Territorial variation in the wolves' diet? - A comparison of 11 territories in Sweden

(Summary of the diploma thesis „Das Nahrungsspektrum des Wolfes (*Canis lupus*) in Schweden im territorialen Vergleich", March 2006)

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Abstract

For determining wolves' (Canis lupus) prey species consumption in south-central Sweden 1884 scats collected from different territories, all year round, between the years 1992 - 2005 were analysed. Moose (Alces alces) were clearly the primary prey and were found in 78 % of all scats. Roe deer (Capreolus capreolus) and beaver (Castor fiber) were the next most important prey species but their remains were found in only 7 % and 3 % respectively of all scats. Apart from moose every prey species had to be classified as secondary or less important. The results of 11 territories were compared to find out about territorial variation. The territorial comparison showed a great similarity regarding prey species occurrence (similarity values for binary presence absence data: 66,7 % - 100 %). Moose were evidently the primary prey in every territory, but there were significant differences found (biomass data) between the territories. The importance or consumption of roe deer and beaver differed significantly between the territories. Other small and medium sized mammals differed non-significantly between the territories when pooled together.

There was no correlation between prey densities and consumption (frequency) found. When comparing results from fieldwork and laboratory work a potential underestimation of smaller mammals was found.

Introduction

Ungulates, particularly cervids have been demonstrated to be the preferred prey of wolves (*Canis* lupus) by many studies throughout the world (e.g. BIBIKOV 1990; MECH 1970; OKARMA 1995). Locally and seasonally other mammals such as beaver (*Castor fiber*) may constitute an important part of the wolves' diet (e.g. FORBES & THEBERGE 1996).

Moose (*Alces alces*) is the main and most preferred prey in Scandinavia (GADE-JØRGENSEN & STAGEGAARD 2000; KOJOLA et al. 2004; OLSSON et al. 1997).

OLSSON et al. (1997) presented in their study moose, roe deer (*Capreolus capreolus*) and badger (*Meles meles*) as most important prey species. Several other species like hare (*Lepus timidus*), beaver (*Castor fiber*), smaller rodents and birds were found during analyses of the wolves' diet in Scandinavia (e.g. GADE-JØRGENSEN & STAGEGAARD 2000).

For investigating the wolves' diet scat analysis was chosen in the present study. Analyses of scats are a common, often used and non-invasive method to analyse an animal's diet. When compared to analyses of stomach contents in particular, this method is non-invasive, simple, and practical and data collection is in high numbers realizable (REYNOLDS & AEBISCHER 1991). Hence this method was used in several carnivore studies (e.g. GOSZCZYŃSKI 1974; GOSZCZYŃSKI 1976; HELLDIN 2000; JOHNSON & HANSEN 1979; REYNOLDS & AEBISCHER 1991; ZABALA & ZUBEROGOITIA 2003), as well in wolves' studies worldwide (e.g. Ballard et al. 1987; GADE-JØRGENSEN & STAGEGAARD 2000; KOJOLA et al. 2004; MATTIOLI et al. 1995; MERIGGI et al. 1991; OLSSON et al. 1997; SCOTT & SHACKLETON 1980; SUMIŃSKI & FILIPIAK 1977).

After becoming a full protected species in 1966 the Swedish wolf population increased and consists of approximately 100 individuals to date. Hence better knowledge about this species and additional acceptance of the local population is more and more needed (ERICSSON & HEBERLEIN 2003; WABAKKEN et al. 2000). With the purpose to offer with increased knowledge the base for a better management the results of the present study should be presented, analysed and discussed. The aim of the present study was to examine the wolves' diet particularly regarding territorial variation in prey species consumption.

The objectives were:

A general current overview about wolves' diet and prey species consumption in south-central Sweden:

- Are cervids the most preferred prey compared to other vertebrates or do we overestimate their importance as wolves' prey?
- Is the cervids' consumption uniform and even? Or will moose be confirmed as the most preferred prey?

Regarding potential territorial variation in prey species consumption and wolves' diet respectively the following questions were of higher interest and relevance:

- Do differences between the analysed territories exist regarding consumption of moose, roe deer, beaver or other small and medium-sized mammals?
- Are cervids, specifically moose the important prey species in every territory or are there territories with preferences for other prey?
- Is the consumption of cervids correlated with their different abundances / densities?

