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SHORT COMMUNICATION

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Six scat-analysis methods were compared and tested for differential assessment of a wolf *Canis lupus* diet in the Northern Apennine Mountains, Italy. A sample of 217 wolf scats was analysed using standardised laboratory techniques, and the recovered undigested remains were quantified according to the following diet measurements: frequency of occurrence, dry weight (estimated and measured), relative volume, and biomass ingested (two methods). With the exception of one of the biomass methods, there was no significant disagreement between the procedures examined. However, some discrepancies between rankings from different methods indicated the sources of bias that should be accounted for to avoid misleading conclusions. Frequency data can be corrected to reduce some of the associated forms of bias, whereas rankings by weight and volume appear affected by the structure of undigested remains. Although to different extents, all the methods which rank food items according to direct measures of the undigested remains, i.e. by frequency, weight, and volume, suffer from the surface to volume ratio bias of varying prey sizes. Linear-regression biomass models correct for the surface/volume bias, but there are some drawbacks when applying them, and they are limited to mammalian prey. Applicability of the biomass models should be evaluated on the basis of diet composition and prey sizes, and results carefully interpreted in concert with other field-collected information. Interpretation of scat-analysis data in order to assess the diet of wolves, as well as of other carnivores, would be greatly enhanced by comparing results obtained with two or more methods.

Key words: Canis lupus, wolf diet, scat-analysis, method comparisons, biomass intake

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An increasing number of studies concerning food habits of wolves *Canis lupus* has recently been carried out throughout Europe (e.g. Salvador & Abad 1987, Lesniewicz & Perzanowski 1989, Fernández et al. 1990, Vila et al. 1990, Cuesta et al. 1991, Jedrzejewski et al. 1992, Mattioli et al. 1992, Meriggi et al. 1992, Barrientos 1993, Ionescu 1993, Patalano & Lovari 1993, Smietana & Klimek 1993, Ciucci 1994, Papageorgiou et al. 1994, Poulle et al. 1995). Knowledge of wolf feeding ecology is critical not only in an ecological context but also in terms of economics and conservation, particularly in light of the recent and on-going expansion of the wolf range in Europe (cfr. Promberger & Schröder 1993). However, it is imperative that food habit studies be reli-

able, their results correctly interpreted, and limits of the applied methodology be accounted for. This is particularly relevant for scat-analysis, a technique widely used for studying carnivore food habits (Putman 1984) and frequently adopted to assess the diet of wolves. Compared to other techniques, scat-analysis is easy to apply, allows relatively large sample sizes and, most importantly, is non-intrusive and compatible with the endangered and/or threatened status of the wolf in most countries. However, scat-analyses can present both technical and interpretational difficulties (Reynolds & Aebischer 1991), and involve methods which differ in the procedure of quantifying undigested remains from scat samples, e.g. frequency, volume and biomass, thus limiting meaningful comparisons between studies.

Both interpretation among and comparability between diet studies would benefit from a better understanding of the sources of error associated with each method of analysis, i.e. measures of accuracy and precision. One approach is to design feeding trials in order to develop models to accurately estimate the relative importance of prey types in the diet from faecal samples. This has been done for several carnivore species (Scott 1941, Lockie 1959, Goszczynski 1974, Johnson 1981, Ackerman et al. 1984, Kelly 1991), including wolves (Floyd et al. 1978, Weaver 1993). Alternatively, different scat-analysis methods can be compared in order to test their differential assessment of the diet (e.g. Corbett 1989). No such approach has been designed for wolves, although this appears desirable given the wide spectrum of scat-analysis methods currently adopted by different authors to assess the diet of wolves. In this perspective, the aim of our work was to evaluate to what extent different scat-analysis methods influence the assessment of the wolf diet. To do this we applied Corbett's (1989) comparative approach to six methods: frequency of occurrence, estimated dry weight, measured dry weight, relative volume, and two procedures for biomass intake. Comparisons between indices do not tell us much about their inherent accuracy unless they are validated against the population to be estimated (e.g. White 1992). We do not intend to offer a measure of accuracy for each method nor to single out the most reliable method for estimating the diet of wolves. Rather, we statistically evaluate concordance among the different methods, and interpret discrepancies between them in terms of sources and amplitude of inherent biases. Pros and cons, and the interpretational limits of each method are pointed out and discussed by elucidating the nature of the biases involved. This could prove useful in designing future food habit studies for wolves and other large carnivores, in setting priorities for methodological research and, most importantly, in enhancing the interpretation and comparability of studies.

Methods

Study area

Wolf scats were collected from June 1991 to November 1993 in a mountainous region which encompasses the Orecchiella Natural Park (5,218 ha) and adjacent territory along the Northern Apennines, Italy. Altitude ranges from 800 to 2,054 m a.s.l., and about 72% of the area is covered by beech *Fagus sylvatica* and mixed forests, followed by alpine meadows (11%), and pastures (8%). With the exclusion of two small villages inhabited mostly in summer, there are no human settlements in the area due to a steady and constant decline in the local population during the past 30 years. Local wolf recolonisation occurred recently after a period of at least 60 years since their extirpation (Cagnolaro et al. 1974). As a consequence of local large game introductions (mouflon *Ovis orientalis*) and reintroductions (red deer *Cervus elaphus* and roe deer *Capreolus capreolus*) by the Forest Service beginning in the 1960s, and the range expansion of the wild boar *Sus scrofa* throughout Italy (Apollonio 1992), wild ungulate populations today are locally abundant and form the bulk of the wolf diet (Ciucci 1994). Feral and/or stray dogs do not reside in the Park, although occasional vagrant domestic dogs were captured by the Forest Service probably after being abandoned following the hunting and tourist seasons. During our study, we estimated that one local wolf pack consisting of 2-5 individuals in early winter, and one possibly transient individual frequented the area.

