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SHORT COMMUNICATION

Short communication articles are short scientific entities often dealing with methodological problems or with byproducts of larger research projects. The style is the same as in original articles

Evaluating scat analysis methods to assess wolverine *Gulo gulo* diet

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A feeding trial was carried out on two captive wolverines *Gulo gulo* to evaluate methods to assess wolverine diets through scat content. During the feeding trial, wolverines were offered known quantities of five prey species. All scats were collected and their contents analysed. We evaluated four widely used methods of quantifying dietary composition: dry weight, index of relative contribution, frequency of occurrence, and percentage of occurrence. Based on the outcome of this evaluation, percentage of occurrence was found to be the most appropriate method for wolverine diet studies given the extreme variation in prey items (e.g. prey type and age) and undigested items (e.g. hide and bones) in the wolverine's diet. Dry weight may provide additional information on the amount of biomass consumed, which is biologically more meaningful than just the composition assessment derived from using the percentage of occurrence.

Key words: captive wolverines, dry weight, food experiment, foraging behaviour, frequency of occurrence, percentage of occurrence

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Food habit studies are an important prerequisite to understanding animal ecology, conservation and management (Korschgen 1980, Litvaitis 2000). Although diet preferences of several Mustelidae have been studied (Goszczynski 1976, Kruuk & Parish 1981, Wise et al. 1987, Cumberland et al. 2001), the food habits of wolverines *Gulo gulo* are relatively poorly understood (Landa et al. 2000).

Wolverines depend on both hunting and scavenging for food (Krott 1959, Haglund 1966), and their diet has been described in various areas of North America (Hornocker & Hash 1981, Magoun 1987, Banci 1994) and Fennoscandia (Haglund 1966, Myhre & Myrberget 1975, Landa et al. 1997). Most analyses have used frequency of occurrence to quantify diet composition (Berducou et al. 1983, Corbett 1989). Using this standardised methodology enables comparisons among different wolverine populations, but might overrepresent scavenged prey since these consist of relatively more fur and bones than hunted prey (Banci 1994, Landa et al. 1997).

Because separation and identification of individual diet items is labourious, visual estimation of the percentage of occurrence is often used when conducting scat analyses (Ciucci et al. 1996, Grosse et al. 2003). However, both measurements of dry weights of foods (Johnson & Hansen 1979, Reig & Jedrzejewski 1988) and an index of relative contribution have also been used (Berducou et al. 1983). How closely these various methods reflect actual prey biomass consumed is as yet unclear (Mills 1996), and precise comparisons across studies are difficult because no standard protocol has been developed (Sato et al. 2000).

Our study evaluated whether the actual species composition fed to wolverines was reflected in their scat contents. We assessed the accuracy of four analytical methods used to examine food habits or prey selection: 1) dry weight, 2) the index of relative contribution based on dry weight, 3) frequency of occurrence, and 4) percentage of occurrence. Frequency of occurrence and percentage of occurrence are used to estimate the impact of predation on the prey species (i.e. how often does the predator eat a certain prey species). Dry weight and the index of relative contribution give insight into the nutritional significance of each prey species to the predator (i.e. how much nutrition the different prey species render to the predator). This evaluation can serve as a useful tool for future studies on wolverine food habits.

Methods

Feeding trial

During 27 March - 17 April 1998, a feeding trial was carried out with two adult wolverines at Polar Zoo, Troms, Norway. Both wolverines were housed in a semi-natural enclosure of 15,000 m^2 consisting of natural birch forest. Two days prior to the feeding trial, their normal diet of traffic-killed moose *Alces alces* and culled goat *Capra hircus* kids was withheld. Immediately prior to the trial, the enclosure was cleaned of scats and food remains entirely.

During the trial, five important prey species for wolverines in Norway (Landa et al. 1997; see Table 1) were offered at the normal feeding time (between 13:00 and 15:00) to avoid behavioural changes due to different feeding regimes. Both animals were observed until all food was either consumed or hoarded to enable collection of hoarded food remains at the same time when scats were collected. Large prey (reindeer *Rangifer tarandus* and sheep *Ovis aries*) were provided in chunks, whereas small prey (hare *Lepus timidus*, grouse *Lagopus* spp. and rodent *Microtus* spp.) were provided whole. During the feeding trial, three consecutive feeding days were alternated with a 48-hour fasting period (*cf*. Floyd et al. 1978, Weaver 1993) to ensure all food was consumed and digested.