Moreover field- and lab work data should be compared to examine if smaller prey species would be underestimated without laboratory analyses.

Material and Methods

Scat collecting and dietary analyses

During research and monitoring projects (*Grimsö Research Station, Wildlife Damage Center, Skandulv*) a total of 1884 fresh wolf scats were collected in different territories all year round and multi-annual between the years 1992 - 2005. During snow- and radio tracking and carcass searches scats were identified according to their size (WEAVER & FRITTS 1979), shape, odour (CHAVEZ & GESE 2005) and location. Scats were collected in small plastic bags labelled with coordinates and date and then stored in a freezer until analyses.

To investigate potential territorial variation within the Swedish wolf population scats from 11 territories were analysed.

Prior analyses scats were dried (48 h, 90^{o} C), weighed and stored in small plastic boxes.

The scat analyses followed the standard methods described by e.g. CIUCCI et al. (1996) and REYNOLDS & AEBISCHER (1991). For increased accuracy the samples were not washed through a sieve for dividing in micro- and macro-components (REYNOLDS & AEBISCHER 1991). This enabled a higher number of analysed samples and therefore a higher level of generality and applicability of the results, too.

Prior analyses observers were coached. A training phase of about 25 h with known reference samples followed. During analyses the observers' skills were tested by means of a "testbox" with 30 samples.

The identification of prey species was based on undigested prey remains, mostly hairs, feathers, teeth and bones. To see every component scat samples were broken by hand and spread out. Prey remains were identified by comparing the microscopic and macroscopic characteristics with a reference collection and by using identification keys (TEERINK 1991; DEBROT et al. 1982). To distinguish between roe deer (*Capreolus capreolus*) and moose (*Alces alces*) hairs also the hair width was measured while squeezing under a binocular/microscope (pers. comment: HELLDIN, J-O).

Distinguishing between juvenile and adult moose by hair is only possible during summer (ŚMIETANA 1993; VOIGT et al. 1976) because of the red fur. Hence distinction was only done for samples collected between May and September. Samples containing moose collected in other seasons were classified as "adults".

To avoid falsification puppy scats were not included in analyses.

The percentage volume of every component category was estimated visually by spreading out the sample on special squared paper.

Two types of frequency of occurrence (calculated as the number of times a prey type was identified in all scats divided by the total number of items identified = **FOC occ**. (excl. non food); calculated as the number of times a prey type was identified in all scats divided by the total number of scats = **FOC sample size**), ingested biomass of mammalian prey using Weavers (y = 0,439 + 0,008 x; WEAVER 1993) and Ruehes (y = 0,00554 + 0,00457 x; RUEHE 2003) linear regressions models where y is the biomass ingested (kg) per scat and x is the live mass (kg) of the prey and the relative volume of every remnant prey species were calculated. The biomass values were multiplied with the equivalent number of scats calculated by using and summing the relative proportions (volumes) of an individual prey species accounting for the scats that contain more than one prey species (CIUCCI et al. 1996; CORBETT 1989; FLOYD et al 1978).

The mean body mass of prey species were recalculated from hunting bags and taken from internal data of the Grimsö Wildlife Research Station: adult moose: 368 kg, juvenile moose: 78,4 kg, adult roe deer: 28 kg, juvenile roe deer 9,3: kg, beaver: 18 kg, badger: 10,5 kg, red fox: 6,5 kg, hare: 3,5 kg, smaller rodents: 0,025 kg, sheep: 25 kg.

Due to finding that higher than 50 % volume in more than 5 % of all scats including identified wolf remnants FOC were calculated for this species. On account of negligible volume proportions in the most cases (in 76 % lower than 5 %) which suggested being own hairs and ingestion by grooming the category wolf were not included in biomass calculations.

Food niche breadth was calculated according to the following formulas of Levin using the FOC occ. values (unidentified Cervids were accounted for moose and roe deer in equal proportions):

$$B = \frac{1}{\sum p_j^2} ,$$

where B ranges between 1 (minimum niche breadth, maximum specialisation) and n (total number of resource states) and for standardized niche breadth B_a:

$$B_a = \frac{(b-1)}{(n-1)} ,$$

which ranges on a scale from 0 (high specialisation) and 1 (KREBS 1989).

