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Correction factors for estimating food consumption by red fox *Vulpes vulpes* from scats

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Assessments of terrestrial carnivore diet are often required for ecological management and conservation purposes. Analysis and identification of food remains in scats is an important method often employed for these objectives. Proportions of consumed biomass estimated from scat samples may provide an accurate approximation of the actual diet when correction factors (CFs) are used. The red fox *Vulpes vulpes* is a widespread generalist carnivore that includes a wide range of foods in its diet, including livestock and plays a potential role as wildlife predator. We performed controlled feeding trials with red foxes to derive CFs for eight food categories, including both from animal and vegetal origin. CFs were calculated on a daily basis as the ratio between eaten fresh mass and total dry mass of the resulting scats. Red foxes consumed daily 615 ± 19 g (mean \pm SE) of food and produced 6.4 ± 0.3 scats weighing 31 ± 1.2 g. The CFs varied significantly among food types, with the lowest values for partridges *Alectoris rufa* (CF = 12.5 ± 0.7) and the highest for red deer *Cervus elaphus* (CF = 47.3 ± 7.3), increasing linearly and significantly in relation to the individual body mass for the animal food types. CF precision was low for deer, fruit and hare *Lepus granatensis*, but more importantly, the CFs differed considerably among food types. We recommend considering intra-food variability when using CFs for estimating proportions of ingested biomass in studies of generalist carnivores such as red fox as a better support for management and conservation decisions.

Keywords: correction factors, diet estimation, food remains, ingested biomass, predation, red fox, scat analysis

Predator diet assessments are required for ecological and conservation purposes, such as studying predator–prey relationships, energy transfer in food webs, population dynamics, competitive interactions, conservation and management (Donadio and Buskirk 2006, Wilson and Wolkovich 2011, Fernandez-de-Simon et al. 2015, Monterroso et al. 2016). The understanding of predator diets is an ecological topic but is also a fundamental part of socioeconomic, psychological and even political aspects of conservation (Chetri et al. 2017, Khan et al. 2018).

Several methods have been employed to assess the diet of mammalian carnivore predators. Due to predator elusive behaviour and the low probability of directly observing feeding events, indirect methods are usually employed. Novel indirect methods (e.g. stable isotopes, DNA metabarcoding) have become more frequently employed (Kelly 2000, Pompanon et al. 2012), though they are limited by their relatively high cost and reduced availability. The study of

food remains in faeces and gut contents is currently the most commonly employed tool to assess carnivore diets (Reynolds and Aebischer 1991). Food remains in faecal samples is an abundant and valuable source of information on feeding behaviour (Ciucci et al. 1996, Klare et al. 2011). Methods for representing the proportion of food items in a predator's diet include: 1) frequency of occurrence (Carvalho and Gomes 2004), 2) volume proportion (McDonald and Fuller 2005) and 3) proportion of ingested biomass (Reynolds and Aebischer 1991). The pros and cons of each quantification method depend on the study objective. Frequency of occurrence is a method traditionally used in studies of carnivore diet since it is easy to calculate (Carvalho and Gomes 2004). While this method is acceptable for making comparisons among study areas or seasons, it tends to overestimate the importance of small prey species and underestimate that of large prey species in the diet (Floyd et al. 1978, Klare et al. 2011). Moreover, this method does not consider differences in digestibility among food classes (Goszczyński 1974). Consumed biomass provides one of the best approximations for carnivore diet but it is less frequently used (Klare et al. 2011). This is probably because information about how to convert data from scats to ingested biomass is not readily available (Reynolds and Aebischer 1991). Some research

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objectives require estimating the biomass contribution of each food category, such as food web flows, predation impact, predator–prey relationships and predator requirements (Fernandez-de-Simon et al. 2015).

Several methods to reconstruct actual biomass intake have been derived from controlled feeding trials in which carnivores consume different foods and the produced scats are subsequently quantified (Rühe et al. 2008, Klare et al. 2011). Several approaches can be employed to estimate prey biomass from scats, including: 1) specific correction factors (Stahl 1990), also known as conversion factors (Rühe et al. 2007) or coefficients of digestibility (Goszczyński 1974, Webbon et al. 2006, Rühe et al. 2008); 2) linear functions of dry mass of indigestible remainders in scats to prey body mass (Rühe et al. 2007); 3) the number of individual prey detected in scats (Weaver 1993) or 4) biomass regression models that relate prey biomass consumed per excreted scat to prey body mass (Floyd et al. 1978, Weaver 1993, Rühe et al. 2003). The main advantage of biomass regression models is that a single model can be used for the full range of prey sizes. However, these models are only applicable to carnivores feeding chiefly on mammalian prey species that are not completely consumed (Wachter et al. 2012). For carnivore species with an omnivorous diet, the use of food-specific correction factors (CFs) estimated from feeding trials is the most commonly recommended method to estimate the actual diet (Reynolds and Aebischer 1991, Klare et al. 2011, Wachter et al. 2012).

Correction factors are defined differently by different authors. Lockie (1959) and Goszczyński (1974) calculated CFs as (fresh weight of food given)/(dry weight of egested remains), whereas Artois et al. (1987) calculated CFs as (fresh weight ingested)/(dry weight of egested remains). These two definitions are bound to yield different results because most carnivores avoid consuming animal parts of no nutritional benefit, such as large feathers or deer fur (Reynolds and Aebischer 1991). In this paper, we use the Artois et al. (1987) definition and will consider CF as the number which, when multiplied by the dry mass of indigestible matter in scats corresponding to a food item, will convert this dry mass into the total fresh mass of original food eaten.

Correction factors are not exempt from criticism – for example, they can be subject to uncertainty (Soe et al. 2017) and potential bias (Reynolds and Aebischer 1991). A common practice when estimating carnivore diet from scats is to use those CFs for other predator species, if they are not available. However, great deviations from true biomass consumption can be obtained when using CFs derived for other species (Rühe et al. 2008). Consequently, applying predator- and prey-specific CFs is recommended for obtaining unbiased estimates of consumed biomass (Rühe et al. 2008).

