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Source: Wildlife Biology, 14(4) : 500-506

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/0909-6396-14.4.500

SHORT COMMUNICATION

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Conversion factors in carnivore scat analysis: sources of bias

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Rühe, F., Ksinsik, M. & Kiffner, C. 2008: Conversion factors in carnivore scat analysis: sources of bias. - Wildl. Biol. 14: 500-506.

Scat analyses are commonly applied to study feeding ecology of carnivores. Factors developed in feeding trials are often used to convert dry matter mass of scat remainders to fresh matter mass of killed or scavenged prey. In our study, we aimed at: 1) presenting conversion factors (CFs) of roe deer *Capreolus capreolus*, European hare *Lepus europaeus* and house mice *Mus musculus* digested by wolf *Canis lupus*, Eurasian lynx *Lynx lynx* and red fox *Vulpes vulpes*, 2) comparing CFs derived from fox exposed to different feeding levels (fasted vs non-fasted before each feeding trial), 3) comparing effects of using different mesh sizes in the lab procedure on CFs, 4) comparing effects of applying CFs derived from wolf, lynx and fox to wolf scats, and 5) quantifying biases caused by inappropriate procedures in scat analyses. Feeding level, use of different mesh sizes, and application of predator-specific CFs affected the estimated number of killed prey individuals. The greatest deviations were found for the feeding level in regard to roe deer and European hare, and for the application of lynx CFs of roe deer and European hare to wolf scats. The strong relationship between prey use and CFs in our study may be used to estimate prey numbers from scats more precisely: in cases of low prey use, we suggest applying CFs derived from non-fasted carnivores, and in cases of high prey use CFs from fasted conspecifics are more appropriate. We recommend applying predator-prey specific CFs and using the same mesh size on which these CFs are based. The presented CFs allow recalculation of prey masses and prey numbers from scat analyses, which had been gained by using inappropriate CFs.

Key words: diet, functional response, predation, prey preference

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Received 19 June 2007, accepted 28 March 2008

Associate Editor: Henrik Andrén

Scat analysis is a basic method to study feeding ecology of elusive carnivores (e.g. Ciucci et al. 1996). Estimating numbers of prey individuals killed by carnivores is essential for studying prey preferences of carnivores, prey overlap of sympatric carnivores, and for describing functional responses of carnivores to changing prey densities (e.g. Jędrzejewska & Jędrzejewski 1998).

Biomass models (Floyd et al. 1978, Traves 1983, Ackerman et al. 1984, Weaver 1993, Rühe et al. 2003, Jethva & Jhala 2004, Rühe et al. 2007) and conversion factors (CFs) are often applied to estimate prey biomasses from scats. Conversion factors convert the dry mass of scat fractions to fresh matter of prey biomass. They are based on feeding trials with prey individuals of different body masses or prey classes. All scats resulting from the digestion of one prey individual are washed through a sieve and the remainders in the sieve are used to compute the specific conversion factor. CFs are often presented as single values for specific prey species or prey classes (Lockie 1959, Goszczynski 1974, Stahl 1990, Webbon et al. 2006) and are rarely used in a linear regression, linking CFs to prey mass (Artois et al. 1987).

One major issue in applying CFs to scat fractions from field studies is that the reference parameter of the CF is chosen according to the aim of the study (Reynolds & Aebischer 1991): There are two types of CFs, one based on prey mass presented and another one based on prey mass consumed. When aiming at estimating the number of killed or scavenged, further on summarised as 'killed' prey individuals, it is appropriate to use the CFs based on the presented prey mass (e.g. Lockie 1959, Goszczynski 1974) whereas it would be reasonable to use CFs based on the consumed prey mass (e.g. Artois et al. 1987, Stahl 1990, Webbon et al. 2006) when studying energetics of free-ranging carnivores. This basic differentiation equally concerns the application of biomass models (*cf.* 'prey consumed' (Floyd et al. 1978) and 'prey presented' (Weaver 1993)). Focussing on the utilisation of our results for studying predator-prey relationships, we aim at providing CFs based on presented prey masses. A second issue is the experimental set up of feeding trials. In some studies, the predators were given supplementary food prior to and at the end of each trial (Goszczynski 1974, Artois et al. 1987), whereas in most other studies (Lockie 1959, Floyd et al. 1978, Traves 1983, Weaver 1993, Rühe et al. 2003, Webbon 2006, Rühe et al. 2007) predators were fasted for 24-72 hours. We hypothesise that fasted predators consumed more undigestible matter of the presented carcasses which resulted in smaller CFs than those of their non-fasted conspecifics. In our study, feeding trials were carried out with fasted carnivores and the resulting CFs were compared with published CFs derived from feeding trials with non-fasted predators.