For statistical analyses the computer programs StatView (contingency table, Spearman), SPSS (Kruskal-Wallis, Friedman) and BioDiversity Professional (cluster analyse) were used. Calculated significances were tested and located with a post hoc Schaich-Hamerle-Test (BORTZ et al. 2000).

Study area

The study area was located in south-central Sweden between 54° - 75° N and 27° -14° E.

The 11 territories included in the later analysis Bograngen (n=51), Filipstad (n=66), Furudal (n=91), Grangärde (n=234), Hagfors (n=175), Hasselfors (n=213), Leksand (n=353), Nyskoga (n=193), Tisjön (n=113), Tyngsjö (n=115) und Årjäng (n=61) are located in the counties Örebro län, Värmland and Dalarna respectively.

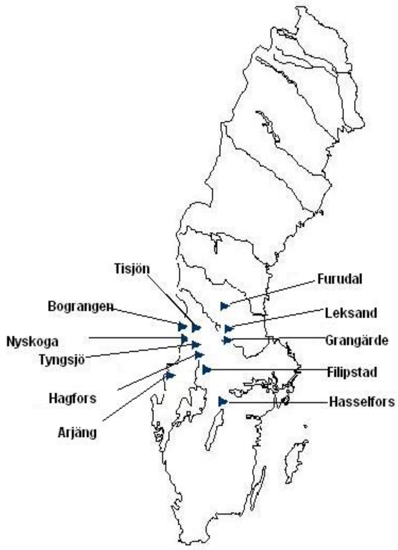

Fig. 1: Locations of studied territories

Vegetation period ranges from 150 - 180 days in Dalarna and the northern parts of Värmland to 180 - 210 days in south Värmland and Örebro län (NILSSON 1990).

Average temperature ranges from 3° C (Dalarna) to 4°-5° C (Värmland, Örebro län). Annual precipitation varies from 700 - 900 mm in Dalarna, 600 - 1000 mm in Värmland and 600 - 700 mm in Örebro län (www.smhi.se).

Forests cover 575 000 ha, 1 330 000 ha and 1 935 000 ha in Örebro län, Värmland and Dalarna, respectivly. The boreal forest is dominated by coniferous species like Norway spruce (*Picea abies*) and Pine (*Pinus silvestris*) and a relative low proportion of deciduous tree species, mainly Birch (*Betula spec.*) (www.svo.se).

Potential available wolf prey species in this area are moose (*Alces alces*), roe deer (*Capreolus capreolus*), beaver (*Castor fiber*), badger (*Meles meles*) as well as smaller rodents (MITCHELL-JONES 1999). Moose and roe deer densities for the different territories range between 8,51 and 27,08 moose per 1000 ha and 0,07 and 34,51 roe deer per 1000 ha (table 1).

Table 1: Densities in the 11 different territories

Territory	Moose / 1000 ha	Roe / 1000 ha
Bograngen	27,03	0,07
Filipstad	12,70	n.d.*
Hagfors	10,07	0,29
Nyskoga	10,86	0,66
Årjäng	n.d.*	n.d.*
Tisjön	n.d.*	n.d.*
Tyngsjö	10,82	0,89
Furudal	n.d.*	n.d.*
Grangärde	10,28	1,78
Leksand	8,51	0,6
Hasselfors	9,46	34,51

*n.d.=no data

Other carnivores beside the wolf are brown bears (*Ursus arctos*) in the northern parts of the area, lynx (Lynx lynx) and several medium sized and small carnivore species e.g. fox (*Vulpes vulpes*) or Mustelidae (MITCHELL-JONES 1999). Regarding wolf prey the avifauna contains grouse (esp. *Tetrao urogallus* and *Tetrao tetrix*).

Wolf pack size varies in the different territories (table 2).