Scat collection and laboratory procedure

Wolf scats were collected according to an opportunistic sampling (*sensu* Frenzel 1974) along travel routes used by wolves (paths, trails, and dirt roads: hereafter scat-trails) and by following wolf tracks in the snow. We estimated the age of scats based on the time elapsed since the last sampling effort (maximum 2-8 weeks), the scat appearance, exposure of deposition site, and weather conditions. In most field conditions, no single criterion allows distinction between scats of wolves and dogs; therefore we adopted a conservative multi-criteria approach to differentiate wolf scats from those of other canids (Ciucci 1994). Of all the scats collected, and for the scope of this study, only those non-weathered (Reynolds & Aebischer 1991) and considered as 'collectable' (*sensu* Floyd et al. 1978) were included in the analysis.

Scats were collected in nylon bags, labelled, and frozen (-30°C) prior to analysis. Laboratory procedures followed Reynolds & Aebischer (1991). Prior to treatment, each scat was thawed, oven-dried (90°C for 24 hours), and weighed (0.01 g precision). Each scat was soaked in water for 24-48 hours, and micro and macro-components

of each scat were separated by thorough washing in a sieve with a mesh size of 0.5 mm. The microscopic fraction of the scat was represented by water-soluble particles and components fragmented finely enough to pass through the sieve, whereas all other remains, larger than the mesh size, represented the macro-components and were further identified in the analysis. The microscopic fraction is generally discarded assuming it originates from food items in the same proportions as the macroscopic remains. Reynolds & Aebischer (1991), however, found this not to be true for remains of birds recovered in fox scats, and demonstrated that examination of the sole macroscopic fraction might result in underestimation of birds and earthworms consumed by foxes. Since birds were only rarely represented in the diet of wolves in our study area, and earthworms were not believed to be an important food source for wolves, the microscopic fraction of the scat was not analysed further assuming this would not significantly affect the results.

For each scat, macro-components were hand separated by food item (e.g. hairs, bones, seeds), dried (90°C for 1.5 hours), weighed, and their relative proportions by volume estimated by eye with the aid of a superimposed reference grid (Reynolds & Aebischer 1991). Items of little or no nutritive value, believed to be ingested either intentionally, i.e. *Graminae*, or involuntarily, i.e. leaves, soil, rumen content, plastic and other man-made materials, were excluded from the analysis. Macroscopic remains of birds, invertebrates, and seeds were identified by comparison with reference material. Hairs of mammals recovered in wolf scats were identified by colour, length and texture and by microscopic examination of the cuticular pattern, the medulla (Teerink 1991) and, in some cases, the cross-section (Mathiak 1938). Comparisons were made with hairs of mammals collected locally and the reference manual of Teerink (1991). Bone remains were identified by referencing to museum specimens. Skin and other undigested flesh remains of mammals were identified by association with the hairs (Corbett 1989), whereas nails and teeth were pooled with the bones for weighing. Among wild ungulates, juveniles (≤ 5 months) were identified on the basis of characteristic microscopic hair features, detectable from birth to the first autumn molt (Pimlott et al. 1969, Voigt et al. 1976, Scott & Shackleton 1980, Potvin et al. 1988), and size and structure of bone remains (Schmid 1972). The accuracy of trained observers (E.R.P., M.R., I.G.) in identifying mammal hairs was assessed through a blind test on a sample of 120 hairs from local mammals, of which 54 (45%) were from wild ungulate species, and the rest from other species. Reported accuracy averaged 99.7% (range: 99.2 - 100%; N = 360) at the species level and 100% (N = 41) at the age-class level for wild ungulates; in both cases high enough to prevent the use of correction factors (cfr. Reynolds & Aebischer 1991). The lower accuracy reported for age classes for domestic ungulates ($\bar{x}$ = 96.8%, range: 95.2 - 100%, N = 21) depended entirely on errors in identifying age classes of horses which, therefore, were not accounted for in the analysis. When identification at the species level was not possible, food items were grouped (e.g. unidentified mammals, unidentified ruminants) or referred to a higher taxonomic level (e.g. Coleoptera, birds).

