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Biases in the analysis of the diet of the red fox *Vulpes vulpes*

Paolo Cavallini & Teresa Volpi

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The diet of red foxes *Vulpes vulpes* from the province of Pisa, Central Italy, was compared on the basis of analysis of the contents of 320 guts (stomachs and intestines), and of 211 faecal samples. The faeces and guts were collected in the same area during the same period. Mammal remains (in particular of small mammals) were more abundant in faeces than in stomachs and intestines, whereas invertebrates and grass were more abundant in guts. This may be due to different sampling methods which included hunting (guts) which may lead to an overweight of young, inexperienced foxes, eating less preferred food items, being represented in the sample, and collection of faeces which might primarily come from resident, dominant individuals. Bird frequency, but not volume, decreased significantly from stomachs to intestines, and from intestines to faeces. Studies based on stomach contents report a higher percentage of bird remains than studies based on faeces (frequency of occurrence: 19.4 ± 10.3% vs. 9.1 ± 6.9%; $P = 0.014$). The bias presented may be related to the mechanics of digestion and suggestions to limit such biases are put forward.

Key words: Diet analysis, methods, bird consumption, red fox, Vulpes vulpes

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The diet of the red fox *Vulpes vulpes* is highly variable, both in space and time, owing to the species' enormous geographic range (Stains 1975) and adaptability to variable food availability (Cavallini & Lovari 1991). Main food items include rodents (e.g. Yoneda 1982), lagomorphs (Reynolds 1979), fruits and insects (Ciampalini & Lovari 1985), and earthworms (Macdonald 1980b). The feeding ecology of the red fox has been widely studied, especially because of the importance of the fox as a predator of small game (Pils & Martin 1978), and because of the influence of food on the social organisation of carnivores (Macdonald 1983). Analysing stomach contents and faeces composition have been the primary methods employed in studies of fox diet. Each method has its advantages: gut contents are more easily determined (Witt 1980), whereas faeces are more easy to collect and furthermore minimise interference, i.e. destruction of individuals, with the population being studied. It is not clear how the various techniques affect the estimation of dietary intake. Witt (1980) suggested that results based on stomach contents are incomparable with those based on investigations of excrements, and that even the contents of stomachs and intestines may differ considerably. No data, however, have been reported to support his suggestions. Therefore, we have tried to clarify interpretations based on different techniques. The aims of the present study were: 1) to compare estimates of food habits of the red fox obtained by different sampling methods; this will be done by comparing a sample of guts with a sample of faeces collected in the same area during the same period; and 2) to identify food items systematically over- or underestimated in the analysis of stomach contents, intestines and faeces.

Study area and methods

The study area covering 2,448 km^2 was situated in the province of Pisa, in Central Italy (43°N, 10-11°E), which consists of flat and intensively cultivated land (mainly cereals) in the north, becoming increasingly hilly (up to 800 m a.s.l.) and wooded towards the south. The climate is Mediterranean, with mild winters and dry, hot summers. In 1992, monthly averages of minimum temperatures ranged from 3.4°C to 19°C, and of maximum temperatures from 12°C to 31°C. Monthly means were below 10°C for three months, and above 20°C for four months. Rainfall is heaviest 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 (<20 mm of rain per month) were January, February, March, August, and May (in increasing order; Cavallini 1994).

Hunters collected foxes in the whole province during the main fox hunting season from January to the beginning of May 1992. We collected foxes (N= 330; 125 females and 205 males) from hunters within six hours after death and stored the carcasses in plastic bags at -2°C until dissection which took place within 48 hours after refrigeration. We removed the entire gut (from oesophagus to rectum) and stored it at -20°C until processing. Stomachs and intestines were analysed separately. Their contents were weighed, filtered, and macroscopically sorted out into categories. We microscopically analysed hair and feather fragments (Day 1966, Debrot et al. 1981), and classified other items by comparison with reference material.