Table 2: Wolf individuals in the studied territories (acc. ARONSON et al. 2000-2004; pers. comment: SAND; WABAKKEN et al. 2004)

	Year of scat collecting								
Territory	1992	--- - --	1997	1998	1999	2000	2001	2002	2003
Bograngen	---	---	---	2 Pa*	4 F	3 F	2 Pa	3 Pa	n.d.**
Filipstad	---	---	---	5 F	5-7 F	6 F	6-7 F	6-7 F	7 F
Hagfors	---	---	7 F	9-10 F	0-1 S	---	---	---	---
Nyskoga	n.d.	---	n.d.	n.d.	2 Pa	4 F	7-8 F	5-7 F	4 F
Årjäng	---	---	---	8-9 F	6-7 F	6 F	8-9 F	---	---
Tisjön	---	---	---	n.d.	0-1 S	1 S	2 Pa	2 Pa	---
Tyngsjö	---	---	---	---	---	2 Pa	6 F	2 S	n.d.
Furudal	---	---	---	---	1 S	2 Pa	9 F	11 F	10-11 F
Grangärde	---	---	---	1 W	2 Pa	5 F	0-1 W	---	---
Leksand	---	---	6 F	8 F	3 F	1 S	2 Pa	(1 S)	n.d.
Hasselfors	---	---	---	---	2 F	8 F	7-8 F	4-5 F	6-7 F

* Pa=pair, F=family / pack, S=stationary, W=other

** n.d.= no data

Results

Remains from moose (*Alces alces*), roe deer (*Capreolus capreolus*), unidentified cervids, beaver (*Castor fiber*), hare (*Lepus timidus*), domestic animals (sheep), badger (*Meles meles*), red fox (*Vulpes vulpes*), wolf (*Canis lupus*), unidentified carnivores, smaller rodents, birds, insects, berries and other plant material (mainly grams) were found during analyses of all samples.

Frequency:

Significant differences in using various prey species / food components were found (χ^2= 2111, 429; p < 0,0001). Cervids were clearly the preferred wolf prey; particularly moose dominated in the diet and were found in 78 % while roe deer were only found in 7 % of the scats. The third frequent mammalian prey species were beaver. Its remains were found in 3 % of the scats. All other prey species had to be considered as negligible however the other small and medium sized mammals were - when pooled together - detected in 12 % of the samples (table 3).

Table 3: Occurrence of remains from various prey species and other remains

	Number of occurrences	FOC sample size	FOC occ.
Moose	1466	78%	43%
Roe deer	126	7%	4%
Unid. Cervidae	244	13%	7%
Sum Cervidae	**1836**	**97%**	**54%**
Beaver	58	3%	2%
Other small and medium sized mammals*	233	12%	7%
Birds	71	4%	2%
Insects	45	2%	1%
P/Mat.	1139	60%	34%
Other**	329	17%	---

*incl.: hare, sheep, badger, red fox, wolf, unid. carnivores, smaller rodents
**incl.: non food, e.g. stones

Volume:

Considering the relative volumes of the remains found in scats the dominance of moose in the wolf's diet was confirmed.

All categories beside insects and birds reached the maximum volume of 100 % per scat and were found as only remain per scat in these cases (table 4).

Table 4: Relative Volumes of remains

	Moose	Roe deer	Unid. Cervidae	Beaver	Small, medium sized mammals	Birds	Insects	P/Mat.
Vol. Min %	1	5	1	1	1	1	1	1
Vol. Max %	100	100	100	100	100	98	20	100
Sum Vol.%	**134757**	**11236**	**20209**	**4501**	**5391**	**1396**	**133**	**9733**
Average %	92	89	83	78	23	20	3	9
Rel. Vol.	0,719	0,060	0,108	0,024	0,029	0,007	0,001	0,052
Rel. Vol.	**72%**	**6%**	**11%**	**2%**	**3%**	**1%**	**0%**	**5%**

Biomass:

In terms of biomass according to the models of WEAVER (1993) and RUEHE (2003) dominated moose clearly (table 5).

Table 5: Biomass values of mammalian prey

	Sum [kg]	Relation	Ranking
Moose Ruehe Model	2026,82	99,1%	1
Moose Weaver Model	4127,12	97,2%	1
Roe deer Ruehe Model	14,28	0,7%	2
Roe deer Weaver Model	73,15	1,7%	2
Beaver Ruehe Model	3,92	0,2%	3
Beaver Weaver Model	26,24	0,6%	3
small, medium mammals Ruehe Model	0,77	<<0,1%	4
small, medium mammals Weaver Model	18,08	0,4%	4

Statistical analyses documented significance (Friedman: χ^2=3426,977 (Weaver) and 3482,227 (Ruehe); df: 3; asymptotic significance: 0,00). This was found only between moose and all the other categories. Biomass values for roe deer, beaver and other small and medium-sized mammals (pooled together) differed non-significantly (Schaich-Hamerle-Test: χ^2=7,815; df: 3, α: 0,05; $DeltaR_{crit}$: 198,2).