The red fox *Vulpes vulpes* is the most widespread terrestrial carnivore species, distributed across the entire Northern Hemisphere (Macdonald and Reynolds 2004). It is a generalist and opportunistic predator, including a wide range of foods in its diet from animal to vegetal sources and even food of human origin (Díaz-Ruiz et al. 2013, Soe et al. 2017). Red fox populations are managed because of their role as a vector of disease and as a predator of livestock, game and threatened species (Reynolds and Tapper 1996, Baker et al.

2006). Management of fox predation is attempted mainly by culling (Harris and Saunders 1993, Reynolds and Tapper 1996). However, the acceptability and effectiveness of wild-life culling is increasingly questioned (Slagle et al. 2017). In this debate, knowledge about the impact of foxes on prey species is urgently needed, requiring unbiased data on the diet of foxes in different contexts.

When assessing the extent of predator impact on prey or human–predator conflict, applying potentially inaccurate methods to estimating prey consumption could be problematic (Lumetsberger et al. 2017). If CFs are to be used for obtaining unbiased estimates of ingested biomass, they must be accurately estimated. CFs for the red fox have been previously estimated only for some foods (Lockie 1959, Goszczyński 1974, Frank 1979, Artois et al. 1987, Stahl 1990), and their precision is rarely reported. Hence, accurate estimations of CFs for prey and other foods consumed by red foxes is a priority for evaluating the impact of red fox on prey species of economic or conservation concern, and therefore for fox management and the conservation of its prey.

We aimed to derive CFs for the transformation of scat mass into biomass of different food categories consumed by red fox based on controlled feeding trials. We were interested in determining 1) whether CFs differed among an array of food categories and 2) whether precision of the estimates of these factors varies with the type of food. Additionally, we aimed to estimate: 3) daily food requirements of red foxes and 4) whether daily production of scats depends on the food type.

Material and methods

Feeding trials

We conducted feeding trials between September 2005 and February 2007 in Finca Dehesa de Galiana experimental facilities of Castilla-La Mancha University (central Spain). Trials were performed with three adult wild-captured foxes, one female (two years; 6.2 kg) and two males (two and three years; 6.5 and 6.6 kg respectively). Foxes were housed in individual 3 × 4 m outdoor covered kennels on a concrete substrate covered in sawdust. Foxes were kept and handled in accordance with animal welfare guidelines (Choate et al. 1998, Council of the European Union 1999). The staple diet fed to the foxes usually consisted of standard dry dog feed with occasional chicken (*Gallus* sp.) carcasses, portions of red deer *Cervus elaphus* carcasses and dead wild rabbits *Oryctolagus cuniculus*.

A feeding trial was defined as a number (6–10) of consecutive daily tests when an experimental fox was fed daily with the same type of food (Table 1). Foxes were fasted for 24 h before each feeding trial to clean their gut contents and all faecal pellets were cleared from the enclosure. We performed feeding trials with eight types of food: 1) domestic chicken carcasses, 2) red deer carcasses divided into approximately 0.8 kg pieces, 3) Iberian hares *Lepus granatensis* (a half-eviscerated individual), 4) European rabbits (an eviscerated individual), 5) domestic lamb *Ovis orientalis aries* (a half-eviscerated young individual), 6) red-legged partridges

Table 1. Number (n) of daily tests performed, fresh biomass offered and consumed daily and number and dry mass of scats produced for each type of food. Standard errors are provided after average values. p-values indicate significant differences among types of food according to ANOVA F tests.

	n	Offered fresh biomass (g)	Consumed fresh biomass (g)	No. scats	Dry mass of scats (g)
Deer	23	772.4 ± 35.3	602.8 ± 33.4	5.6 ± 0.6	19.4 ± 2.8
Grapes	20	871.1 ± 36.9	624.8 ± 47.7	6.1 ± 0.8	24.0 ± 2.4
Chicken	18	716.6 ± 43.4	563.0 ± 47.1	4.4 ± 0.5	22.6 ± 2.6
Lamb	12	2052.9 ± 115.6	970.3 ± 89.1	8.3 ± 1.1	37.7 ± 3.0
Hare	20	867.4 ± 24.7	651.3 ± 30.9	6.4 ± 0.5	38.8 ± 3.1
Rats	20	820.8 ± 27.8	737.7 ± 26.7	6.2 ± 0.5	45.5 ± 1.7
Rabbit	16	867.8 ± 32.5	537.3 ± 44.1	9.4 ± 1.1	35.0 ± 3.1
Partridge	20	422.4 ± 22.7	353.6 ± 22.5	6.5 ± 0.5	29.7 ± 2.3
p		<0.001	<0.001	<0.001	<0.001
Total	149				
Average		820.8 ± 27.8	614.7 ± 18.8	6.4 ± 0.3	31.0 ± 1.2

Alectoris rufa (a full individual), 7) laboratory rats *Rattus norvegicus* (three–four individuals) and 8) grapes (approximately 0.8 kg full bunches; Table 1). On average 820.8 ± 27.8 g of food were provided daily to each fox (Table 1), which is above daily food requirements reported for adult red foxes (Sargeant 1978, Lloyd 1980, Artois et al. 1987, Stahl 1990).

The food was offered each day in the morning and all uneaten prey remainders were collected from the enclosure the following day, when new fresh food was offered. Water was available ad libitum. The food offered and the food remainders were weighed daily to the nearest gram with an electronic balance. The daily consumed biomass was calculated as the difference between the offered food mass and the mass of uneaten remainders collected the day after. Scats were collected daily, weighed, dried to constant mass at 60°C and reweighed to the nearest 0.001 g with an electronic balance.