Scat-analysis methods

Scat-analysis methods differ in their procedure of quantifying undigested food remains. Of those most often adopted to assess the diet of wolves or other large carnivores, we compared the following: A) frequency of occurrence (Murie 1944, Cowan 1947, Mech 1966, Pimlott et al. 1969, Scott & Shackleton 1980, Peterson 1977, Guitian et al. 1979, Ackerman et al. 1984, Peterson et al. 1984, Ballard et al. 1987), B) measured weights of remains (Johnson & Hansen 1977, Reig & Jedrzejewski 1988); C) estimated weights of remains (Lockie 1959, Johnson & Hansen 1977, 1979, Corbett 1989); D) relative volume of remains (Peyton 1980, Fritts & Mech 1981, Fox & Streveler 1986, Hellgren & Vaughan 1988, Windberg & Mitchell 1990, Mattioli et al. 1992); E) biomass ingested, using the model of Floyd et al. (1978) (Carbyn & Kingsley 1979, Scott & Shackleton 1980, Fritts & Mech 1981, Ballard et al. 1987, Potvin et al. 1988, Gasaway et al. 1992, Mattioli et al. 1992, Huggard 1993, Jhala 1993), and F) biomass ingested, using the model of Weaver (1993). Frequency data are calculated as percentage of occurrence (Lockie 1959), where the frequency with which each food item occurs is expressed as a percentage of the total number of occurrences of all food items, rather than a percentage of the total number of scats. We believe the former measure to be more meaningful in terms of diet composition as it expresses the frequency of a food item relative to the other food items recovered in the scat sample. In addition, different prey items can be grouped together (e.g. by prey type, taxonomic group) and their frequency expressed independently by group (e.g. large ungulates, mammals) (Kelly 1991). In order to reduce the bias occurring when food items contributing different amounts to a scat's volume are equated by frequency (i.e. equating of occurrences bias; cfr. Kelly 1991: 68), we did not consider in the analysis remains whose proportions in a scat were <3%. This accounted also for the potential bias due to the occasional presence, in trace amounts, of long guard hairs of large ungulates (especially wild boar and red deer). Since these hairs are long relative to the diameter of the pyloric sphincter, they might have been 'trapped' by the stomach and their passage through the gut delayed (cfr. Reynolds & Aebischer 1991). Relative weights of remains were ob-

tained in two ways: a) by hand separation and dry-weighing each food item, and b) by visually estimating the proportion of each food item in the scat and multiplying by the dry weight of the scat; with this procedure, macroscopic remains of different items (including non-food items) are assumed to have equal densities (cfr. Reynolds & Aebischer 1991). Relative volumes of remains were visually estimated with the aid of a superimposed reference grid, and each food item was expressed as a percentage of the volume of each scat. Biomass ingested was estimated on the basis of the known relationship between prey biomass consumed per collectable scat produced, using the models of Floyd et al. (1978) and Weaver (1993) obtained by feeding trials with packs of captive wolves. Both biomass models are in the form of linear regressions, where the dependent variable (y) represents the biomass ingested/collectable scat, and the independent variable (x) is the live weight of the prey species recovered in the scat. The regression parameters of the two models [$y = 0.383 + 0.02x$, $r^2 = 0.97$ (Floyd et al. 1978); $y = 0.439 + 0.008x$, $r^2 = 0.78$ (Weaver 1993)] yield different estimates of prey body mass (kg) per collectable scat as the two models differ in their experimental design. Prey consumed by wolves in feeding trials by Floyd et al. (1978) ranged in size from snowshoe hares *Lepus americanus* to a single adult white-tailed deer *Odocoileus virginianus*, whereas Weaver (1993) incorporated a greater array of large cervid prey (mule deer *Odocoileus hemionus*, elk *Cervus elaphus* and moose *Alces alces*) and integrated results from his feeding trials with those by Floyd et al. (1978) and Traves (1983).

To account for the scats containing more than one prey item, we applied the biomass models to the equivalent number of scats containing a given prey species (Floyd et al. 1978, Corbett 1989). The equivalent number of scats was calculated by visually estimating the relative proportions of an individual prey species in the scat and summing the proportions obtained for all the scats where that prey species had been recovered. Live weights of the prey species were taken from the literature (Maoli 1973, Perco & Perco 1979, Perco 1986, Pedone et al. 1991). For large prey, live weights were adjusted to account for differences in body size between age classes (Floyd et al. 1978, Fritts & Mech 1981) by weighing juvenile and adult weights on the basis of their relative proportions in the scat sample (Corbett 1989). Adjusted weight for 'unidentified ruminant' category was calculated from adjusted weights of the identified ruminant species, assuming their relative proportions were the same in the identified and unidentified samples.

The statistical design to assess the relative performance of the different methods followed Corbett (1989), where results obtained by each method are expressed as ranks of importance of the food items, and the rankings resulting from different methods are then compared simultaneously to obtain an overall measure of agreement (Kendall coefficient of concordance, W). Significance of W-values was tested by Friedman's method (Sokal & Rohlf 1981: 609). To further assess the agreement between pairs of methods, Spearman correlation coefficients were calculated for the rankings and, because $N > 10$ in all cases, their significance was tested as ordinary product/moment correlation coefficients (Sokal & Rohlf 1981: 607). Comparisons were run to allow assessment of concordance both within and between groups of methods that differ by nature, i.e. measurement of undigested remains vs. actual biomass intake, evaluating the influence of a particular method on the overall concordance, i.e. Kendall's W, by its selective removal/addition/substitution in sets of simultaneous comparisons. Simultaneous and pairwise comparisons included: i) measured dry weight, estimated dry weight; ii) percentage of occurrence, estimated dry weight, relative volume; iii) percentage of occurrence, estimated dry weight, relative volume, biomass (Floyd et al. 1978); iv) biomass (Floyd et al. 1978), biomass (Weaver 1993); v) percentage of occurrence, estimated dry weight, relative volume, biomass (Weaver 1993). Unlike Corbett (1989), for both simultaneous and pairwise comparisons involving the biomass models, rankings were limited to food items represented by mammal species only, as we believe applicability of the models to food items structurally different from those originally tested (Floyd et al. 1978, Weaver 1993) cannot be assumed to be valid for both statistical and biological considerations.