Territorial Variation:

Composition of food remains in scats was similar in all 11 territories (table 6, figure 2).

Table 6: Overview remains in samples out of different territories

	Bograngen	Filipstad	Furudal	Grangärde	Hagfors	Hasselfors	Leksand	Nyskoga	Tisjön	Tyngsjö	Årjäng
Moose	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Roe deer	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Unid. Cervidae	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Beaver	no	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Hare	yes	no	no	no	yes	yes	yes	yes	yes	yes	yes
Badger	yes	no	no	no	no	yes	yes	yes	yes	no	no
Wolf	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Fox	no	no	no	no	no	yes	no	no	no	no	no
Unid. Carniv.	no	no	no	yes	no	yes	yes	no	no	no	yes
Sheep	no	no	no	yes	no	no	no	yes	no	no	no
S/Rod	yes	yes	no	yes	yes	yes	yes	yes	yes	yes	yes
Unid. Mammals	no	yes	no	yes	no	yes	no	no	no	no	no
Bird	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	no
Insects	yes	yes	no	yes	yes	yes	yes	yes	yes	yes	yes
Berries	yes	no	no	yes	yes	yes	yes	yes	yes	yes	yes
P/Mat	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Other	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes

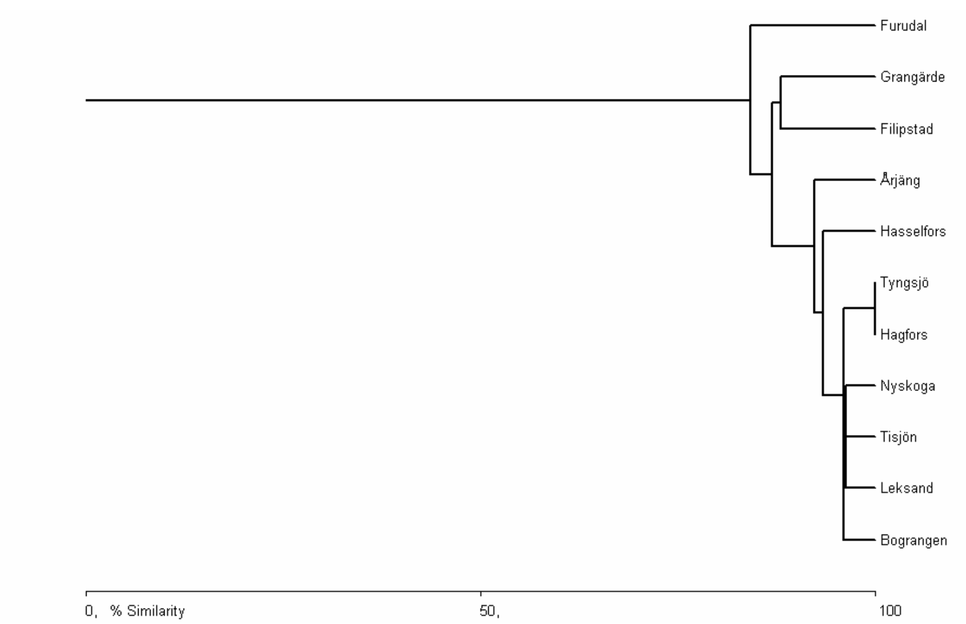

Figure 2: Diet's composition (Clusteranalysis with presence-absence data)

The standardized Levins' Index B_a for measuring the food niche breadth were low in every territory and showed a relative high degree of specialisation. It ranged between 0,089 and 0,175 (table 7).