Statistical analyses

The existence of differential digestibility among food types was tested with linear mixed models fitted to scat dry mass, with ingested biomass and type of food as fixed factors and individual as a random factor. We controlled for autocorrelation resulting from repeated measurements on the same animal and the same food by including an autocorrelation structure in the models with the 'nlme' package (Pinheiro et al. 2018) in the R statistical software (<www.r-project.org>). We used Nagelkerke pseudo R² estimated with the 'rcompanion' package (Mangiafico 2018) in R as a measure of how well the full model explained the data.

If the type of food was included in our model for scat mass, CFs for each food type were calculated on a daily basis as the ratio between eaten fresh mass and total dry mass of the resulting scats (Rühe et al. 2007) produced during the subsequent 24 h. The precision of these estimates were assessed by their coefficient of variations and by bootstrap 95% confidence intervals with 10 000 iterations.

The relationship between the CF values and corresponding prey size was tested through linear regression between the individual full body mass (log-transformed) and the CF estimated for each animal food type (Rühe et al. 2007). Average adult body mass was obtained from the literature

except for young lambs for which the average full weight of animals used in feeding trials was used.

We estimated apparent digestibility for different food types as ((mean fresh mass consumed – mean fresh scat mass)/(mean fresh mass consumed) × 100) (Rühe et al. 2008). We qualified this digestibility as 'apparent' because the water content in scats could not be attributed to the ingested food alone with certainty; an unknown proportion may be made up of metabolic components from the animal or have resulted from drinking water intake (Rühe et al. 2008, Wachter et al. 2012). We tested whether apparent digestibility differed significantly among types of food through a linear model. Differences between types of food were tested through Tukey's post hoc tests.

Results

Consumed biomass and defecation rate

Foxes consumed daily 614.7 ± 18.8 g (mean ± SE) of food on average (n = 149 daily feeding tests), differing significantly among food types ($F_{7,141} = 15.23$, $p < 0.001$; Table 1). Each fox produced an average of 6.4 ± 0.3 scats per day, representing 31.0 ± 1.2 g dry mass, with significant differences among food types (number of scats: $F_{7,141} = 4.588$, $p < 0.001$; dry mass: $F_{7,141} = 12.639$, $p < 0.001$; Table 1). The proportion of daily offered food that was consumed was negatively and significantly related with the amount of offered food ($F_{1,131} = 40.53$, $p < 0.001$). The type of food also had a significant effect on the proportion of food consumed ($F_{7,131} = 2.10$, $p = 0.048$), suggesting food preferences.

Our model for scat mass included the biomass of consumed food ($F_{1,131} = 45.719$, $p < 0.001$), the type of food ($F_{7,131} = 10.378$, $p < 0.001$) and the interaction between ingested biomass and type of food ($F_{7,131} = 3.944$, $p < 0.001$) as fixed factors and the individual as a random factor. According to the Nagelkerke pseudo R² (60.9%), our model acceptably explained the variability of data. According to this model, the dry mass of scats is positively and significantly related to consumed biomass, but this relationship also depends on the type of food. The slope of this relationship for deer and lamb is significantly lower than the average slope estimated by the model (Table 2, Fig. 1).

Table 2. Parameter estimates for fixed effects according to our model for dry mass of scats. Asterisks indicate significant differences from zero (* $p < 0.05$, ** $p < 0.01$).

	Estimate	SE	t value	p
Intercept	-1.635	9.587	-0.171	0.865
Biomass	0.076	0.023	3.392	0.001**
Chicken	-5.276	10.881	-0.485	0.629
Rabbit	6.650	11.482	0.579	0.563
Hare	4.519	13.715	0.330	0.742
Rats	40.558	15.929	2.546	0.012*
Lamb	31.446	13.091	2.402	0.018*
Grapes	2.410	10.698	0.225	0.822
Deer	28.942	12.294	2.354	0.020*
Biomass × Chicken	-0.032	0.025	-1.241	0.217
Biomass × Rabbit	-0.029	0.027	-1.084	0.281
Biomass × Hare	-0.028	0.028	-1.001	0.319
Biomass × Rats	-0.073	0.029	-2.531	0.013*
Biomass × Lamb	-0.073	0.025	-2.938	0.004**
Biomass × Grapes	-0.046	0.025	-1.860	0.065
Biomass × Deer	-0.090	0.026	-3.414	0.001**