Line transect searches of the entire enclosure for scats and food remains were conducted twice a day at 12:00 and 17:00. We assumed that all food was entirely consumed since no hoarded food remains were found during our searches. During the feeding trial the presence of occasional light snowfall increased our ability to find scats and possible food remains. All scats were collected, labelled and frozen. Frozen scats were transported back to the laboratory where each scat was oven dried at 70°C for 24 hours and weighed using an electronic balance to the nearest 0.001 g. Afterwards each scat was stored until further analysis.

Scat analyses

Each scat was washed in a sieve with a diameter of 0.5 mm until the water was clear. Remains were

Table 1. Composition of wolverine diet using four quantification methods of analysis; dry weight (DW), index of relative contribution (IRC), frequency of occurrence (FO) and percentage of occurrence (PO), based on the hair and feather category found in the scats (N = 135) compared to the actual diet provided. Species ranking of importance are given between brackets (1 = highest rank). For each method, the proportional contribution (%) is listed per species followed by its deviation from the actual diet (Δ). The average absolute deviation (AAD) from the diet provided is given for each method for all species.

	Fresh weight in diet (g)	%	DW (g)	%	Δ	IRC (%)	%	Δ	FO (%)	%	Δ	PO (%)	%	Δ
Reindeer	6150 (1)	32.7	48.552 (1)	43.6	10.9	35.1 (1)	35.1	2.4	83.0 (1)	39.6	6.9	39.7 (1)	39.7	7.0
Sheep	6000 (2)	31.9	12.176 (4)	10.9	-21.0	11.1 (4)	11.1	-20.8	26.7 (4)	12.7	-19.2	12.8 (4)	12.8	-19.1
Grouse	3750 (3)	19.9	13.058 (3)	11.7	-8.2	22.6 (2)	22.6	2.7	43.7 (2)	20.8	0.9	20.6 (2)	20.6	0.7
Hare	2000 (4)	10.6	10.929 (5)	9.8	-0.8	9.7 (5)	9.7	-0.9	19.3 (5)	9.2	-1.4	9.2 (5)	9.2	-1.4
Rodent	900 (5)	4.8	26.697 (2)	24.0	19.2	21.4 (3)	21.4	16.6	37.0 (3)	17.6	12.8	17.7 (3)	17.7	12.9
AAD					12.0			8.7			8.2			8.2

separated into categories: hairs and feathers, rodent bones, other mammal bones, bird bones, unidentifiable bones, plant material, soft tissue (e.g. skin and internal organs), dirt and non-food items (e.g. rope and plastic). Each category was oven dried at 70°C for 24 hours. The relative contribution of each category to the entire scat was visually estimated using a superimposed grid. Hairs and feathers were identified to species level using macroscopic and microscopic characteristics following published identification keys (Williamson 1951, Day 1966, Teerink 1991) and reference collections. We visually estimated the contribution of each species in the hair and feather category to the nearest 5%. The hair and feather category and the other eight categories of the scat were weighed separately.

Data analyses

Dry weights (DW) for the different prey species within the hair and feather category were calculated by multiplying the visual estimation of the contribution for each prey species with the dry weight of the entire hair and feather category. For calculating the index of relative contribution (IRC), each species was given a value ($a_{i,c}$) between 0 and 5 based on relative contribution (after Berducou et al. 1983). For each scat the sum of the values was always 5. For calculation of the 'weight value' A_i of species i in the diet (based on all scats collected), we used

$$A_i = \sum_{ni} (a_{i,c} + p_c),$$

where p_c is the dry weight of scat c. IRC was calculated as

$$IRC_i(\%) = \frac{Ai}{\sum Ai} \cdot 100 \text{ (Berducou et al. 1983).}$$

Frequency of occurrence (FO) was calculated as

$$FO_i\ (\%) = \frac{n_i}{N} \cdot 100$$

where N is the total number of scats and n_i the number of scats containing species i (Berducou et al. 1983, Corbett 1989), whereas percentage of occurrence (PO) was calculated as

$$PO_i\ (\%) = \frac{n_i}{\sum n_i} \cdot 100 \text{ (Ciucci et al. 1996).}$$

Diets calculated using the four methods, based on the species found within the hair and feather category, were compared with the diet provided to the wolverines through concordance of species ranking of importance. In addition, the proportional contribution of each species calculated using each of the four methods (i.e. contribution of a species divided by the sum of contributions over all five species) was compared with the proportional contribution for the actual diet provided. The average absolute deviation (AAD) from the actual diet was calculated by averaging the absolute differences of the proportional contributions for each method with the actual diet over all species.