Table 7: Levins' standardized niche breadth

	Furudal	Leksand	Gran-gärde	Filipstad	Nyskoga	Hagfors	Tyngsjö	Hassel-fors	Bogran-gen	Årjäng	Tisjön
B_a	0,089	0,102	0,117	0,120	0,131	0,138	0,138	0,148	0,156	0,161	0,175

In every territory moose were clearly the most frequent and most important prey species (table 8). The differences in frequency of occurrence were significant in every territory (Bograngen: χ^2= 60,529; p < 0,0001; Filipstad: χ^2= 61,178; p < 0,0001; Furudal: χ^2= 154,443; p < 0,0001; Grangärde: χ^2= 236,743; p < 0,0001; Hagfors: χ^2= 189,216; p < 0,0001; Hasselfors: χ^2= 284,548; p < 0,0001; Leksand: χ^2= 341,263; p < 0,0001; Nyskoga: χ^2= 334,824; p < 0,0001; Tisjön: χ^2= 168,091; p < 0,0001; Tyngsjö: χ^2= 162,936; p < 0,0001; Årjäng: χ^2= 61,493; p < 0,0001). In all territories - except Tisjön and Tyngsjö - were roe deer the second most frequent prey species, while in the two territories Tisjön and Tyngsjö beaver were more frequent (non-significant).

Table 8: Frequency of occurrence in the different territories

		Moose	Roe deer	Unid. Cervids	Beaver	S / M Mammals	Birds	Insects	P/Mat.	Other
Bograngen	**N**	36	2	10	0	10	2	3	36	6
	FOC ss	**71%**	**4%**	**20%**	**0%**	**20%**	**4%**	**6%**	**71%**	**12%**
Filipstad	**N**	52	6	8	1	9	1	1	30	3
	FOC ss	**79%**	**9%**	**12%**	**1,5%**	**14%**	**1,5%**	**2%**	**45%**	**5%**
Furudal	**N**	81	4	6	3	2	2	0	86	5
	FOC ss	**89%**	**4%**	**7%**	**3%**	**2%**	**2%**	**0%**	**95%**	**5%**
Grangärde	**N**	189	21	25	1	14	21	3	108	32
	FOC ss	**81%**	**9%**	**11%**	**0%**	**6%**	**9%**	**1%**	**61%**	**14%**
Hagfors	**N**	133	14	21	7	19	5	6	102	28
	FOC ss	**76%**	**8%**	**12%**	**4%**	**11%**	**3%**	**3%**	**58%**	**16%**
Hasselfors	**N**	145	28	38	1	41	7	7	191	51
	FOC ss	**68%**	**13%**	**18%**	**0%**	**19%**	**3%**	**3%**	**90%**	**24%**
Leksand	**N**	294	17	35	9	37	12	1	133	39
	FOC ss	**83%**	**5%**	**10%**	**3%**	**10%**	**3%**	**0%**	**38%**	**11%**
Nyskoga	**N**	167	4	19	3	33	9	10	170	57
	FOC ss	**87%**	**2%**	**10%**	**2%**	**17%**	**5%**	**5%**	**88%**	**30%**
Tisjön	**N**	77	5	23	14	26	6	4	100	62
	FOC ss	**68%**	**4%**	**20%**	**12%**	**23%**	**5%**	**4%**	**88%**	**55%**
Tyngsjö	**N**	87	3	20	7	11	2	4	103	14
	FOC ss	**76%**	**3%**	**17%**	**6%**	**10%**	**2%**	**3%**	**90%**	**12%**
Årjäng	**N**	41	5	12	1	14	0	3	25	17
	FOC ss	**66%**	**8%**	**19%**	**2%**	**23%**	**0%**	**5%**	**40%**	**27%**

The relative volumes of food remains showed a similar result: Cervids, in particular moose, dominated in the wolves' diet in all territories. Relative volumes of moose remains ranged between 57 % and 85 % (table 9).

Table 9: Relative Volumes of food types' remains

	Moose	Roe deer	Unid. Cervids	Beaver	S / M Mammals	Birds	Insects	P/Mat.
Bograngen	60%	4%	18%	~~	6%	1%	0%	11%
Filipstad	74%	8%	12%	2%	2%	<< 0,1%	<< 0,1%	2%
Furudal	85%	4%	5%	<< 0,1%	1%	<< 0,1%	~~	4%
Grangärde	77%	8%	9%	<< 0,1%	1%	1%	<< 0,1%	4%
Hagfors	71%	8%	9%	4%	2%	1%	<< 0,1%	6%
Hasselfors	60%	11%	16%	<< 0,1%	4%	<< 0,1%	<< 0,1%	9%
Leksand	77%	4%	9%	2%	3%	1%	<< 0,1%	4%
Nyskoga	81%	2%	8%	1%	4%	1%	<< 0,1%	4%
Tisjön	57%	5%	16%	10%	3%	2%	<< 0,1%	8%
Tyngsjö	68%	3%	14%	5%	1%	<< 0,1%	<< 0,1%	9%
Årjäng	64%	7%	15%	2%	7%	~~	<< 0,1%	5%