A third issue concerns the laboratory methods for deriving and applying CFs. Most cited CFs were derived by washing scats through a sieve with 2-mm meshes (Lockie 1959, Goszczynski 1974), whereas others used 1.0-mm sieves (Stahl 1990), 0.5-mm sieves (Reynolds & Aebischer 1991, Webbon et al. 2006) or 0.3-mm sieves (Artois et al. 1987). In field studies, sieves with 0.5 mm (e.g. Ciucci et al. 1996, Ansorge et al. 2006) or 1.0 mm (e.g. Jędrzejewska & Jędrzejewski 1998) meshes were used to gain macroscopic scat remainders. The masses of these remains were multiplied with CFs derived from 2.0-mm sieves to estimate the prey masses represented by the scats. We hypothesise that this procedure might lead to overestimations of prey masses.

A fourth issue deals with the cross-predator-species use of CFs. Because CFs of wolves *Canis lupus* and Eurasian lynx *Lynx lynx* had then not been published, CFs of red foxes *Vulpes vulpes* had been applied to estimate prey masses of lynx (Jędrzejewska & Jędrzejewski 1998) and wolves (Jędrzejewska & Jędrzejewski 1998, Ansorge et al. 2006). We present CFs for red fox, Eurasian lynx and wolves after feeding on frequent prey species of these carnivores. In this regard, we hypothesise that the CFs of the same prey type differ between carnivore species.

We illustrate the effects of: 1) differing feeding level, 2) differing laboratory procedures and 3) cross-predator-species use of CFs by estimating the number of killed prey individuals from scats of free-ranging wolves in Germany.

Material and methods

Feeding trials

We kept two adult Eurasian lynx (1.5-2 years of age; weighing 29 and 31 kg; Burmester 2005), one adult wolf (3-3.5 years; 29 kg) and three adult red foxes (1-1.5 years; 6, 8 and 8 kg, respectively; R. Willecke, pers. comm.) in paved enclosures, which were 390, 278 and 60 m^2 in size, respectively. The animals were treated regularly with anthelmintics and were kept and handled according to animal welfare guidelines.

The feeding followed Lockie (1959); i.e. before each trial, the animals were fasted for 48 hours, and we removed all scats from the enclosures. In each trial, we offered a roe deer *Capreolus capreolus* (17.5-20.0 kg), European hare (2.8-4.7 kg) and a daily diet of house mice *Mus musculus* (1.2-4.0 kg) to each carnivore group. We offered most prey as unopened bodies. Roe deer were fed to the wolf and the foxes during summer and they were divided in portions to prevent decay.

During the trials, we collected scats twice a day whereby all scats were collectable and distinguishable from each other (*cf*. Floyd et al. 1978, Traves 1983, Weaver 1993, Rühe et al. 2003). The end of each trial was reached when the animals did not feed on the carcass for 48 hours. At the end of each trial, we removed all uneaten prey remainders from the enclosures and weighed them to a precision of 10 g.

Scat analysis

We carefully cleaned each collected scat from attached non-scat particles, weighed them to a precision of 0.1 g fresh matter (fm), sealed them in a consecutively numbered air-tight plastic bag and stored them at -18°C. We calculated the consumed prey mass as the difference between offered and not eaten prey mass. Following Lockie (1959) and Goszczynski (1974), we washed all scats of the feeding trials, after they had been soaked sufficiently in water, through a 2-mm sieve and an underneath fixed 0.5-mm sieve and determined the dry matter (dm) of undigested, macroscopic scat remainders. For the dm determination, we dried all scat remainders for 24 hours at 105°C and weighed them to a precision of 0.1 g. Thus, conversion factors to the presented fm prey mass were calculated from the dm mass of macroscopic scat remainders after washing the scats through a 2-mm sieve ($CF_{2.0}$) and the sum of the dm masses of scat remainders after washing through the 2-mm and a 0.5-mm sieve ($CF_{0.5}$).

We defined apparent fm digestibility (in %) as follows: (ingested fm food mass - fm scat mass) $*$ 100/ ingested fm food mass. Because the water content in the scats could not be attributed to the ingested prey alone with certainty (an unknown proportion might have resulted from drinking water intake), we named it apparent fm digestibility.

Application of conversion factors to field data

We used recently published and unpublished field data on wolves to show the effects of using different CFs. Wolf diet was represented by 192 scats. Relative volumes of scat fractions per prey type were estimated. Remainders of non-fawn roe deer, non-leveret hare, small rodents and other prey amounted to 38.6, 3.0, 0.1 and 58.3%, respectively (Ansorge et al. 2006; H. Ansorge, pers. comm., G. Kluth, pers. comm.). The number of killed individuals of each prey species (N) was calculated as follows: N = dm mass of macroscopic prey remainders in the washed scats $\times$ CF/mean total body mass of a prey individual.