Results

A total of 263 wolf scats was collected from June 1991 to November 1993. Mean number of scats collected varied neither by season (winter: $\bar{x} = 26.3$; spring: $\bar{x} = 21.3$; summer: $\bar{x} = 16$; fall: $\bar{x} = 24$) (ANOVA, $F = 0.24$, $P > 0.7$), nor by year on a seasonal basis (1990-91: $\bar{x} = 19.5$; 1991-92: $\bar{x} = 20.7$; 1992-93: $\bar{x} = 25.2$) (ANOVA, $F = 0.08$, $P > 0.9$). Of the total collected, 79 scats (30%) were deposited in winter, 64 (24%) in spring, 49 (19%) in summer, and 71 (27%) in fall, and the seasonal distribution of the sample did not differ from a theoretically uniform one ($\chi^2 = 7.56$; $P > 0.05$). Forty-six scats were not included in the analysis because they were weathered ($N = 21$) or of loose, semi-liquid appearance (i.e. non-collectable; $N = 25$), thus leaving a sample of 217 scats for the methodological comparison. Mean ($N = 217$) scat dry weight (± SE) was 31.1 ± 1.7 g, whereas mean dry weights of macro and micro-components per scat were 14.3 ± 0.8 g and 16.8 ± 1.3 g, respectively. Micro-components represented on average (± SE) 42.1 ± 0.3% of each scat dry weight.

The relative importance of the food items recovered in the scat sample as quantified by the different methods is shown in Table 1, where food items are ranked in ascending order according to percentage of occurrence in the diet. Mammals were the dominating category in the diet, accounting for 88.7% of all the occurrences and ranging from 96.4% (relative volume) to 98.1% (estimated and measured dry weight) of the diet. With regard to the main food categories in the diet (Fig. 1), wild ungulates (especially wild boar, mouflon and roe deer) composed the bulk of the diet, their share ranging from 60.8% by percentage of occurrence to 72.1% by estimated dry weight. Also in terms of biomass eaten, wild ungulates predominated representing 58.9% and 62.3% of the total biomass consumed according to the models of Floyd et al. (1978) and Weaver (1993), respectively. Domestic mammals were of secondary importance, although in terms of biomass ingested they represented 30.6% and 37% of the diet according to the models of Weaver (1993) and Floyd et al. (1978), respectively (see Fig. 1). Biomass values for domestic mammals were mostly affected by large domestic ungulates, i.e. horses and cattle, which were consumed only occasionally (i.e. 3.3% by percentage of occurrence) but whose large weights (see Table 1) were reflected in large bio-

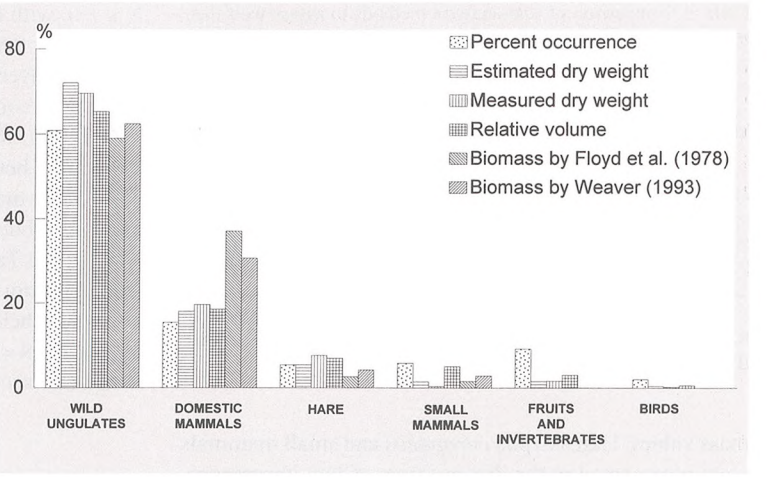

Figure 1. Main food categories in the wolf diet (Northern Apennines, Italy), as assessed by six scat-analysis methods (N = 217).

Table 1. Composition of the wolf diet and food item rankings by six quantification methods of analysis (217 scats) in the Northern Apennines, Italy.