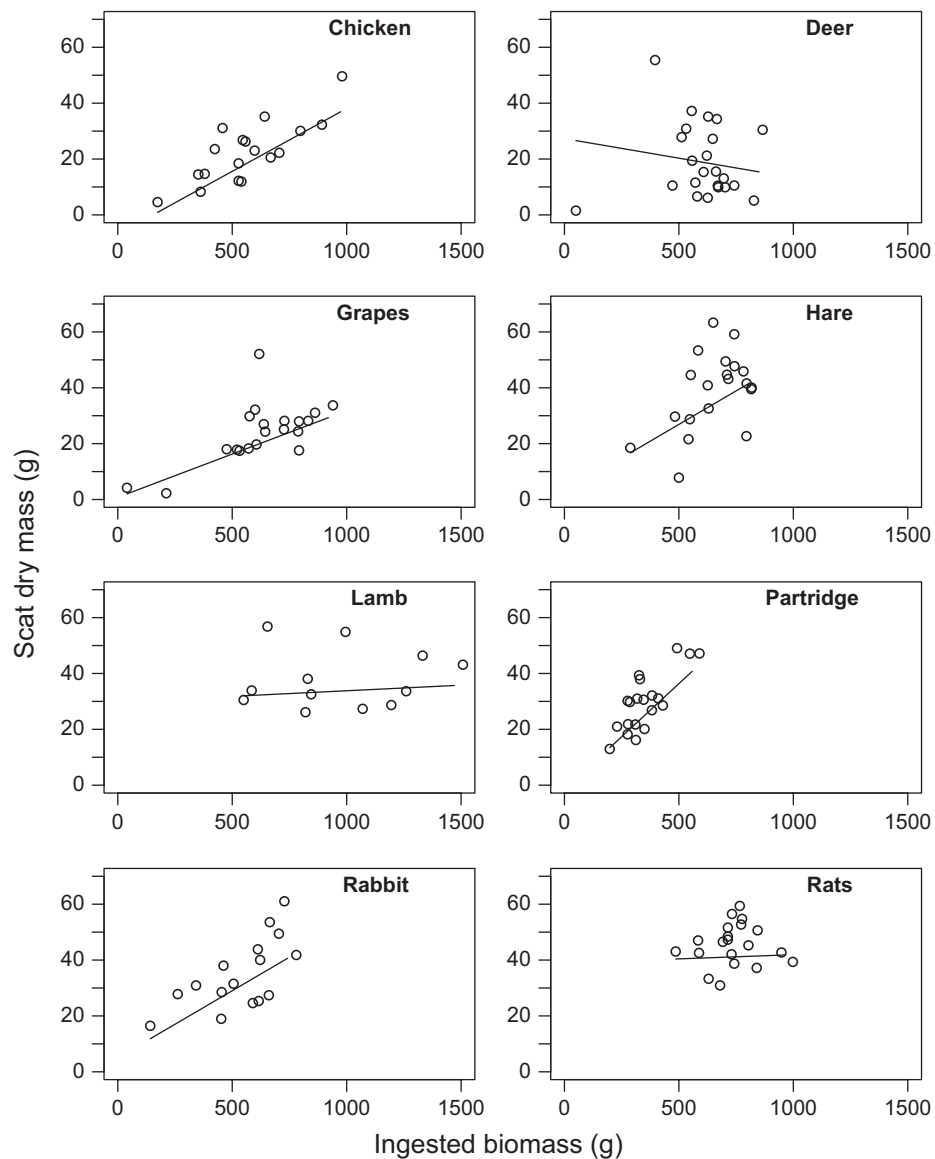


Figure 1. Relationships between ingested biomass and scat dry mass for each food type. Lines show the predicted linear relationship for each type of food according to the selected mixed model.

Table 3. Correction factors (CF) for the diet of the red fox as the mass ratio between fresh consumed food and dry scats. Estimated average, standard error, coefficient of variation and 95% confidence intervals, derived from bootstraps with 10 000 iterations. n represents the number of daily tests performed for each food type. Consumed biomass for a given food type should be estimated from dry mass of this food found in scats by the equation: Fresh consumed biomass = CF × Dry mass of scats.

Food	n	CF estimate	SE	CV	95% Confidence interval
Deer	23	47.3	7.3	0.74	36.4–65.1
Grapes	20	29.8	3.8	0.56	25.1–41.7
Chicken	18	28.0	2.2	0.33	24.2–32.6
Lamb	12	27.1	2.9	0.36	21.8–32.4
Hare	20	19.7	2.6	0.59	16.4–28.3
Rats	20	16.6	0.9	0.24	15.1–18.5
Rabbit	16	16.0	1.4	0.34	13.6–18.9
Partridge	20	12.5	0.7	0.23	11.3–13.9

Variation of CFs and apparent digestibility among food types

The CFs varied significantly among food types ($F_{7,141} = 9.691$, $p < 0.001$), from 12.5 g of fresh ingested biomass/g of dry scat for partridges to 47.3 g for deer (Table 3). The precision for the CFs was high (C.V. < 0.4) for partridge, rat, chicken and rabbit, but low for deer, grapes and hare (C.V. > 0.5 ; Table 3). The average CF increased linearly and significantly ($R^2 = 0.877$, $F_{1,5} = 35.644$, $p = 0.0019$) with the individual body masses (log transformed) for the animal food types (Fig. 2).

Apparent digestibility differed significantly among food types ($F_{7,141} = 7.123$, $p < 0.001$). Chicken, deer, hare and lamb were significantly more digestible (post hoc Tukey test) than grapes, which showed the lowest digestibility. Partridge, rabbits and rats had intermediate values (Fig. 3).

Discussion

Daily food intake and defecation rate

The average daily food intake estimated for captive red foxes in this study (614.7 g day^{-1}) agrees with the values estimated by Yoneda (1982) and Stahl (1990), but is lower than the value reported by Webbon et al. (2006) and higher than those reported in other studies (Lockie 1959, Ryszkowski et al. 1973, Sargeant 1978, Lloyd 1980, Artois et al. 1987). These discrepancies could be due to differences in the body mass of test individuals, or differences in activity or environmental conditions among studies (Frafjord 1993). However, in most studies the body mass of foxes used in the feeding tests is not stated and it is unclear whether food was provided ad libitum (Webbon et al. 2006). These facts could contribute to explain the differences in daily food intake among studies. Since the estimation of food requirements is extremely difficult for wild animals, estimates from captive animals can serve as a guide for wild animals, even though the lower activity levels of captive animals may reduce their food requirements (Nagy 1987).

The negative relationship between the amount of offered food and the proportion consumed suggests satiation,

since as more food was offered, a lower proportion was consumed. The variation in daily intake among food types could be related to differences in palatability, ease of consumption determining food preferences (Kondo and Shiraki 2012), or homeostatic nutrient intake regulations (Kohl et al. 2015).

The mean defecation rate estimated in this study ($6.4 \text{ scats day}^{-1}$) is lower than the value reported by Webbon et al. (2006; 8 scats day^{-1}), which is in agreement with higher daily food intake in the latter study. This indicates that about one scat is produced per 100 g of ingested food. Our significant differences in daily defecation rates among food types contrast with findings by Webbon et al. (2006). Our average dry mass of scats produced daily ($31.0 \pm 1.2 \text{ g}$) was above the value (22 g) estimated by Artois et al. (1987) in similar feeding trials, and close to the values (25–30 g) obtained by Faliu and Griess (1974) from foxes fed with a commercial food.