For comparing the estimated number of killed prey individuals, we assumed the following mean prey body masses: roe deer: 19 kg (according to F. von Plettenberg (pers. comm.) and von Raesfeld (1978)), hare: 4 kg, and small rodent: 0.025 kg. We mainly used the values based on the wolf-$CFs_{0.5}$ as references, because macroscopic prey remainders of the field data had been obtained using 0.5-mm sieves (by Ansorge et al. 2006). We computed Spearman rank correlations (r_s) with SigmaStat 1.0.

Table 1. Prey presented, prey eaten and scat mass excreted by one adult wolf, two adult lynx and three adult red foxes as well as conversion factors from scat remainders to presented prey mass in nine feeding trials in an enclosure of the University of Göttingen, Germany, in 2003 (lynx) and 2006 (wolf, red fox); fm = fresh matter, Dm = dry matter.

Predator species	Prey species	Prey mass (g fm) presented	Prey mass (g fm) eaten	Prey use (%)	Apparent fm digestibiliy (%)	Dm mass (g) of scat remainders after washing through a 2-mm sieve	Conversion factor to prey mass presented $CF_{2.0}$
Wolf	Roe deer	20 000	19 066	95	87	396.3	50
Wolf	European hare	3 263	3 260	100	84	139.7	23
Wolf	95 House mice	3 425	3 425	100	85	100.0	34
Lynx	Roe deer	17 500	12 600	72	96	155.0	113
Lynx	European hare	4 700	4 570	97	92	88.1	53
Lynx	123 House mice	4 000	4 000	100	86	143.7	28
Red fox	Roe deer	19 900	18 728	94	91	380.0	52
Red fox	European hare	2 766	2 741	99	84	112.1	25
Red fox	40 House mice	1 200	1 200	100	85	36.8	33

Table 2. Conversion factors of dry matter (dm) mass of scat remainders after washing through a 2-mm sieve, derived from feeding trials with red fox, and differentiated according to the feeding level. Goszczynski's (1974) foxes were fed with pig hearts prior to and in the final stage of each trial ('Fed'), whereas Lockie's (1959) and our foxes were fasted 48 hours before each trial ('Fasted').

	Feeding level		
	Fed	Fasted	
Prey	Goszczynski (1974)	Lockie (1959)	Our study
Roe deer	118		52
Lagomorph	50	41	25
Small rodents	23	23	33

Table 3. Conversion factors of dry matter mass of scat remainders after washing through a 2-mm sieve ($CF_{2.0}$) and after washing through a 0.5-mm sieve ($CF_{0.5}$).

Predator species	Prey species	$CF_{2.0}$	$CF_{0.5}$	$CF_{0.5}/CF_{2.0}$
Wolf	Roe deer	50	37	0.74
Wolf	European hare	23	22	0.96
Wolf	95 House mice	34	28	0.82
Lynx	Roe deer	113	81	0.72
Lynx	European hare	53	48	0.91
Lynx	123 House mice	28	24	0.86
Red fox	Roe deer	52	44	0.85
Red fox	European hare	25	22	0.88
Red fox	40 House mice	33	28	0.85

Results

Conversion factors of wolf, lynx and red fox

The prey-specific conversion factors ($CF_{2.0}$) in wolf were similar to those in red fox. In lynx, the CFs of roe deer and hare were greater than in the canids. The CF for house mice was smaller in lynx than in wolf and fox. The lynx consumed smaller proportions of roe deer and European hare, thus selecting higher apparent digestible parts of the prey body than the wolf and the foxes did (Table 1).

Feeding selectivity of the three carnivore species focussed on highly apparent digestible prey items as apparent fm digestibility rose with a decrease in prey use (r_s = -0.76, N = 9, P = 0.01). The relationships of $CF_{2.0}$ to apparent fm digestibility (r_s = 0.94, N = 9, P < 0.01) and to prey use (r_s = -0.77, N = 9, P = 0.01) were strong.

Effect of feeding level

Feeding roe deer to fasted foxes resulted in a considerably smaller CF compared to the CF derived from feeding roe deer to non-fasted foxes. Differences among CFs for lagomorphs were less pronounced. CFs for small rodents were not consistent with the general tendency that CFs from foxes which received supplementary food were greater than those of fasted conspecifics (Table 2).