To evaluate concordance among the four methods, all categories were ranked according to their importance in the diet based on the results obtained by each method. Kendall's τ coefficient of concordance (Zar 1999) was used to measure agreement between the methods. Values approaching 1 indicate that two methods rendered similar results, whereas values near 0 indicate a lack of concordance between the methods. Significance of W-values was tested using Friedman's method (for $N < 6$) and χ^2 method ($N > 6$; Zar 1999). Spearman's rank correlation was calculated to test for differences between pairs of methods (Zar 1999).

Results

During the feeding trial, 159 scats were collected and analysed. The scats had a mean (± SE) dry weight of 6.269 ± 0.707 g. On average, half of the scat contents consisted of microscopic fragments (< 0.5 mm, 3.265 ± 0.373 g vs 2.990 ± 0.379 g macroscopic fragments). The macroscopic fragments consisted mostly of unidentifiable bones (0.968 ± 0.210 g), hair and feathers (0.705 ± 0.098 g) and non-food items (0.559 ± 0.118 g). Of the 159 scats collected, 24 scats did not contain any hair or feathers of the prey species provided.

Ranking of reindeer within the four methods agreed with the ranking of reindeer within the diet provided, as did the ranking of grouse using DW (Table 1). The average absolute deviation, as measure for difference between method and actual diet provided, was lowest for FO and PO and highest for DW. Sheep was underestimated and rodent overestimated in all four methods (see Table 1).

The different categories recovered in the scats, as quantified by each method, is presented in Table 2. The different categories were ranked in descending

Table 2. Composition of wolverine diet and ranking of importance (r) using four quantification methods of analysis (i.e. dry weight, DW, index of relative contribution, IRC, frequency of occurrence, FO, and percentage of occurrence, PO) based on 15 categories found in 159 scats. Ranks 1, 2 and 3 are given in italics.

	DW		IRC		FO		PO	
	g	r	%	r	%	r	%	r
Mammalian bones	11.430	9	2.3	13	5.7	15	1.8	10
Reindeer hair	48.552	4	14.3	*2*	70.4	*1*	16.2	*2*
Sheep hair	12.176	8	5.0	8	22.6	9	4.9	8
Hare hair	10.929	10	4.3	9	16.4	11	4.7	9
Rodent bones	9.267	11	4.0	10	9.4	12.5	1.4	12.5
Rodent hair	26.697	6	9.1	5	31.4	6	7.7	6.5
Bird bones	2.241	12	3.1	12	9.4	12.5	1.4	12.5
Feathers	13.058	7	1.0	*3.5*	40.9	4	7.7	6.5
Wolverine hair	0.348	15	3.4	11	30.8	7	0.4	15
Unidentifiable bones	153.984	*1*	15.1	*1*	62.9	*2*	20.1	*1*
Unknown hair	0.578	14	2.0	14	17.6	10	1.0	14
Soft tissue	2.093	13	1.5	15	6.3	13	1.6	11
Plant material	44.561	5	8.3	6	36.5	5	9.7	4
Dirt	50.600	*3*	7.7	7	28.3	8	8.9	5
Non-food items	88.882	*2*	1.0	*3.5*	41.5	*3*	12.4	*3*

order of occurrence in the entire diet. Agreement among rankings within the 15 categories was significant in all simultaneous comparisons ($0.85 \leq W \leq 1.00$; Table 3), except for the combination FO and DW ($W = 0.83$, n.s.). This was supported by Spearman's correlation coefficients in pairwise comparisons ($0.75 \leq r_s \leq 1$). The Kendall's coefficient of concordance was highest for PO together with DW ($W = 0.98$, $r = 0.97$).

Discussion

Of the four quantification methods, FO and PO resulted in the lowest deviation from the actual diet provided. Although FO had a low concordance with the other three methods, it may still be advisable to include FO in wolverine diet analyses since it enables comparison with former wolverine diet studies (e.g. Myhre & Myrberget 1975, Magoun 1987, Landa et al. 1997). Both FO and PO can be derived from the same dietary analytical procedure (i.e. counting the occurrence of a species within the hair and feather category). Given wolverines' opportunistic and varied diet, PO provides, however, a better indication of the relative frequency with which each prey species was consumed (Berducou et al. 1983, Ciucci et al. 1996). Not only does it indicate how common a prey species is in the diet, but it also accounts for various prey species being found in a scat (Ackerman et al. 1984).