During the same period (January to April inclusive), we collected fresh red fox faeces (identified by smell, size and shape; Bang & Dahlström 1974) monthly along fixed transects in seven areas uniformly distributed in the study area (see Cavallini 1994, for the location of areas). The sampling areas were part of the area in which foxes were killed by hunters. To be able to compare techniques we discarded faecal samples from two areas where no hunting occurred. The diet of the red fox in the seven study areas was homogeneous (Cavallini & Volpi, in press) and therefore we pooled the material from these areas. We stored faeces in a deep-freezer and later they were analysed in the same way as the digestive tracts.

Indices of diet based on occurrence usually overestimate small items eaten often, but in small quantities (Putman 1984). We did not use conversion factors (Lockie 1959) due to the lack of published factors for many categories, and to the high variability between estimates of different studies (Lockie 1959, Liberg 1982, Palomares & Delibes 1990, Roger et al. 1990, Stahl 1990, Reynolds & Aebischer 1991). We therefore used estimated volume according to the method described by Kruuk & Parish (1981) recently used to analyse the diet of the red fox and other carnivores (e.g. Cavallini & Nel 1990, Cavallini & Lovari 1991, Saunders et al. 1993, Serafini & Lovari 1993, Weber & Aubry 1994).

To estimate the relative volume, we counted (or estimated from the number of remains) the total number of each kind of prey in each sample; we multiplied the number of prey items by the bulk of each prey before ingestion (known from reference material), and the proportion of each food category to the total bulk was estimated; the average proportion across samples is therefore an estimate of the volume of ingested food (Kruuk & Parish 1981).

To compare the relative volumes of the various categories, we used three tests: 1) for the overall difference between methods, we used the Kruskal-Wallis one-way ANOVA (H); 2) when the ANOVA detected a significant difference, we tested for the difference between stomachs and intestines, matching pairs of samples (stomach and intestine of the same individual) by use of the Wilcoxon test (Z); 3) for difference between intestines and faeces (and for differences among published studies) we used Mann-Whitney test (U). Differences between frequencies were tested by use of chi-square test (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.

Results and discussion

Study in the province of Pisa

Due to 10 damaged samples, we only analysed 320 guts out of the 330 collected; 176 of these originated from the northern parts of the study area, and 144 from the southern parts. Of the 320 guts analysed, 266 stomachs and 310 intestines held measurable contents ($\geq$ 6 g). The higher number of empty stomachs than of empty intestines may probably be ascribed to faster passage through the stomach section.

Table 1. Comparison of diet composition (volume in percent) estimated by analysing the contents of stomachs (N = 262), intestines (N = 304), and faeces (N = 211) of red foxes from the province of Pisa, Central Italy, during January-May 1992. H = Kruskal-Wallis ANOVA; Z = Wilcoxon test; U = Mann-Whitney test.

	Stomachs	Intestines	Faeces	Overall		Stomach vs. intestines		Intestines vs. faeces	
				H	P	Z	P	U	P
Total mammals	56.8	53.9	68.0	23.0	<0.001	0.973	0.331	39618	<0.001
Small mammals	19.2	18.7	30.5	10.4	0.006	1.080	0.280	36692.5	0.002
Large mammals (wild)	8.6	8.8	4.1	5.8	0.05	-	-	-	-
Large mammals (domestic)	29.1	26.3	33.5	3.5	0.17	-	-	-	-
Total birds	20.5	11.8	7.8	29.8	<0.001	5.837	<0.001	28669.5	0.010
Wild birds	9.5	5.0	4.2	8.9	0.012	4.189	<0.001	31563	0.60
Domestic birds	10.9	6.8	3.5	21.4	<0.001	4.083	<0.001	28707	0.001
Invertebrates	6.6	7.0	2.8	35.9	<0.001	0.618	0.537	24169.5	<0.001
Total plants	10.5	16.2	13.1	4.9	0.08	-	-	-	-
Wild fruits	0.5	1.0	1.8	0.7	0.70	-	-	-	-
Cultivated fruits	4.4	7.9	6.9	2.1	0.34	-	-	-	-
Other vegetable matter	5.7	7.3	4.4	16.0	<0.001	2.250	0.024	27420.5	<0.001
Refuse	5.5	11.2	8.2	5.8	0.05	-	-	-	-

We collected 221 faeces in the seven sampling areas averaging 30 faeces ± 23 (SD) per area; 124 originated from the northern and 97 from the southern parts of the study area.