Biomass:

According to biomass moose constituted more than 90 % of the wolf's diet in every territory. Apart from two territories (Tisjön, Tyngsjö) where consumption of beaver was higher than consumption of roe deer, roe deer were the second most important prey species in every territory (table 10). The differences in prey species consumption considering biomass were significant between moose and other mammalian prey species. Consumption of roe deer, beaver and other small and medium sized mammals (pooled together) showed no significant difference (Bograngen: Friedman χ^2= 87,747 (Weaver) and 90,400 (Ruehe); df: 3; asymptotic significance: 0,00; Schaich-Hamerle-Test χ^2= 7,815; df: 3; α: 0,05; DeltaRcrit: 32,7; Filipstad: Friedman χ^2= 125,510 (Weaver) and 129,496 (Ruehe); df: 3; asymptotic significance: 0,00; Schaich-Hamerle-Test: χ^2= 7,815; df: 3; α: 0,05; DeltaRcrit: 37,2; Furudal: Friedman χ^2= 217,402 (Weaver and Ruehe); df: 3; asymptotic significance: 0,00; Schaich-Hamerle-Test: χ^2= 7,815; df: 3; α: 0,05; DeltaRcrit: 43,6; Grangärde: Friedman χ^2= 467,407 (Weaver) and 480,046 (Ruehe); df: 3; asymptotic significance: 0,00; Schaich-Hamerle-Test: χ^2= 7,815; df: 3; α: 0,05; DeltaRcrit: 69,9; Hagfors: Friedman χ^2= 286,155; df: 3; asymptotic significance: 0,00; Schaich-Hamerle-Test: χ^2= 7,815; df: 3; α: 0,05; DeltaRcrit: 60,4; Hasselfors: Friedman χ^2= 308,207 (Weaver) and 331,778 (Ruehe); df: 3; asymptotic significance: 0,00; Schaich-Hamerle-Test: χ^2= 7,815; df: 3; α: 0,05; DeltaRcrit: 66,7; Leksand: Friedman χ^2= 718,936 (Weaver) and 756,265 (Ruehe); df: 3; asymptotic significance: 0,00; Schaich-Hamerle-Test: χ^2= 7,815; df: 3; α: 0,05; DeltaRcrit: 85,8; Nyskoga: Friedman χ^2= Chi-Quadrat: 444,349 (Weaver) and 452,179 (Ruehe); df: 3; asymptotic significance: 0,00; Schaich-Hamerle-Test: χ^2= 7,815; df: 3; α: 0,05; DeltaRcrit: 63,5; Tisjön: Friedman χ^2= 149,665 (Weaver) and

164,761 (Ruehe); df: 3; asymptotic significance: 0,00; Schaich-Hamerle-Test: χ^2= 7,815; df: 3; α: 0,05; DeltaRcrit: 48,6; Tyngsjö: Friedman χ^2= 209,126 (Weaver) and 222,613 (Ruehe); df: 3; asymptotic significance: 0,00; Schaich-Hamerle-Test:: χ^2= 7,815; df: 3; α: 0,05; DeltaRcrit: 49,0; Årjäng: Friedman χ^2= 87,370 (Weaver) and 91,742 (Ruehe); df: 3; asymptotic significance: 0,00; Schaich-Hamerle-Test: χ^2= 7,815; df: 3; α: 0,05; DeltaRcrit: 36,0).