		Quantification methods											
		Percentage of occurrence		Estimated dry weight		Measured dry weight		Relative volume		Biomass (Floyd et al. 1978)		Biomass (Weaver 1993)	
Food item	Adjusted weight (kg)	N	rank	g	rank	g	rank	%	rank	kg	rank	kg	rank
Wild boar *Sus scrofa*	42.95	64	1	1,271	1	521.70	1	3,570	1	46.6	1	29.3	1
Mouflon *Ovis orientalis*	19.56	33	2	693	2	318.70	2	2,477	2	19.2	5	14.7	2
Roe deer *Capreolus capreolus*	19.39	26	3	517	3	311.90	3	1,928	3	14.9	6	11.4	4
Domestic sheep	43.90	24	4	393	4	179.40	4	1,579	4	19.9	4	12.5	3
Small mammals*	0.06	14	5	55	12	5.70	16	703	6	2.7	11	3.1	10
Hares *Lepus europaeus*	4.20	13	6	219	5	141.20	5	983	5	4.6	9.5	4.6	8
Invertebrates		11	7.5	27	16	15.33	14	179	14				
Fruits		11	7.5	33	14	15.20	15	248	11				
Undetermined ruminants	35.16	10	9	143	7	53.40	7	475	8	5.2	8	3.4	9
Red deer *Cervus elaphus*	108.60	9	10	156	6	52.30	8	511	7	13.0	7	6.7	7
Horses	234.00	5	11.5	118	9	84.20	6	445	9	22.5	2	10.2	5
Birds		5	11.5	16	17	4.60	17	79	17				
Fallow deer *Dama dama*	65.87	4	13	121	8	30.30	11	269	10	4.6	9.5	2.6	11
Undetermined mammals**		3	15	35	13	20.10	12	113	16				
Cattle	447.21	3	15	81	11	33.60	10	218	12	20.3	3	8.7	6
Dogs	22.00	3	15	114	10	46.60	9	210	13	1.7	12	1.3	12
Cats	4.20	2	17	29	15	19.10	13	165	15	0.8	13	0.8	13

* Including Rodentia and Insectivora
** Except small mammals

Table 2. Comparison of scat-analysis methods to assess wolf diet, as tested by simultaneous concordance (Kendall coefficient of concordance, W), supported by pairwise correlation (Spearman rank correlation coefficient, r).

Method comparison*	Coefficient of concordance (Kendall's W)	P	Coefficient of correlation (Spearman's r)
P.O. / E.D.W. / R.V.	0.86	<0.001	0.63 - 0.91
P.O. / E.D.W. / R.V. / Bio 1	0.78	<0.001	0.47 - 0.91
P.O. / E.D.W. / R.V. / Bio 2	0.88	<0.001	0.77 - 0.91

* P.O.: Percentage of occurrence; E.D.W.: Estimated dry weight; R.V.: Relative volume; Bio 1: Biomass model of Floyd et al. (1978); Bio 2: Biomass model of Weaver (1993)

mass values. Hares *Lepus europaeus* and small mammals were represented in the diet as items of low importance, the latter being ranked proportionally higher by percentage of occurrence (5.8%) and relative volume (5%) than by the other methods (see Fig. 1). Other items of low importance in the diet were fruits and invertebrates as well as birds, all three being ranked higher by percentage of occurrence than by the other methods (see Fig. 1).

Agreement among rankings was significant in all simultaneous comparisons ($0.78 \leq W \leq 0.88$, Table 2), being lowest for the one involving the biomass model of Floyd et al. (1978) and highest when this was substituted by Weaver's (1993) model (see Table 2). This was supported by Spearman's correlation coefficients in pairwise comparisons ($0.63 \leq r_s \leq 0.94$; $0.01 < P < 0.001$; $13 < N < 17$, Table 3). With the exception of the model of Floyd et al. (1978), agreement among the different methods was particularly strong for the most important food items, i.e. rank ≤ 4 (see Table 1).

Higher correlations between rankings were obtained in pairwise comparisons involving variants of the same method (see Table 3), being highest for variants involving dry weight data ($r_s = 0.94$; $P < 0.001$; $N = 17$).

The biomass model of Floyd et al. (1978) did not agree with any of the other methods ($0.47 \leq r_s \leq 0.55$; $P > 0.05$; $N = 13$), with the exception of Weaver's (1993) biomass model ($r_s = 0.89$; $P < 0.001$; $N = 13$, see Table 3). Ranking by Weaver's (1993) model correlated well with rankings relative to the other methods ($0.77 \leq r_s \leq 0.81$; $0.01 < P < 0.001$; $N = 13$, see Table 3). However, although the correlation between rankings of the two biomass models was higher than that obtained between rankings of each biomass model and any of the others ($0.47 \leq r_s \leq 0.81$; $N = 13$, see Table 3), it accounted mostly for food items from medium to low importance (see Table 1), as it did not hold when referred to high-ranking food items only ($r_s = 0.09$; $N = 6$, representing 61.3% of the total biomass consumed according to the model of Floyd et al. 1978).

Discussion

Concordance and correlation coefficients resulting from the simultaneous and pairwise comparisons showed that, with the exception of the biomass model of Floyd et al. (1978), the selected methods ranked food items quite similarly, especially for high ranked food items (ranks 1-4), which comprised 61.2% of all occurrences and 68.5% of total mammal biomass consumed according to Weaver's (1993) model. However, it is important to stress that the methods we tested differ profoundly in nature: frequency data, dry weights, and relative volume represent measurements of undigested food remains in the scat sample, whereas biomass models estimate relative importance of food items in terms of actual biomass ingested. Thus, our statistical comparison of the different rankings implies that they should not be interpreted the same way.

The differences among rankings reported for individual food items did not significantly affect the overall assessment of the diet by the selected methods, as the relative importance of the main food categories (i.e. wild ungulates, domestic mammals, etc.) was similarly revealed by all methods (see Fig. 1). However, discrepancies among rankings, especially for food items of lower rank

Table 3. Pairwise comparisons (Spearman rank correlation coefficients, r) between six methods of scat-analysis used to assess the wolf diet in the Northern Apennines, Italy.

