcome [12]. Reynolds and Aebischer [11] suggested that the fox stomach acts as a separator of the micro- and macro-fragments of bird feathers; as a consequence, the presence of bird remains in the micro-fraction does not always correspond with that of large feather fragments in the macro-fraction, and only the routine analysis of the first one would allow the correct estimation of bird occurrence in scat analysis. In contrast, mammalian hairs are well preserved during the digestive process and easily found in the faecal samples [11]. Conflicting results have been reported for digestion processes found in other small mammals such as martens [6,8], suggesting that the separation of feather fragments could be a peculiarity of the physiology of digestion of foxes.

The higher frequency of occurrence of earthworms in faecal samples may depend on their short residence time in the stomach [5], which consequently increases the risk of underestimating their presence in the stomach contents [15].

Anthropogenic food is easier to identify in stomach contents than in faecal samples: the occurrence of scavenged meat, bread, and other processed food may be overlooked when analysing digested remains, which are often assigned to 'garbage' only in the presence of non-edible matter of human origin. Moreover, fox consumption of slaughtered remains of both domestic rabbits and poultry can be erroneously attributed to fox predation on their wild counterparts.

Logistic Regression Analysis showed that the variable "method of analysis" was the main factor determining the occurrence of food items in the fox diet, supporting the hypothesis that the resulting variation in the overall diet depended on methodological constraints. Nonetheless, faecal and stomach samples were collected in different ways – the first one along transects distributed in the main habitats, the latter from road-killed animals – possibly introducing some form of sampling bias. Although our results seem to exclude both age- and sex-related bias [12,43] (the road-killed samples included both males/females and young/adult foxes in similar proportions), road killed foxes may include a disproportionately high representation of synanthropic animals, which usually rely on highly profitable, anthropogenic food sources [15]. Accordingly, Cavallini and Volpi [12], who compared faeces to stomach and intestine contents of hunted foxes, did not find any variation in the frequency of occurrence of waste food, although they found a higher frequency of domestic birds in fox intestines than in faeces, suggesting that the diet of hunted foxes can also be biased (specifically toward farmyard-ranging animals). Considering our results, cultivated fruit prevailed in stomach contents, and rats (associated with anthropogenic activities) were preyed upon only by road-killed foxes, supporting the hypothesis that foxes feeding in urban and suburban areas may be more prone to be killed by cars.

In conclusion, using Kruuk and Parish's technique, the analysis of faecal samples proved to be as reliable as that of stomach contents in the quantification of food volumes. We suggest that scat analysis is more suitable to adequately represent the food habits of foxes living in mountain habitats (provided that the micro-fraction is sampled to identify both earthworm and bird remains), although the diet of the sub-population relying on anthropogenic food may be partially overlooked.

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Appendix 1. Diet of the red fox in the western Italian Alps, as assessed by the analysis of stomach contents (N=121) and faecal samples (N=117).