Factors affecting correction factors

We found significant differences in the CFs between food types, in contrast to results obtained by Webbon et al. (2006). Rodents are poorly digested because they contain relatively large proportions of indigestible parts such as fur and bones, and are swallowed in whole by foxes. As a result, they produce a large amount of remains in the faeces and their CF is low (Table 3). Similarly, the large proportion of indigestible parts of partridges, such as feathers and bones, would explain their low CF (Table 3). Large mammals, such as deer, are assimilated to a higher degree, due to the relative small amounts of indigestible parts such as bones and fur, which would explain the large CF for this food (Table 3).

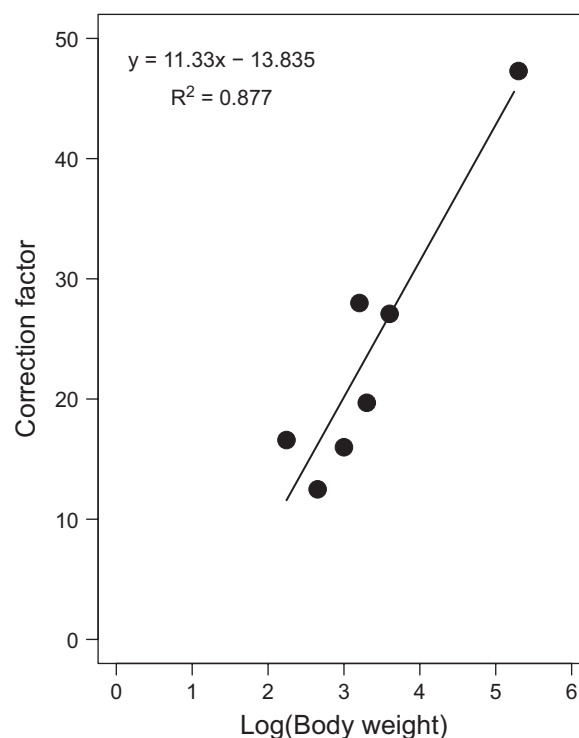


Figure 2. Relationship between correction factors and average individual body mass for each animal prey type.

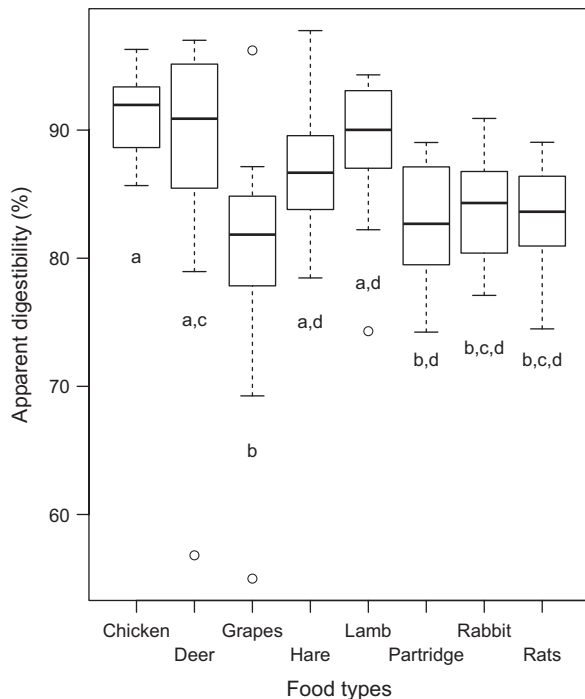


Figure 3. Boxplot of apparent digestibility ($[(\text{ingested biomass} - \text{fresh scat mass}) / \text{ingested biomass}]$) for each of the tested foods. Different letters indicate significant differences among food types according to post hoc Tukey tests.

We found differences among studies in red fox CFs for a given food type (Table 4). Differences in the age of experimental individuals could partially explain these variations (Stahl 1990), since the digestive system of young carnivores is less efficient than that of adults, resulting in lower CFs (Reynolds and Aebischer 1991). This trend towards lower CFs for juveniles was reported by Lockie (1959). However Stahl (1990) reported the opposite trend, with higher CFs for juveniles than for adults, explained by varying consumption patterns: cubs choose the easiest parts to eat and leave more prey remains than adults (Stahl 1990). Other differences among studies could be due to differences in the prey species used for each prey group (e.g. small mammals, birds), age, body condition or different parts ingested (Artois 1987).

Differences in the resulting CFs may also be due to the experimental setup of feeding trials (Brzezinski and Marzec 2003) including the frequency, manner and amount of food offered or whether foxes were fasted before and after the trials (Table 4). For instance, we provided new food daily and removed the previous day's remains, whereas prey was provided once at the beginning of each week in other studies (Sargeant 1978) or prey remains were taken out after two days in the case of large prey (Stahl 1990). The frequency with which predators consume prey affect its digestion: feeding prey over time yields bone and hair amounts more consistent with those from field collected scats (Kelly and Garton 1997). In some studies, the predators were given supplementary food prior to each trial (Goszczyński 1974, Artois et al. 1987), whereas in most studies predators were fasted for 24–72 h (Lockie 1959, Weaver 1993, Rühle et al. 2003, 2008, Webbon et al. 2006, this study). Fasted predators consume more indigestible matter of the offered

food, which results in smaller CFs, than those of their non-fasted conspecifics (Rühle et al. 2008). We also divided the hares fed to the foxes into two halves (following Goszczyński 1974), whereas in other studies, hares were offered as whole and the uneaten remains were offered the next day (Stahl 1990).

The CF for a given food type may vary depending on the prey size and on the parts consumed (Goszczyński 1974, Brzezinski and Marzec 2003). The unexpected lack of relationship between consumed biomass and mass of scats for deer and lamb (Fig. 1) could be due to daily variations in the amount of skin and hair consumed with these foods. This was the reason suggested by Hewitt and Robbins (1996) explaining why a single CF for ungulates cannot be used for the grizzly bear *Ursus arctos*. Since ungulate carrion ingested by red foxes in the wild usually contains much larger amounts of indigestible parts than the pieces provided in our feeding tests, CFs lower than the value we obtained could be more appropriate for scat samples collected in the wild. In this sense, Jedrzejewski and Jedrzejewska (1992) suggested a CF of 15 for deer in the diet of the red fox, which contrasts with higher values estimated in our study (47.3) or those previously proposed (118; Goszczyński 1974). CFs also depend on prey use (the percent that a given prey animal is consumed): Rühle et al. (2008) found a strong relationship between the percentage of prey use and CFs and recommended using larger CFs when prey use is low.