	Percentage of occurrence	Estimated dry weight	Relative volume	Biomass (Floyd et al. 1978)	Measured dry weight
Percentage of occurrence	–				
Estimated dry weight	r = 0.63*	–			r = 0.94**
Relative volume	r = 0.84**	r = 0.91**	–		–
Biomass (Floyd et al. 1978)	$r = 0.47^{ns}$	$r = 0.55^{ns}$	$r = 0.51^{ns}$	–	–
Biomass (Weaver 1993)	r = 0.77*	r = 0.79*	r = 0.81**	r = 0.89**	–

* $P < 0.01$
** $P < 0.001$
ns not significant

(see Table 1, rank ≥ 5), indicate location, amplitude, and direction of inconsistencies by the different methods, suggesting sources of bias and their influence.

Frequency data ranked very small food items (invertebrates, fruit) relatively high compared to the other methods; similarly, small and medium-sized mammals (rodents, insectivores, hares) were ranked higher by percentage of occurrence than by both biomass models (see Table 1). This was expected on the basis of the problems associated with frequency data from canid scats, as already discussed by several authors (Scott 1941, Lockie 1959, Meriwether & Johnson 1980, Fritts & Mech 1981, Kelly 1991, Reynolds & Aebischer 1991). In particular, by equating the occurrences of food items which contribute in different amounts to a scat's volume (Kelly 1991), items such as small mammals, invertebrates and fruit have been ranked higher by frequency than by the other methods. However, we partially reduced this bias by not considering items occurring in a scat in trace amounts (i.e. <3%).

In mammalian prey the amount of undigestible material (mostly hairs) per unit of biomass decreases with increasing body size (by age and species), according to changes in surface/volume ratio (Floyd et al. 1978, Kelly 1991, Weaver 1993). This explains why frequency data ranked small and medium-sized mammals (rodents, insectivores, hares) higher than large mammals such as red deer, horse and cattle, even though the importance of the former was much lower when expressed in biomass terms (see Table 1). However, we found a significant correlation between rankings by frequency data and Weaver's (1993) biomass model. This suggests that the bias in frequency data due to changes in surface/volume ratio in prey of different sizes is not a serious problem in our case, possibly because a large portion of the diet was composed of prey similar in size (see Fig. 1). Similarly, Weaver (1993) recognised that the largest bias in frequency data occurs when small and large prey (e.g. kit beaver *Castor* spp. and adult moose) each comprise 20-80% of the diet, and bias reduction will occur with the inclusion in the diet of prey intermediate in size. In our study, small prey (small mammals and hares), large prey (horses, cattle, red deer) and prey intermediate in size (wild boar, mouflon, roe deer) represented respectively 13%, 8%, and 79% of mammalian occurrences (see Table 1).

Some sources of bias in frequency data, in particular the equating of occurrences bias, could be avoided by adopting the dry weight and relative volume methods, as these directly measure food remains in the scat sample. Ranking concordance between the dry weight and the relative volume was higher than that observed between either of these two methods and percentage of occurrence (see Tables 1 and 3). This reflects a basic difference in the quantification procedure: whereas frequency data account solely for the presence of a given item, the other two methods also account for its amount in the scat sample. However, it should be noted that, similar to frequency data, dry weight and relative volume methods suffer from biases due to changes in surface/volume ratio in prey of different sizes. In addition, they are sensitive to changes in the structure of the undigested remains (see below).

The estimated dry weight method is simpler and less time-consuming compared to the more labourious manual separation and measurement of each food item recovered in the scat (cfr. Johnson & Hansen 1977). Reliability of dry weight estimates was supported by the close ranking agreement between the estimated dry weight and the measured dry weight methods (see Tables 1 and 3). Reynolds & Aebischer (1991), however, urged that the reliability of the estimated dry weight method be assessed by testing the assumption that macroscopic remains of different food items have equal specific density, since departures from this assumption can lead to significant distortions in weight estimates.

Methods based on weights of undigested remains are sensitive to differential digestibility of prey types (Weaver & Hoffman 1979) and, as our analysis suggests, some additional problems arise by using the same unit of measure (i.e. weight) for remains that are structurally different (structural bias). The most influential discrepancies between rankings by dry weight and percentage of occurrence involve food items (small mammals, invertebrates, fruit and birds) whose remains are structurally different and weigh less than those of large mammals (see Table 1). Most importantly, structural bias can arise also within the same food item category and, in mammalian prey, it could be related to variation in the relative proportions of hair and bone remains recovered in scats. This variation could depend on the age of the predator (Lockie 1959), the differential digestibility of different prey sizes (Weaver & Hoffman 1979, Meriwether & Johnson 1980, Johnson & Aldred 1982), and the differential digestibility, especially of bones, by individual predators (Kelly 1991). In addition, for wolves and other predators that may not eat large prey entirely, structural bias could stem from variation in the parts of the prey which are consumed and could be particularly relevant when predators scavenge on old carcasses. Food items that in our study area were most likely consumed as carrion (horse, cattle, dog), were ranked higher by dry weight than by frequency data (see Table 1), and further inspection revealed that >60% by relative volume of the correspondent scats was composed of bone remains.

