

1 **Conversion factors in carnivore scat analysis: Sources of bias**

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

25 **Abstract**

26 Scat analyses are commonly applied to study feeding ecology of carnivores. Factors
27 developed in feeding trials are often used to convert dry matter mass of scat remainders
28 to fresh matter mass of killed or scavenged prey. In this study we aimed at: (1)
29 presenting conversion factors (CFs) of roe deer (*Capreolus capreolus*), European hare
30 (*Lepus europaeus*) and mice (*Mus musculus*) digested by wolf (*Canis lupus*), Eurasian
31 lynx (*Lynx lynx*) and red fox (*Vulpes vulpes*), (2) comparing CFs derived from fox
32 exposed to different feeding levels (fasted vs. non-fasted before each feeding trial), (3)
33 comparing effects of using different mesh sizes in the lab procedure on CFs, (4)
34 comparing effects of applying CFs derived from wolf, lynx and fox to wolf scats, (5)
35 quantifying biases caused by inappropriate procedures in scat analyses.

36 Feeding level, use of different mesh sizes and application of predator-specific CFs
37 affected the estimated number of killed prey individuals. The greatest deviations were
38 found for the feeding level in regard to deer and hare, and for the application of lynx
39 CFs of deer and hare to wolf scats. The strong relationship between prey use and CFs in
40 our study may be used to estimate prey numbers from scats more precisely: in cases of
41 low prey use we suggest applying CFs derived from non-fasted carnivores, and in cases
42 of high prey use CFs from fasted conspecifics are more appropriate. We recommend
43 applying predator-prey-specific CFs and using the same mesh size on which these CFs
44 are based. The presented CFs allow recalculation of prey masses and prey numbers from
45 scat analyses which had been gained by using inappropriate CFs.

46

47 **Introduction**

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

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

63 One major issue in applying CFs to scat fractions from field studies is that the reference
64 parameter of the CF is chosen according to the aim of the study (Reynolds & Aebischer
65 1991): There are two types of CFs, one based on prey mass presented and another one
66 based on prey mass consumed. When aiming at estimating number of killed or
67 scavenged – further on summarized as “killed” - prey individuals it is appropriate to use
68 the CFs based on the presented prey mass (e.g. Lockie 1959, Goszczynski 1974)
69 whereas it would be reasonable to use CFs based on the consumed prey mass (e.g.
70 Artois et al. 1987, Stahl 1990, Webbon et al. 2006) when studying energetics of free

71 ranging carnivores. This basic differentiation equally concerns the application of
72 biomass models [cf. “prey consumed” (Floyd et al. 1978), “prey presented” (Weaver
73 1993)]. Focusing on the utilisation of our results for studying predator-prey
74 relationships, we aim at providing CFs based on presented prey masses. A second issue
75 is the experimental set up of feeding trials. In some studies the predators were given
76 supplementary food prior to and in the end of each trial (Goszczyński 1974, Artois et al.
77 1987), whereas in most other studies (Lockie 1959, Floyd et al. 1978, Traves 1983,
78 Weaver 1993, Ruehe et al. 2003, Webbon 2006, Rühle et al. 2007) predators were fasted
79 for 24-72 h. We hypothesize that fasted predators consumed also more undigestible
80 matter of the presented carcasses which resulted in smaller CFs than those of their non-
81 fasted conspecifics. In this study, feeding trials were carried out with fasted carnivores
82 and the resulting CFs were compared with published CFs derived from feeding trials
83 with non-fasted predators.

84 A third issue concerns the lab methods for deriving and applying CFs. Most cited CFs
85 were derived by washing scats through a sieve with 2 mm-meshes (Lockie 1959,
86 Goszczyński 1974), whereas others used 1.0 mm-sieves (Stahl 1990), 0.5 mm-sieves
87 (Reynolds & Aebischer 1991, Webbon et al. 2006) or 0.3 mm-sieves (Artois et al.
88 1987). In field studies, sieves with 0.5 mm (e.g. Ciucci et al. 1996, Ansoerge et al. 2006)
89 or 1.0 mm (e.g. Jedrzejewska & Jedrzejewski 1998) meshes were used to gain
90 macroscopic scat remainders. The masses of these remains were multiplied with CFs
91 derived from 2.0 mm-sieves to estimate the prey masses represented by the scats. We
92 hypothesize that this procedure might lead to overestimations of prey masses.

93 A fourth issue deals with the cross-predator-species use of CFs. Because CFs of wolves
94 (*Canis lupus*) and lynx (*Lynx lynx*) had then not been published, CFs of red foxes

95 (*Vulpes vulpes*) had been applied to estimate prey masses of lynx (Jedrzejewska &
96 Jedrzejewski 1998) and wolves (Jedrzejewska & Jedrzejewski 1998, Ansorge et al.
97 2006). We present CFs for red fox (*Vulpes vulpes*), Eurasian lynx (*Lynx lynx*) and
98 wolves (*Canis lupus*) after feeding on frequent prey species of these carnivores. In this
99 regard we hypothesize that the CFs of the same prey type differs between carnivore
100 species.