Another group of factors explaining the numerical differences among studies concerns the laboratory methods. CFs are usually estimated after washing scats through a sieve with mesh size varying between 0.5 mm and 2.0 mm (Table 4). Using smaller meshes generally results in smaller CFs (Webbon et al. 2006, Rühle et al. 2008, Fig. 4). Our CF values, estimated using dry mass of whole unwashed scats, are similar to the values estimated previously using this method (Stahl 1990) and close to the values using 0.5 mm mesh size (Webbon et al. 2006), but smaller than those estimated by washing scats through 2.0 mm sieves (Lockie 1959, Goszczyński 1974, Stahl 1990, Rühle et al. 2008, Table 4). Considering all the values reported in the studies performed so far (Table 4), this trend towards larger CF values for larger mesh sizes (Fig. 4) is not significant ($F_{1,33} = 0.759$, $p = 0.390$), probably because the large variation among studies due to other factors.

Beyond these numerical differences among studies, some common patterns arise when comparisons are made. For instance, ungulates and lagomorphs are the foods with the largest CF values while small birds, small rodents and fruits have the smallest CF values across studies (Table 4).

While CFs represent a simplification of the actual digestibility values, the percentage of biomass estimated with CFs provides a relatively accurate estimate of the amount of food eaten by carnivores (Goszczyński 1974, Roger et al. 1990, Brzezinski and Marzec 2003). When CFs for some foods are not available for a given carnivore species, using those values estimated for other predator species for the same food is a common practice. According to other authors this is fully inadvisable since the values of CFs for the same food types may differ notably among predators (Rühle et al. 2007, 2008).

Table 4. Correction factors (CF; fresh ingested biomass/dry mass of remainders in scats) of the red fox according to previous studies using feeding trials. CFs were obtained using dry weight of full unwashed scats (CF₀), after washing through 0.3 mm (CF_{0.3}), 0.5 mm (CF_{0.5}), 1.0 mm (CF₁) or 2.0 mm (CF₂) sieves.

Reference	Fasted	CF	Ungulates			Birds			Rodents			Lagomorphs	Fruit
			Small	Large	Small+ large	Small	Large	Small	Large				
Lockie 1959 ¹	Yes	CF ₂	—	61	45–61	23	44	43	—	—	—	—	
Goszczyński 1974 ¹	No	CF ₂	118	—	35	23	—	50	—	—	—	—	
Frank 1979 (cub foxes)	No	CF ₂	—	107	37–107	—	—	120	—	—	—	—	
Rühe et al. 2008	Yes	CF ₂	52	—	—	33	—	25	—	—	—	—	
Stahl 1990	No	CF ₂	—	33.4	—	23.9	—	41.8	—	—	—	13.6	
Stahl 1990	No	CF ₁	—	28.3	—	23.1	—	38.9	—	—	—	12.5	
This study ²	Yes	CF _{0.5}	76.3	20.2	—	—	26.8	25.8–31.8	—	—	—	48.1	
Webbon et al. 2006	Yes	CF _{0.5}	22.4	13.9	—	—	20.7	31.4	—	—	—	—	
Rühe et al. 2008	Yes	CF _{0.5}	44	—	—	28	—	22	—	—	—	—	
Artois et al. 1987	Yes	CF _{0.3}	—	81	—	41	—	—	—	—	—	18	
This study	Yes	CF ₀	47.3	12.5	—	—	16.6	16.0–19.7	—	—	—	29.8	
Stahl 1990	No	CF ₀	—	13.5–15.8	—	—	—	15.7–16.4	—	—	—	15.5	

¹ Lockie (1959) and Goszczyński (1974) calculated the CF as (fresh weight of food given)/(dry weight of egested remains) while the remaining studies calculated CFs as (fresh weight of food ingested)/(dry weight of egested remains); ² CF_{0.5} was derived from CF₀ in our study as CF_{0.5}/0.62, with 0.62 being the average proportion of macroscopic dry weight remains in 115 wild fox scats collected in Central Spain (authors' own data), in agreement with values reported by Reynolds and Aebischer (1991).

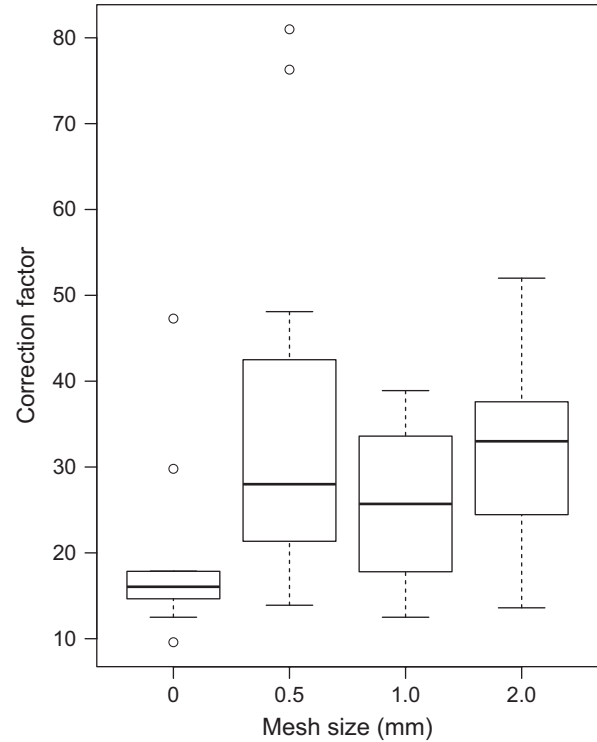


Figure 4. Boxplot of correction factor values as a function of mesh size according to the values reported in this and previous studies.