With respect to relative volume, ranking discrepancies with frequency data were intermediate to those observed between frequency and dry weight data (see Tables 1 and 3). Quantification by relative volume also appears sus-

ceptible to structural bias (cfr. Table 1: invertebrates, fruit, birds), although to a lesser extent than by dry weight data (cfr. Table 1: small mammals, cattle, dog). Relative ranks of small mammals and large domestic mammals (horses and cattle) as obtained by relative volume and measured dry weight (see Table 1), suggest that the bias due to changes in surface/volume ratio in prey of different sizes might be more relevant for the volume than the dry weight method (i.e. undigested remains of smaller prey weigh less than those of large prey, thus contrasting the amplitude of the surface/volume bias).

By correcting for the surface/volume bias which occurs when undigested remains are measured directly, biomass models assigned proportionally higher ranks to large mammals (i.e. domestic sheep, horses, cattle, red deer) and proportionally lower ranks to small mammals (i.e. rodents, insectivores, hares) than the other methods (see Table 1). The model of Floyd et al. (1978) assigns proportionally more relevance to large prey than Weaver's (1993), and this is particularly distorting in the case of large domestic animals: even though horses and cattle occurred at low frequency, they were top-ranked by the model of Floyd et al. (1978) (see Table 1). When applied to prey larger than white-tailed deer, the largest included in the original feeding trials, the model of Floyd et al. (1978) tended to overestimate the corresponding biomass value (Kelly 1991, Weaver 1993). This accounts for the lack of agreement between the two biomass models if limited to food items with rank ≤ 6, and between Floyd et al.'s (1978) model and all the other methods (see Table 3). The higher simultaneous concordance (see Table 2), as well as the significant correlation in pairwise comparisons (see Table 3) obtained using Weaver's (1993) model in place of that of Floyd et al. (1978), reflect calibration of the former model on larger prey. Large domestic animals were ranked proportionally lower by Weaver's (1993) than by Floyd et al.'s (1978) model.

In assessing the diet of dingoes *Canis familiaris dingo* Corbett (1989) reported significant agreement between Floyd et al.'s (1978) model and two scat-analysis methods (frequency of occurrence, estimated dry weight). This did not agree with our findings, possibly because the adjusted weights of large domestic animals (feral buffalo, feral pig, feral cattle) used in the biomass model of Corbett (1989: Table 1) were lower than those we calculated (see Table 1). It follows that the definition of the live weight of the prey is a critical step when applying the biomass models. Prey weights have to account for differences in size with the age of the prey (Floyd et al. 1978), and need to be adjusted for the prey's age structure in the wolf diet. When the age structure of the prey is not available from kill figures, it is estimated by analysing characteristics of ungulate hairs recovered in the scat sample (e.g. Carbyn & Kingsley 1979, Scott & Shackleton 1980, Potvin et al. 1988, Corbett 1989). However, this procedure, is applicable only for ungulates from birth to 4-5 months of age (Pimlott et al. 1969), and cannot account for differences between yearlings and adults, or females and males.

Interpretation of results by linear-regression models should take into account other factors that potentially affect estimation of the amount of prey mass per collectable scat. In particular, the application of regression parameters obtained in feeding trials where wolves had time to consume the prey entirely (cfr. Floyd et al. 1978, Weaver 1993) might result erroneous when kills by wild wolves are only partially utilised. Wolves are often reported not to eat their prey entirely (e.g. Pimlott et al. 1969, Peterson 1977, Carbyn 1983, Miller et al. 1985, Potvin et al. 1988, Bobek et al. 1992) and to preferentially feed on soft tissues (Carbyn 1983, Miller et al. 1985). Both feeding patterns are particularly common for domestic prey (Ciucci et al., unpubl. data). In addition, specification of prey weights in the biomass models does not take into account loss of biomass due to scavengers, or the poor physical condition of individual prey. However, the same problems, along with differences in digestibility between wild and captive animals (see Kelly 1991), apply to all biomass estimators obtained by feeding trials in captivity, including those that use calibration factors (e.g. Scott 1941, Lockie 1959, Goszczynski 1974, Weaver & Hoffman 1979, Johnson 1981, Ackerman et al. 1984, Kelly 1991). It is important to emphasise that both biomass models (Floyd et al. 1978, Weaver 1993) have been developed according to an array of North American prey species. Consequently, their wide application throughout the entire wolf distribution needs further testing. Furthermore, these models should not be considered applicable to non-mammalian food items (e.g. Corbett 1989), which are structurally different and whose digestibility and nutritive value cannot be compared to those of mammalian prey.

Conversion factors obtained through feeding trials in captivity can be multiplied by dry weights to estimate actual biomass ingested (e.g. Lockie 1959, Goszczynski 1974, Johnson & Hansen 1979). For wolves, however, no such factors have been computed and, if those obtained for other carnivore species are extrapolated to the wolf (e.g. Reig & Jedrzejewski 1988, Jedrzejewski et al. 1992), results should be interpreted solely as indices of relative biomass consumption. Other methods developed to estimate biomass intake for small carnivores (e.g. Kruuk & Parish 1981) do not appear adequate for large carnivores, including wolves, which do not consume prey entirely in a single meal (Kruuk, pers. comm.). For these reasons the linear regression models developed for wolves (Floyd et al. 1978, Weaver 1993) were the only biomass estimators included in our comparison.