Food items	Stomachs		Faeces	
	%FO	%V	%FO	%V
MUSHROOMS (Fungi)	1.65	80.00	-	-
VEGETAL MATTER	50.41	67.54	50.43	67.80
Leaves and grass	1.65	75.00	3.42	85.00
Fruit	47.93	66.72	47.01	66.55
Undetermined fruit	3.31	40.00	0.85	30.00
Rosaceae	32.23	63.08	40.17	67.87
Rosa sp.	-	-	5.13	63.33
Sorbus sp.	-	-	4.27	47.00
Prunus sp.	8.26	61.00	7.69	61.11
Amelanchier ovalis	-	-	0.85	75.00
Cotoneaster integerrima	-	-	1.71	55.00
Rubus sp.	0.83	5.00	5.13	26.67
Apples (*Malus communis*)	15.70	68.42	4.27	69.00
Pears (*Pirus communis*)	2.48	65.00	14.53	78.53
Apricots (*Prunus armeniaca*)	1.65	65.00	-	-
Plums (*Prunus domestica*)	7.44	42.22	-	-
Moraceae (Figs *Ficus carica*)	4.13	54.00	0.85	70.00
Vitaceae (Grapes *Vitis vinifera*)	9.92	48.75	1.71	65.00
Fagaceae	2.48	58.33	3.41	27.5
Castanea sativa	1.65	85.00	2.56	26.67
Quercus sp.	0.83	5.00	0.85	30.00
Ericaceae (*Rhododendron ferrugineum*)	-	-	1.71	25.00
Ebenaceae (Persimmons *Diospyros kaki*)	0.83	60.00	3.42	20.00
Maize (*Zea mays*)	0.83	100	-	-
EARTHWORMS (Lumbricidae)	12.40	35.00	30.77	31.25
INSECTS	19.83	32.92	17.09	31.00
Undetermined insects	3.31	11.25	0.85	100.00
Orthoptera	9.09	37.73	9.40	34.55
Hymenoptera	-	-	0.85	15.00
Coleoptera	4.13	24.00	8.55	15.00
Dermaptera	0.83	5.00	-	-
Larvae	7.44	43.89	3.29	44.00
Undetermined larvae	0.83	20.00	0.85	100.00
Coleoptera	3.31	36.25	1.71	37.50
Lepidoptera	1.65	50.00	-	-
Diptera	1.65	65.00	-	-
FISH (*Salmo trutta* sp.)	0.83	30.00	-	-
FROGS (Anura)	-	-	2.56	63.33
REPTILES	4.13	23.00	-	-
Lacerta sp.	3.31	18.75	-	-
Natrix sp.	0.83	40.00	-	-
BIRDS	14.88	67.50	4.27	39.00
Undetermined birds	0.83	100	-	-
Passeriformes	11.57	63.21	4.27	39.00
Columbiformes	1.65	75.00	-	-
Galliformes	0.83	80.00	-	-

continued **Appendix 1.** Diet of the red fox in the western Italian Alps, as assessed by the analysis of stomach contents (N=121) and faecal samples (N=117).

Food items	Stomachs		Faeces	
	%FO	%V	%FO	%V
MAMMALS	31.40	71.32	56.41	76.97
Insectivores	2.48	36.67	5.98	51.43
Rodents	23.14	58.93	32.48	65.26
Undetermined rodents	2.48	48.33	5.98	56.43
Sciuridae (*Marmota marmota*)	1.65	60.00	1.71	50.00
Gliridae	4.13	68.00	3.42	52.50
Eliomys quercinus	1.65	75.00	0.85	40.00
Muscardinus avellanarius	2.48	63.33	0.85	30.00
Glis glis	-	-	1.71	70.00
Muridae	11.57	53.92	22.37	66.03
Chionomys nivalis	3.31	40.00	6.84	54.38
Microtus sp.	1.65	65.00	7.69	62.78
Myodes glareolus	0.83	30.00	4.27	79.00
Apodemus sp.	2.48	53.33	5.13	70.00
Rattus sp.	3.31	68.75	-	-
Lagomorphs	1.65	75.00	5.98	92.14
Lepus sp.	1.65	75.00	3.42	91.25
Lepus timidus	-	-	2.56	93.33
Ungulates	9.09	80.00	5.98	55.71
Undetermined ungulates	1.65	55.00	-	-
Sus scrofa	2.48	93.33	0.85	100
Rupicapra rupicapra	2.48	100	5.13	48.33
Capreolus capreolus	1.65	55.00	0.85	100
Carnivores	4.13	78.00	8.55	87.00
Undetermined carnivores	-	-	1.71	70.00
Vulpes vulpes	-	-	1.71	97.50
Mustela sp.	0.83	100	-	-
Martes sp.	-	-	-	-
Felis catus	3.31	72.50	2.56	81.67
GARBAGE	20.66	70.60	5.13	65.00