Effect of using different mesh sizes

Using smaller meshes generally resulted in smaller CFs: values of $CF_{0.5}$ amounted to 72-96% of the corresponding values of $CF_{2.0}$. In trials with red foxes, these quotients were similar for different prey species, but varied considerably among different prey types in the lynx and wolf trials (Table 3).

Effect of cross-predator-species application of conversion factors

We estimated the numbers of killed prey individuals as represented by 80 scats of free-ranging wolves (details in Fig. 1). In accordance with the laboratory procedure used by Ansorge et al. (2006) we applied $CF_{0.5}$. We applied the factors from feeding trials with fox, lynx and wolf to the wolf data: The $CF_{0.5}$ of fox resulted in a similar estimate for the number of roe deer (2.69), whereas the CF of lynx resulted in a more than two times greater estimated number of killed roe deer (4.96) compared to the $CF_{0.5}$ of the wolf trial (2.27). Comparing the estimated numbers of killed European hares yielded a similar pattern as found in roe deer ($CF_{0.5}$ fox: 0.67 hares, $CF_{0.5}$ lynx: 1.46, $CF_{0.5}$ wolf: 0.67). The estimated numbers of killed small rodents were identical between $CF_{0.5}$ fox and $CF_{0.5}$ wolf (0.90), whereas the number derived from $CF_{0.5}$ lynx was slightly smaller (0.77; see Fig. 1).

Discussion

Conversion factors of wolf, lynx and red fox

Greater CFs of roe deer in lynx than in the canids may be attributable to the fact that this felid fixed the hide with its claws and teeth, tore off the hide, consumed nutritious parts and left over the hide, hoofs and hard, thick parts of the skeleton (Burmester 2005, Rühe et al. 2007). The canids were apparently not able to separate the prey parts as the lynx did and ingested a greater amount of less digestible matter.

Effect of feeding level

According to the optimal diet model hypothesis, animals should rank food types in terms of their energetic profitability, always include the most profitable food type and include less profitable food

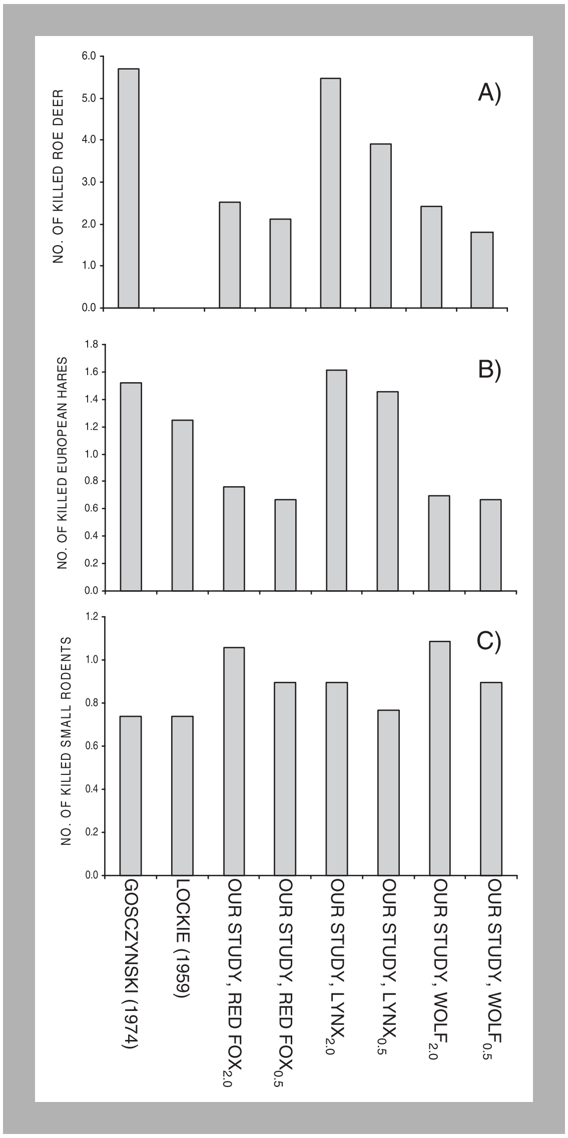

Figure 1. Estimated numbers of prey killed by free-ranging wolves as represented by 80 scats. In each scat, the relative volume of the undigested remainders of each prey species was estimated. They added up to A) 74.04 scats consisting of roe deer parts, fawns excluded, B) 5.79 scats composed of particles of European hare, leverets excluded, and C) 0.20 scats made up of components of small rodents according to the results presented in Ansorge et al. 2006, and by H. Ansorge, pers. comm., G. Kluth, pers. comm., and our study.

when the expected rate of gain by specialising in more profitable food matches the profitability of poorer food (Sinclair et al. 2006).