In conclusion, we stress that results from this study, similar to most food habit studies on wolves and other large carnivores, were based on analysis of the macroscopic undigested remains recovered in the scats. Although the microscopic fraction represents a large proportion of each scat (Johnson & Hansen 1977, Reynolds & Aebischer 1991, this study), it is generally discarded assuming it originates from food items in the same proportions as macro-components. Reynolds & Aebischer (1991) demonstrated this to be a misleading assumption for birds and earthworms consumed by foxes, and the same could be true for wolves with particular feeding habits. In an area of Italy where wolves were reported to feed at garbage dumps, a large number of scats contained only 'amorphous' material, which consisted of microscopic fragments difficult to identify and measure (Macdonald et al. 1980, Boitani 1982). Similar situations might occur in other areas of the wolf distribution in Eurasia (e.g. Spain, Israel, Saudi Arabia). In these cases, quantification of macroscopic remains from scat samples should be interpreted cautiously and additional sources of data should integrate assessment of the diet (e.g. Boitani 1982).

Conclusions

Differences between the selected scat-analysis methods were mostly found in ranks for food items of secondary and low importance. Therefore, all methods offered a similar overall assessment of the wolf diet, especially with regard to the main food categories (see Fig. 1). However, various method-specific sources of bias determined some differences among food item rankings, and each of the selected methods appeared associated with some interpretational limitation. These findings lead us to some conclusive considerations:

- In terms of accuracy, there is no single most reliable method, as each method is affected by some form of bias. Therefore, the choice of the method in future food habit studies should be dictated not only by its inherent accuracy but also by the aims of the study (e.g. qualitative description of the diet, quantification of relative amount of food items in the diet, comparisons with other studies).
- When different food habit studies adopted different methods of scat-analysis, comparisons among them should be qualitative rather than quantitative. In addition, as the method of analysis could affect quantification of the relative importance of different prey items in the diet, application of preference indices (e.g. Jacobs 1974, Chesson 1978) to scat-analysis data might be misleading.
- Correct interpretation of results from scat-analysis studies should take into account the biases associated with each method, and should also be supported by utilisation of multiple methods.

In this perspective, frequency data remain appealing because of the less time and effort they require, and their simplicity compared to other methods. The percentage of occurrence method realistically depicts the qualitative composition of the diet, including those food items otherwise difficult to measure with other methods (i.e. garbage). Although various sources of bias potentially limit interpretation of frequency data, some could be partially reduced (e.g. by removing from the analysis items occurring in trace amounts; see also Kelly 1991). In addition, if prey items in the diet are of similar size, the surface/volume bias might not be relevant. Interpretation of frequency data should be enhanced by simultaneously utilising other scat-analysis methods. With little additional labwork, macroscopic remains of the scats could be separated, and this would allow the quantification of relative volume and estimated dry weight. By comparing volume and/or dry weight with frequency data, it is possible to determine whether diet assessment by the latter was affected by the equating of occurrence bias (i.e. equating items contributing different amounts to a scat's volume). Relative volume proportions are also needed to apply biomass models when there is more than one prey/scat (Floyd et al. 1978), and they offer a correction for frequency data (see Kelly 1991). By measuring the dry weight of the scat, relative volume data are easily converted to estimated dry weight data which appear slightly less affected by the surface/volume bias. However, as relative volume and dry weight data are sensitive to the structure of undigested remains, the relative proportions of structurally different remains (e.g. hair/bone ratios) in the scat sample should be quantified and reported for each prey item.

If the biases associated with frequency, volume and dry weight data are not accounted for, scat-analyses should be interpreted with caution, as quantification of undigested remains in scats does not necessarily correspond to the relative amount of prey consumed. If used in conjunction with methods that allow estimates of biomass intake, frequency, relative volume or dry weight data still offer a qualitative description of the diet, represent a broader interpretational basis and, being the most frequently used, also facilitate comparisons with other studies (e.g. Scott & Shackleton 1980, Fritts & Mech 1981, Peterson et al. 1984, Ballard et al. 1987, Jedrzejewski et al. 1992).

Diet assessment in terms of biomass ingested is biologically more meaningful and should be preferred to methods based on direct measures of undigested remains in scat samples. However, biomass models are not void of

interpretational difficulties and are not suitable for all conditions. Linear regression models (Floyd et al. 1978, Weaver 1993) are easily applicable to frequency data, and their choice depends on the range in size of prey represented in the diet. However, Weaver's (1993) model is believed to be more robust to varying field conditions, as it incorporates results from three different studies (Floyd et al. 1978, Traves 1983, Weaver 1993). Further testing in captivity is needed to apply the biomass models to prey species structurally different from those originally included in the feeding trials, and to better simulate conditions in the wild (e.g. composition of the diet, feeding patterns, predator activity). In addition, field research should complement assessment of the diet using biomass models, especially by providing detailed information about the prey's age structure in the wolf diet, the prey's conditions, the degree of prey consumption by wolves, and the amount of prey biomass lost to scavengers. Field research should also integrate assessment of food habits in those areas where wolves show a highly diversified diet, mostly composed of items difficult to quantify with traditional scat-analysis methods (e.g. garbage, fruit, invertebrates).

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