The diet was predominated by mammals, whereas birds, invertebrates, fruits and refuse were volumetrically less important (Table 1). Several food items were found in statistically different percentages in stomachs, intestines and faeces. The volume of small mammals (mostly rodents) differed between sample types. Volumes in stomachs and intestines were similar, but the volume in faeces was higher than in intestines. As a consequence, the total volume of mammals also differed between sample types and was higher in faeces, but occurred in similar quantities in stomachs and intestines. Large mammals (both wild and domestic) were equally represented in the three sample types.

Total bird volume (including eggs) differed between sample types, and decreased progressively from stomachs to intestines, and from intestines to faeces. Similar results were obtained when considering separately domestic birds, and wild birds, but the difference between intestines and faeces was not significant for wild birds. When present, the average volume did not differ between sample types (all birds: $N = 261, H = 3.1, df = 2, P < 0.208$; wild birds: $N = 120, H = 1.2, df = 2, P < 0.539$; domestic birds: $N = 143, H = 2.6, df = 2, P < 0.276$), but frequency of occurrence decreased from stomachs to intestines to faeces (all birds: $\chi^2 = 28.75, P < 0.001$; wild birds: $\chi^2 = 8.34, P < 0.015$; domestic birds: $\chi^2 = 21.94, P < 0.001$, all N's = 777, df = 2; Fig. 1).

Invertebrate (mainly insects) volume differed between sample types; it was similar in stomachs and intestines, but significantly lower in faeces. The volume of plant matter and fruits (both wild and cultivated) were similar across methods, but grass, leaves and other vegetable matter of uncertain trophic value were less represented in faeces than in intestines, with little difference between stomachs and intestines.

Our results caution against directly comparing the diet of the red fox as shown by different studies, employing different sampling methods (stomachs, intestines, faeces). Several of the differences found in our study may be due to sampling bias. Hunting and trapping are used to collect digestive tracts, and the animals killed are often young, inexperienced foxes (Lindström 1983). Converse-

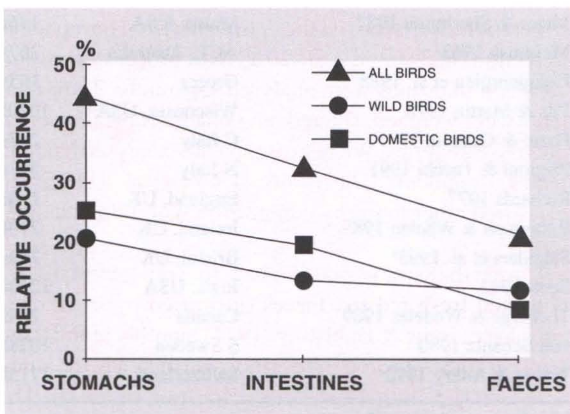

Figure 1. Relative frequency of occurrence of birds (i.e. percentage of samples with remains of birds) according to different sampling methods in red foxes from the province of Pisa, Central Italy, during January-May 1992.

ly, faeces of dominant, resident foxes might be more easily visible, due to their territorial functions (Macdonald 1980a), and thus collected more often. Therefore, we predict that food items which are less valuable or easier to catch would be overrepresented in guts (without difference between stomachs and intestines), whereas preferred food items would be more abundant in faeces. Our data are consistent with this hypothesis: mammals and in particular small mammals, a preferred food item according to Macdonald (1977), are more abundant in faeces, whereas invertebrates, which are easy to catch, and vegetable matter (excluding fruits, and therefore of dubious trophic value) are more abundant in guts (see Table 1).

Sampling biases, however, cannot explain the significant decrease in volume and frequency of bird remains from stomachs to intestines to faeces (see Table 1 and Fig. 1). Differential passage through the pyloric sphincter may explain this pattern, as large fragments of feathers may remain trapped in the stomach, whereas small fragments that are usually overlooked in food analyses pass more rapidly (Reynolds & Aebischer 1991). Stomach analysis may therefore overestimate bird consumption, whereas intestine and especially excrement analyses may systematically underestimate it.