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

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106 **Material and Methods**

107 **Feeding trials**

108 We kept 2 adult Eurasian lynx (1.5 to 2 years of age; weighing 29 and 31 kg; Burmester
109 2005), 1 adult wolf (3 to 3.5 years; 29 kg) and 3 adult foxes (1 to 1.5 years; 6, 8 and 8
110 kg; R. Willecke, pers. comm.) in paved enclosures which were 390, 278 and 60 m² in
111 size, respectively. The animals were treated regularly with anthelmintics and were kept
112 and handled according to animal welfare guidelines.

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

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

124

125 **Scat analysis**

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

138 We defined apparent f m digestibility (%) as follows: ingested f m food mass – f m scat
139 mass * 100 / ingested f m food mass. Because the water content in the scats could not
140 certainly be attributed to the ingested prey alone (an unknown proportion might have
141 resulted from drinking water intake), we named it apparent f m digestibility.

142

143 **Application of conversion factors to field data**

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

152 For comparing estimated number of killed prey individuals, we assumed the following
153 mean prey body masses: roe deer: 19 kg [according to F. von Plettenberg (pers. comm.)
154 and von Raesfeld (1978)], hare: 4 kg, small rodent: 0.025 kg. We mainly used the
155 values based on the wolf-CF_{s0.5} as references because macroscopic prey remainders of
156 the field data had been obtained with 0.5 mm-sieves (by Ansorge et al. 2006). We
157 computed Spearman rank correlations (r_s) with SigmaStat 1.0.

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160 **Results**

161 **Conversion factors of wolf, lynx and red fox**

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

167 Feeding selectivity of the three carnivore species focussed on highly apparent digestible
168 prey items as apparent f m digestibility rose with a decrease in prey use ($r_s = -0.76$, $N =$
169 9 , $P = 0.01$). The relationships of $CF_{2.0}$ to apparent f m digestibility ($r_s = 0.94$, $N = 9$, P
170 < 0.01) and to prey use ($r_s = -0.77$, $N = 9$, $P = 0.01$) were strong.

171

172 **Effect of feeding level**

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

178

179 **Effect of using different mesh sizes**

180 Using smaller meshes generally resulted in smaller CFs: values of $CF_{0.5}$ amounted to 72
181 - 96 % of the corresponding values of $CF_{2.0}$. In trials with red foxes, these quotients
182 were similar for different prey species, but varied considerably among different prey
183 types in the lynx and wolf trials (Table 3).

184

185 **Effect of cross-predator-species application of conversion factors**

186 We estimated numbers of killed prey individuals as represented by 80 scats of free
187 ranging wolves. In accordance with the lab procedure used by Ansorge et al. (2006) we
188 applied $CF_{0.5}$. We applied the factors from feeding trials with fox, lynx and wolf to the
189 wolf data: The $CF_{0.5}$ of fox resulted in a similar estimate for the number of roe deer
190 (2.69) whereas the CF of lynx resulted in a more than two times greater estimated

191 number of killed roe deer (4.96) compared to the $CF_{0.5}$ of the wolf trial (2.27).
192 Comparing estimated numbers of killed hares yielded a similar pattern as found in roe
193 deer ($CF_{0.5}$ fox: 0.67 hares, $CF_{0.5}$ lynx: 1.46, $CF_{0.5}$ wolf: 0.67). Estimated numbers of
194 killed small rodents were identical between $CF_{0.5}$ fox and $CF_{0.5}$ wolf (0.90) whereas the
195 number derived from $CF_{0.5}$ lynx was slightly smaller (0.77) (Fig. 1).

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198 **Discussion**

199 **Conversion factors of wolf, lynx and red fox**

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

205

206 **Effect of feeding level**

207 According to the optimal diet model hypothesis, animals should rank food types in
208 terms of their energetic profitability, always include the most profitable food type and
209 include less profitable food when the expected rate of gain by specializing on more
210 profitable food matches the profitability of poorer food (Sinclair et al. 2006).

211 Fasted foxes were not able to choose between two prey types which resulted in high
212 prey use and corresponding small CFs of roe deer and lagomorph in our study (Table 2).

213 Goszczynski's (1974) foxes - supplemented with additional, highly digestible food -
214 might have used the presented carcasses to a lesser extent than fasted conspecifics. For

215 his foxes, the cost-benefit ratio of consuming alternative food was probably more
216 favourable than of consuming less digestible parts of the carcasses (e.g. bones, hair,
217 skin). The strong relationship between conversion factors, prey use and apparent
218 digestibility in our study fitted in this pattern. However, due to lacking data on
219 digestibility and prey use in Lockie's (1959) and Goszczynski's (1974) foxes, this
220 hypothesis requires further empirical data to be sufficiently tested.