Criticisms and alternatives to correction factors

A limitation of CFs is their high variability for some food types. The precision of our CF estimates for most of the foods tested was similar to that reported by Stahl (1990). However, the precision was much lower (C.V. >0.50) for some foods (e.g. deer, hare and grapes). This low precision is probably due to the variability in the indigestible parts contained among different pieces of the same food (e.g. deer or hare) offered in different daily tests. However, this would not explain the low precision of CF for more homogeneous foods such as grapes. Another possible explanation is that our estimates were obtained on a daily basis, in contrast with other studies. Artois et al. (1987) found that red foxes produced faeces between 8 and 48 h after the ingestion of a given meal. Gastrointestinal transit times have been estimated between 22 and 57 h for other canid species (Childs-Sandford et al. 2006, Boillat et al. 2010). Hence, scats can be produced up to three days after food ingestion, which would explain the large variation of daily estimates of CFs in our study. This low precision of some CFs would imply lower precision in the final estimates of diet, predation impact or predator–prey relationships. Increasing the number of tests per type of food could help in obtaining more precise estimates in future studies. Hence, we suggest caution, taking into account this variability, when applying CFs to estimate the proportion of ingested biomass by carnivore predators.

CFs are usually derived from feeding trials with only one food type at a time, but digestibility of a given food type could be affected by the presence of other foods in the gut (Jaslow 1987, Stahl 1990). Different CFs can result from multi-species experiments, but this method is probably

prone to more errors than the simple weighing of scats collected during monospecific experiments (Stahl 1990).

Recommendations

The variability of CFs should be taken into account when they are applied to calculating the consumed biomass from proportions of dry mass of scats. Most of the tested foods in this study have CFs with low variability and can be used to estimate the consumed biomass with high precision. However, the uncertainty of CFs for some foods (ungulates, fruits, hare) should be considered, for instance by performing Monte Carlo simulations with random CF values within the confidence intervals, translating this uncertainty to the consumed biomass estimates. Additionally, caution should be taken when using the CF of a given food as a proxy for a whole group including foods with very likely noticeable variation in digestibility, such as fruits (Hewitt and Robinson 1996). Nevertheless, we believe that considering these sources of variability will allow unbiased diet estimates to support management and conservation decisions.

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References

- Artois, M. et al. 1987. Les fèces du renard (*Vulpes vulpes*) comme indice de consommation ou de préférence alimentaire et d'activité. – Cahiers d'Ethologie Appliquée 7: 275–286.
- Baker, P. et al. 2006. The potential impact of red fox *Vulpes vulpes* predation in agricultural landscapes in lowland Britain. – Wildl. Biol. 12: 39–50.
- Boillat, C. S. et al. 2010. Assessment of the relationship between body weight and gastrointestinal transit times measured by use of a wireless motility capsule system in dogs. – Am. J. Vet. Res. 71: 898–902.
- Brzezinski, M. and Marzec, M. 2003. Correction factors used for estimating prey biomass in the diet of American mink *Mustela vison*. – Acta Theriol. 48: 247–254.
- Carvalho, J. C. and Gomes, P. 2004. Feeding resource partitioning among four sympatric carnivores in the Peneda-Gerês National Park (Portugal). – J. Zool. 263: 275–283.
- Chetri, M. et al. 2017. Snow leopard and Himalayan wolf: food habits and prey selection in the central Himalayas, Nepal. – PLoS One 12: e0170549.
- Childs-Sanford, S. E. and Angel, C. R. 2006. Transit time and digestibility of two experimental diets in the maned wolf (*Chrysocyon brավildchyrus*) and domestic dog (*Canis lupus*). – Zoo Biol. 25: 369–381.
- Choate, J. R. et al. 1998. Guidelines for the capture, handling and care of mammals as approved by the American Society of Mammalogists. – J. Mammal. 79: 1416–1431.
- Ciucci, P. et al. 1996. A comparison of scat-analysis methods to assess the diet of the wolf *Canis lupus*. – Wildl. Biol. 2: 37–48.
- Council of the European Union. 1999. Council Decision of 23 March 1998 concerning the conclusion by the Community of the European Convention for the protection of vertebrate animals used for experimental and other scientific purpose. – Official Journal of the European Communities 1999/575/EC.
- Diaz-Ruiz, F. et al. 2013. Biogeographical patterns in the diet of an opportunistic predator: the red fox *Vulpes vulpes* in the Iberian Peninsula. – Mammal Rev. 43: 59–70.
- Donadio, E. and Buskirk, S. W. 2006. Diet, morphology and interspecific killing in carnivora. – Am. Nat. 167: 524–536.
- Faliu, L. and Griess, D. 1974. Essai d'alimentation de renards roux à l'aide d'un aliment composé complet sec pour le chien. – Rev. Med. Vét. 125: 1215–1224.
- Fernandez-de-Simon, J. et al. 2015. Can widespread generalist predators affect keystone prey? A case study with red foxes and European rabbits in their native range. – Popul. Ecol. 57: 591–599.
- Floyd, T. J. et al. 1978. Relating wolf scat content to prey consumed. – J. Wildl. Manage. 42: 528–532.
- Frafjord, K. 1993. Energy-intake of captive adult-sized Arctic foxes *Alopex lagopus* in Svalbard, in relation to body-weight, climate and activity. – Z. Säugetierkunde 58: 266–274.
- Frank, L. G. 1979. Selective predation and seasonal-variation in the diet of the fox (*Vulpes vulpes*) in NE Scotland. – J. Zool. 189: 526–532.
- Goszczyński, J. 1974. Studies on the food of foxes. – Acta Theriol. 19: 1–18.
- Harris, S. and Saunders, G. 1993. The control of canid populations. – Symp. Zool. Soc. Lond. 65: 441–464.
- Hewitt, D. G. and Robbins, C. T. 1996. Estimating grizzly bear food habits from fecal analysis. – Wildl. Soc. Bull. 24: 547–550.
- Jaslow, C. R. 1987. Morphology and digestive efficiency of red foxes (*Vulpes vulpes*) and gray foxes (*Urocyon cinereoargenteus*) in relation to diet. – Can. J. Zool. 65: 72–79.
- Jedrzejewski, W. and Jedrzejewska, B. 1992. Foraging and diet of the red fox *Vulpes vulpes* in relation to variable food resources in Białowieża National Park, Poland. – Ecography 15: 212–220.
- Kelly, B. T. and Garton, E. O. 1997. Effects of prey size, meal size, meal composition and daily frequency of feeding on the recovery of rodent remains from carnivore scats. – Can. J. Zool. 75: 1811–1817.
- Kelly, J. F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. – Can. J. Zool. 78: 1–27.
- Khan, U. et al. 2018. Predator, prey and humans in a mountainous area: loss of biological diversity leads to trouble. – Biodivers. Conserv. 27: 2795–2813.
- Klare, U. et al. 2011. A comparison and critique of different scat-analysis methods for determining carnivore diet. – Mammal Rev. 41: 294–312.
- Kohl, K. D. et al. 2015. Do wild carnivores forage for prey or for nutrients? Evidence for nutrient-specific foraging in vertebrate predators. – Bioessays 37: 701–709.
- Kondo, A. and Shiraki, S. 2012. Preferences for specific food species of the red fox *Vulpes vulpes* in Abashiri, eastern Hokkaido. – Mammal Study 37: 43–46.
- Lloyd, H. G. 1980. The red fox. – B.T. Batsford Ltd.