Literature review

We then reviewed the literature on the diet of the red fox, excluding the following studies: those with N < 100, those lasting less than one year, and those not reporting annual

Table 2. Comparison of red fox diet composition (frequency of occurrence in percent, recalculated when necessary) according to reference and study area. Due to different methodologies, figures are approximations only.

Reference	Area	N[1]	Mammals	Birds	Invertebrates	Plants	Fruits
Artois & Stahl 1991[2]	N France	203f	87	5	-	-	6
Borkowski 1994	S Poland	144f	45	5	15	29	21
Cavallini & Volpi, in press	C Italy	1261f	32	10	22	32	27
Coman 1973	VIC, Australia	967s	40	9	20	26	0
Doncaster et al. 1990	Oxford, UK	1160f	19	11	33	-	9
Fairley 1970[3]	Ireland	340s	65	35	-	-	-
Goszczynski 1986[2]	Poland	1139f	67	26	1	-	6
Green & Flinders 1981	Idaho, USA	125f	67	6	10	17	-
Harris 1981[4]	London, UK	571s	16	20	21	8	-
Hewson & Kolb 1975[3]	Scotland, UK	523f	93	5	-	-	-
Hockman & Chapman 1983	Maryland, USA	128s	53	21	7	20	-
Jedrzejewski & Jedrzejewska 1992	E Poland	389f	70	10	5	12	-
Jensen & Sequeira 1978[3]	Danmark	169s	52	31	12	-	5
Jones & Theberge 1983	Canada	>200f	52	5	0	-	12
Korschgen 1959	Missouri, USA	1006s	-	17	4	13	-
Leinati et al. 1961	N Italy	5280f	38	2	6	46	13
Lucherini & Crema 1994	N Italy	270f	33	4	39	24	15
Major & Sherburne 1987	Maine, USA	186f	-	6	3	13	-
McIntosh 1963	ACT, Australia	267s	33	4	48	14	-
Papageorgiou et al. 1988	Greece	165s	31	18	21	26	-
Pils & Martin 1978	Wisconsin, USA	1020f	-	19	6	17	-
Pozio & Gradoni 1981	C Italy	257s	49	30	6	12	-
Prigioni & Tacchi 1991	N Italy	223f	47	21	7	20	-
Richards 1977	England, UK	186f	24	6	25	-	3
Robertson & Whelan 1987	Ireland, UK	210f	27	14	28	29	11
Saunders et al. 1993[5]	Bristol, UK	749s	6	9	16	5	-
Scott 1943	Iowa, USA	1220f	44	15	23	18	-
Theberge & Wedeles 1989	Canada	204f	94	0	0	3	-
von Schantz 1980	S Sweden	1028f	71	10	10	5	-
Weber & Aubry 1993	Switzerland	1213f	62	2	10	-	6

[1] f = faeces; s = stomachs
[2] % biomass
[3] excluding minor food items
[4] % importance
[5] % volume

averages. We reported (or recalculated, when necessary) the relative frequency of occurrence (i.e. the percentage of samples containing the item). In a few cases, we reported other methods (estimated volume or biomass) to increase sample size. Due to differences in the methods used (some studies excluded "minor items", some aggregated results in different categories), it was not possible to calculate exact figures for each study, and therefore the results shown in Table 2 should be regarded as approximations only.

When comparing published studies conducted with different sampling methods, birds were more common in stomachs (frequency of occurrence: 19.4 ± 10.3%; N = 10) than in faeces (9.1 ± 6.9%; N = 20; U = 44, P = 0.014). Other categories were similarly represented in the two types of samples (mammals: N = 27; U = 109, P = 0.150, invertebrates: N = 27; U = 67.5, P = 0.487, plants: N = 21; U = 65, P = 0.345, fruits: N = 13; U = 21, P = 0.047, see Table 2). These results suggest that the underestimation of bird consumption in faeces analysis is a general phenomenon, which should be expected if it is a consequence of the physiology of digestion (Reynolds & Aebischer 1991, this study). Similar biases may be expected in other carnivores. We therefore recommend that the contents of both stomachs and intestines should be analysed when studying guts, and that the average of the two should be calculated. Furthermore, when studying faeces, the underestimation of bird consumption may be avoided by the examination and quantification of microscopic fractions of faeces as described by Reynolds & Aebischer (1991).

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