Fasted foxes were not able to choose between two prey types which resulted in high prey use and corresponding small CFs of roe deer and lagomorph in our study (see Table 2). Goszczynski's (1974) foxes, supplemented with additional, highly digestible food, might have used the presented carcasses to a lesser extent than fasted conspecifics. For his foxes, the cost-benefit ratio of consuming alternative food was probably more favourable than of consuming less digestible parts of the carcasses (e.g. bones, hair, skin). The strong relationship between conversion factors, prey use and apparent digestibility in our study fitted in this pattern. However, due to lacking data on digestibility and prey use in Lockie's (1959) and Goszczynski's (1974) foxes, this hypothesis requires further empirical data to be sufficiently tested.

Applying Goszczynski's (1974) $CF_{2.0}$ to the wolf scats (Ansorge et al. 2006) yielded a considerable higher number of roe deer (5.70) than applying the $CF_{2.0}$ of our study (2.51; see Fig. 1A). A greater number of hares was estimated with a conversion factor from additionally fed foxes (Goszczynski 1974: 1.52) compared to the estimates derived with $CFs_{2.0}$ from fasted foxes (Lockie 1959: 1.25, our study: 0.76; see Fig. 1B). The greater $CF_{2.0}$ of small rodents in our study could be due to feeding on house mice which might have contained a lesser amount of indigestible parts (e.g. less hair) than the voles, rats and mice used by Lockie (1959) and Goszczynski (1974). Applying our $CF_{2.0}$ resulted in a greater number of estimated small rodents in the food of free-ranging wolves than applying Lockie's (1959) and Goszczynski's (1974) $CFs_{2.0}$ (see Fig. 1C).

Effect of using different mesh sizes

Applying $CF_{2.0}$ from the wolf-trial to wolf scats washed with 0.5-mm sieves overestimated number of killed deer (2.42 for $CF_{2.0}$ instead of 1.79 for $CF_{0.5}$). A similar difference was found in regard to estimates of mice numbers but not in regard to numbers of hares (see Fig. 1). Macroscopic remainders of the hare (mainly long, thin underhair) were almost entirely retained in the 2-mm sieve, thus resulting in similar CFs for both mesh sizes. In contrast, roe deer and mice remainders were separated by sieving, thus resulting in greater $CF_{2.0}$-values than $CF_{0.5}$-values (see Table 3).

Conclusion

Feeding level, use of different mesh sizes, and application of predator-species-specific CFs affected the estimated number of killed prey individuals to different degrees. The greatest deviations from the reference values were found for the feeding level in

Table 4. Effects of inappropriate procedures on the estimated number of killed prey. Estimates of killed prey are given in percentages of the respective reference value (reference values of (1) feeding level: $CFs_{2.0}$ fox, our study; (2) mesh size: $CF_{0.5}$ of each prey-predator-combination, our study; (3) cross-predator-species application: $CF_{0.5}$ wolf, our study; reference values equal 100%).

		Mesh size 2.0 mm			$CFs_{0.5}$ of red fox and lynx of this study, applied to wolf scats	
Prey species	Supplementary feeding	Red fox	Lynx	Wolf	Red fox	Lynx
Roe deer	227%	118%	140%	135%	119%	219%
European hare	200%	113%	110%	104%	100%	218%
Small rodents	70%	118%	117%	121%	100%	86%

regard to roe deer and European hare, and for the application of CFs of lynx-deer and of lynx-hare to wolf scats (Table 4). The strong relationship between prey use and CFs in our study may be used to estimate prey numbers from scats more precisely: we recommend assessing percentage of prey use found in the field and to apply greater CFs (e.g. Goszczynski 1974) in cases of low prey use and smaller CFs (as shown in Lockie 1959 and in our study) in cases of high degrees of prey use.

Further on, we recommend applying predator-prey-specific CFs and to use the same mesh size on which these CFs are based. The presented CFs allow recalculation of prey masses and prey numbers from scat analyses which had been gained by using CFs based on different mesh sizes or different predator species.

Assessed prey numbers affect calculations of prey preferences and functional responses of carnivores as well as computations of competition and facilitation between them. The shown magnitude of the differences in estimated prey numbers caused by using inappropriate CFs suggests to recalculate these key ecological parameters.

Acknowledgements - this study was partially funded by the Research Institute of Forest Ecology and Forestry of the Federal State of Rhineland-Palatinate, Germany. We thank H. Andrén, P. Ciucci, T. Vor, and an anonymous referee for their helpful comments on earlier drafts of this paper.

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