- Lockie, J. D. 1959. The estimation of the food of foxes. – *J. Wildl. Manage.* 23: 224–227.
- Lumetsberger, T. et al. 2017. Re-evaluating models for estimating prey consumption by leopards. – *J. Zool.* 302: 201–210.
- Macdonald, D. W. and Reynolds, J. C. 2004. Red fox. – In: Claudio Sillero-Zubiri, M. H. and Macdonald, D. W. (eds), *Canids: foxes, wolves, jackals and dogs – 2004 Status Survey and Conservation Action Plan*. IUCN – The World Conservation Union pp. 129–136.
- Mangiafico, S. 2018. rcompanion: functions to support extension education program evaluation. – R package ver. 2.0.0. <<https://CRAN.R-project.org/package=rcompanion>>.
- McDonald, J. E. and Fuller, T. K. 2005. Effects of spring acorn availability on black bear diet, milk composition and cub survival. – *J. Mammal.* 86: 1022–1028.
- Monterroso, P. et al. 2016. Niche partitioning at the edge of the range: a multidimensional analysis with sympatric martens. – *J. Mammal.* 97: 928–939.
- Nagy, K. A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. – *Ecol. Monogr.* 57: 111–128.
- Pinheiro, J. et al. 2018. nlme: linear and nonlinear mixed effects models. – R package ver. 3.1-137. <<https://CRAN.R-project.org/package=nlme>>.
- Pompanon, F. et al. 2012. Who is eating what: diet assessment using next generation sequencing. – *Mol. Ecol.* 21: 1931–1950.
- Reynolds, J. C. and Aebischer, N. J. 1991. Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. – *Mammal Rev.* 21: 97–122.
- Reynolds, J. C. and Tapper, S. C. 1996. Control of mammalian predators in game management and conservation. – *Mammal Rev.* 26: 127–156.
- Roger, M. et al. 1990. Facteurs correctifs de quantification du régime alimentaire du putois (*Mustela putorius* L.). – *Gibier Faune Sauvage* 7: 343–357.
- Rühe, F. et al. 2003. Two models for assessing the prey mass of European ungulates from wolf scats. – *Acta Theriol.* 48: 527–537.
- Rühe, F. et al. 2007. Data for estimating eaten prey masses from Eurasian lynx *Lynx lynx* scats in central and east Europe. – *Acta Theriol.* 52: 317–322.
- Rühe, F. et al. 2008. Conversion factors in carnivore scat analysis: sources of bias. – *Wildl. Biol.* 14: 500–506.
- Ryszkowski, L. et al. 1973. Trophic relationships of the common vole in cultivated fields. – *Acta Theriol.* 18: 125–165.
- Sargeant, A. B. 1978. Red fox prey demands and implications to prairie duck production. – *J. Wildl. Manage.* 42: 520–527.
- Slagle, K. et al. 2017. Attitudes toward predator control in the United States: 1995 and 2014. – *J. Mammal.* 98: 7–16.
- Soe, E. et al. 2017. Europe-wide biogeographical patterns in the diet of an ecologically and epidemiologically important mesopredator, the red fox *Vulpes vulpes*: a quantitative review. – *Mammal Rev.* 47: 198–211.
- Stahl, P. 1990. Influence of age-related changes in prey consumption on correction factors established for important prey of the red fox (*Vulpes vulpes*). – *Gibier Faune Sauvage* 7: 107–125.
- Wachter, B. et al. 2012. An advanced method to assess the diet of free-ranging large carnivores based on scats. – *PLoS One* 7: e38066.
- Weaver, J. L. 1993. Refining the equation for interpreting prey occurrence in gray wolf scats. – *J. Wildl. Manage.* 57: 534–538.
- Webbon, C. C. et al. 2006. Macroscopic prey remains in the winter diet of foxes *Vulpes vulpes* in rural Britain. – *Mammal Rev.* 36: 85–97.
- Wilson, E. E. and Wolkovich, E. M. 2011. Scavenging: how carnivores and carrion structure communities. – *Trends Ecol. Evol.* 26: 129–135.
- Yoneda, M. 1982. Influence of red fox predation on a local population of small rodents: II. Food habits of the red fox. – *Appl. Entomol. Zool.* 17: 308–318.