221 Applying Goszczynski's (1974) $CF_{2.0}$ to the wolf scats (Ansorge et al. 2006) yielded a
222 considerable higher number of roe deer (5.70) compared to applying the $CF_{2.0}$ of this
223 study (2.51) (Fig. 1A). A greater number of hares was estimated with a conversion
224 factor from additionally fed foxes (Goszczynski 1974: 1.52) compared to the estimates
225 derived with $CF_{S_{2.0}}$ from fasted foxes (Lockie 1959: 1.25, this study: 0.76) (Fig. 1B).
226 The greater $CF_{2.0}$ of small rodents in our study could be due to feeding on house mice
227 which might have contained a lesser amount of indigestible parts (e.g. fewer hair) than
228 the voles, rats and mice used by Lockie (1959) and Goszczynski (1974). Applying our
229 $CF_{2.0}$ resulted in a greater number of estimated small rodents in the food of free ranging
230 wolves, compared to applying Lockie's (1959) and Goszczynski's (1974) $CF_{S_{2.0}}$ (Fig.
231 1C).

232

233 **Effect of using different mesh sizes**

234 Applying $CF_{2.0}$ from the wolf-trial to wolf scats washed with 0.5 mm-sieves yielded an
235 overestimated number of killed deer (2.42 for $CF_{2.0}$ instead of 1.79 for $CF_{0.5}$). A similar
236 difference was found in regard to estimates of mice numbers but not in regard to
237 numbers of hares (Fig. 1). Macroscopic remainders of the hare (mainly long, thin
238 underhair) were almost entirely retained in the 2 mm-sieve, thus resulting in similar CFs

239 for both mesh sizes. In contrast, roe deer and mice remainders were separated by
240 sieving, thus resulting in greater $CF_{2,0}$ -values than $CF_{0,5}$ -values (Table 3).

241 **Conclusion**

242 Feeding level, use of different mesh sizes and application of predator-species specific
243 CFs affected the estimated number of killed prey individuals to different degrees. The
244 greatest deviations from the reference values were found for the feeding level in regard
245 to deer and hare, and for the application of CFs of lynx-deer and of lynx-hare to wolf
246 scats (Table 4). The strong relationship between prey use and CFs in our study may be
247 used to estimate prey numbers from scats more precisely: we recommend assessing
248 percentage of use of prey found in the field and to apply greater CFs (e.g. Goszczyński
249 1974) in cases of low prey use and smaller CFs (as shown in Lockie 1959 and in this
250 study) in cases of high degrees of prey use.

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

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

259

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

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324 Table 1. Prey presented, prey eaten and scat mass excreted by 1 adult wolf (W), 2 adult lynx (L) and 3
 325 adult red foxes (RF) as well as conversion factors from scat remainders to presented prey mass in 9
 326 feeding trials in an enclosure of the University of Göttingen, Germany, in 2003 (lynx) and 2006 (wolf, red
 327 fox). PS = Predator species, f m = fresh matter, D m = dry matter.

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PS	Prey species	Prey mass (g f m) presented	Prey mass (g f m) eaten	Prey use (%)	Apparent f m digestibility	D m mass of scat remainders after washing through a 2 mm-sieve	Conversion factor to prey mass presented CF _{2,0}
W	Roe deer	20 000	19 066	95	87	396.3	50
W	European hare	3 263	3 260	100	84	139.7	23
W	95 House mice	3 425	3 425	100	85	100.0	34
L	Roe deer	17 500	12 600	72	96	155.0	113
L	European hare	4 700	4 570	97	92	88.1	53
L	123 House mice	4 000	4 000	100	86	143.7	28
RF	Roe deer	19 900	18 728	94	91	380.0	52
RF	European hare	2 766	2 741	99	84	112.1	25
RF	40 House mice	1 200	1 200	100	85	36.8	33

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345 Table 2. Conversion factors of dry matter mass of scat remainders after washing through a 2 mm-sieve,
 346 derived from feeding trials with red fox, and differentiated according to the feeding level. Goszczynski's
 347 (1974) foxes were fed with pig hearts prior to and in the final stage of each trial ("Fed"), whereas Lockie's
 348 (1959) and our foxes were fasted 48 hrs before each trial ("Fasted").

349

Prey	Feeding level		
	Fed Goszczynski (1974)	Fasted Lockie (1959) This study	
Roe deer	118		52
Lago- morph	50	41	25
Small rodents	23	23	33

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366 Table 3. Conversion factors of dry matter mass of scat remainders after washing through a 2 mm-sieve
 367 ($CF_{2.0}$) and after washing through a 0.5 mm sieve ($CF_{0.5}$). PS=Predator species, W=Wolf, L=Lynx,
 368 RF=Red fox.

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

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

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Prey species	Supple- mentary feeding	Mesh size 2.0 mm			Application to wolf scats of $CF_{0.5}$, this study from	
		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 %

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411 Figure 1: Estimated numbers of prey killed by free ranging wolves (*Canis lupus*) as represented by 80
 412 scats (in each scat the relative volume of the undigested remainders of each prey species was estimated;
 413 they added up to 74.04 scats consisting of roe deer parts (fawns excluded), 5.79 scats composed of
 414 particles of European hare (leverets excluded) and 0.20 scats made up of components of small rodents)
 415 (Ansorge et al. 2006; H. Ansorge, pers. comm., G. Kluth, pers. comm.).