Table 3. Comparison of scat-analysis methods (i.e. dry weight, DW, index of relative contribution, IRC, frequency of occurrence, FO, and percentage of occurrence, PO) based on 15 categories of scat contents to assess wolverine diet, as tested by simultaneous concordance (Kendall's coefficient of concordance, W) and supported by Spearman's rank correlation coefficients in pairwise comparisons (r). An asterisk indicates significant concordance or correlation at $P < 0.05$.

Method	DW	IRC	FO
IRC	W = 0.93*		
	r = 0.88*		
FO	W = 0.83	W = 0.93*	
	r = 0.70*	r = 0.90*	
PO	W = 0.98*	W = 0.94*	W = 0.86*
	r = 0.97*	r = 0.87*	r = 0.75*

Although the use of PO (i.e. estimating occurrences) may be susceptible to subjectivity, it appears to be a good method for analysing prey species within the hair and feather category of wolverine scats. The main disadvantage of using occurrence is that it equates all hairs equally, regardless of prey size (Lockie 1959, Day 1966, Kruuk & Parish 1981). This bias is important because larger prey would constitute more biomass to a predator, particularly to a scavenging species that will return to a carcass for repeated feedings (Cumberland et al. 2001). PO agreed well with DW, which is derived from a different and more labourious procedure, but which may provide additional information on the amount of biomass consumed and on the significance of each prey species to the predator when corrected by digestibility coefficients (see Reynolds & Aebischer 1991). The use of DW may thus be more meaningful biologically than just an assessment of occurrence. It must, however, be stressed that coefficients of digestibility assume that the whole animal was consumed. Since food hoarding is a common practice of wolverines in the wild, this assumption might not always be met.

Digestive fragmentation appears to result in high losses of both macroscopic and microscopic hair and feather characteristics. Microscopic fragments (< 0.5 mm) constituted over half of the entire scat, indicating a high decomposition rate within the digestive system. Differences in the surface area to volume ratio among species may well explain over- or under-representation of prey species found within the diet. Rodents, which are eaten entirely, contain relatively more fur than (chunks of) reindeer and sheep. This could explain the consistent over-representation of rodent within the hair and feather category of scats compared to the actual diet provided.

Although hare and rodent hair and bird feathers are uniquely identifiable macroscopically and microscopically, moose hair is macroscopically identical to reindeer hair (Spaulding et al. 2000). During scat analyses we also found that sheep hair was only identifiable when present in larger amounts. Trace amounts or highly fragmented sheep hair tend to have the same micro- and macroscopic characteristics as reindeer underhair and can therefore easily be mistaken. This might explain our overestimation of reindeer and underestimation of sheep in the diet. Landa et al. (1997) argue that low representation of sheep in their dietary study on wolverines in the wild occurred because sheep wool is likely to fall off during decomposition of sheep carcasses after being hoarded by wolverines during late summer. In our study, however, this could not explain the underrepresentation of sheep since no food was hoarded. Our underrepresentation of sheep may be caused by wolverines plucking the wool from the meat prior to consumption. This behaviour was repeatedly observed when portions of sheep were offered to the wolverines in our study, and we found wool patches where plucking behaviour was observed.

Our experimental design did not allow us to distinguish between scats from the female and the male wolverine. Similarly, our trial could not assess potential differences in food handling (i.e. playing and chewing) between the two individuals nor extrapolate to the wild. Either of these factors could result in a bias with regard to digestibility. The aim of our trial, however, was to evaluate the accuracy of four analytical methods and not to assess (sexual differences in) digestibility of dietary components in wolverines. Therefore, we do not believe that this will affect the main conclusions of our trial, particularly since the comparisons of methods was based on the same source data. Percentage of occurrence seems to be the best available methodology for wolverine diet studies. A combination of this methodology with sexing via DNA extracted from scats (Flagstad et al. 2004) could be useful to gain insight into sex differences in digestibility and diet of wolverines in the wild. Furthermore the semi-natural enclosure stimulated natural behaviour, but it clearly does not reflect all the various conditions wolverines meet in the wild. The possible changes in digestive ability and feeding behaviour among seasons and between feeding regimes (i.e. starvation vs feeding *ad libitum*) will most likely affect the remains found in scats and should be taken into consideration when comparing this dietary study with dietary studies on wolverines in the wild.

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