Table 10: Biomass (Weaver 1993; Ruehe 2003)

		Moose	Roe deer	Beaver	S / M Mammals
Bograngen	Relation* (Ruehe)	99,3%	0,5%	0,0%	0,2%
	Ranking (Ruehe)	1	2	4	3
	Relation (Weaver)	97,5%	1,3%	0,0%	1,2%
	Ranking (Weaver)	1	2	4	3
Filipstad	Relation (Ruehe)	99,0%	0,9%	0,1%	0,0%
	Ranking (Ruehe)	1	2	3	4
	Relation (Weaver)	97,5%	2,1%	0,4%	<0,1%
	Ranking (Weaver)	1	2	3	4
Furudal	Relation (Ruehe)	99,5%	0,4%	0,1%	0,0%
	Ranking (Ruehe)	1	2	3	4
	Relation (Weaver)	98,8%	1,0%	0,2%	0,0%
	Ranking (Weaver)	1	2	3	4
Grangärde	Relation (Ruehe)	99,2%	0,8%	<0,1%	<0,1%
	Ranking (Ruehe)	1	2	4	3
	Relation (Weaver)	97,9%	2,0%	<0,1%	0,1%
	Ranking (Weaver)	1	2	4	3
Hagfors	Relation (Ruehe)	98,6%	1,0%	0,4%	<0,1%
	Ranking (Ruehe)	1	2	3	4
	Relation (Weaver)	95,8%	2,5%	1,2%	0,5%
	Ranking (Weaver)	1	2	3	4
Hasselfors	Relation (Ruehe)	98,6%	1,4%	<0,1%	<0,1%
	Ranking (Ruehe)	1	2	3	4
	Relation (Weaver)	95,9%	3,5%	0,1%	0,5%
	Ranking (Weaver)	1	2	3	4
Leksand	Relation (Ruehe)	99,4%	0,4%	0,1%	<0,1%
	Ranking (Ruehe)	1	2	3	4
	Relation (Weaver)	97,9%	1,1%	0,5%	0,6%
	Ranking (Weaver)	1	2	4	3
Nyskoga	Relation (Ruehe)	99,6%	0,2%	0,1%	0,1%
	Ranking (Ruehe)	1	2	4	3
	Relation (Weaver)	98,8%	0,5%	0,2%	0,5%
	Ranking (Weaver)	1	3	4	2
Tisjön	Relation (Ruehe)	98,3%	0,7%	1,0%	<0,1%
	Ranking (Ruehe)	1	3	2	4
	Relation (Weaver)	94,8%	1,6%	3,1%	0,5%
	Ranking (Weaver)	1	3	2	4
Tyngsjö	Relation (Ruehe)	99,3%	0,3%	0,4%	<0,1%
	Ranking (Ruehe)	1	3	2	4
	Relation (Weaver)	97,8%	0,8%	1,3%	0,1%
	Ranking (Weaver)	1	3	2	4
Årjäng	Relation (Ruehe)	98,3%	1,5%	0,2%	<0,1%
	Ranking (Ruehe)	1	2	3	4
	Relation (Weaver)	95,2%	3,2%	0,6%	0,9%
	Ranking (Weaver)	1	2	3	4

* percentage of biomass ingested (identified mammals)

Considering biomass data territorial variation was found. There were significant differences between the territories in terms of biomass found for consumption of moose (Kruskal-Wallis χ^2= 135,911 (Weaver) and 135,410 (Ruehe); df: 10; asymptotic significance: 0,00) These significant differences were documented between the territories Hasselfors and Grangärde, Hasselfors and Leksand, Leksand and Hagfors, Tyngsjö, Årjäng, Tisjön, Tisjön and Filipstad, Furudal, Grangärde, Nyskoga (Schaich-Hamerle-Test: χ^2= 18,307; df: 10; α: 0,05; $DeltaR_{crit}$: 194,9, 178,6, 190,3, 221,0, 283,4, 222,5, 318,9, 289,9, 235,8, 243,8). Remains of roe deer and beaver differed significantly as well (roe deer: Kruskal-Wallis χ^2= 31,02 (Weaver) and 29,698 (Ruehe); df: 10; asymptotic significance: 0,00; beaver: Kruskal-Wallis χ^2= 55,549 (Weaver) and 53,073 (Ruehe); df: 10; asymptotic significance: 0,00). Remains of other small and medium-sized mammalian prey did not differ significantly between the 11 territories, if they were pooled together (Kruskal-Wallis χ^2= 16,128 (Weaver) and 16,436 (Ruehe); df: 10; asymptotic significance: 0,096 (Weaver) und 0,088 (Ruehe)). There was a slight difference regarding these secondary prey species found, if species were not pooled together (figures 3 and 4).

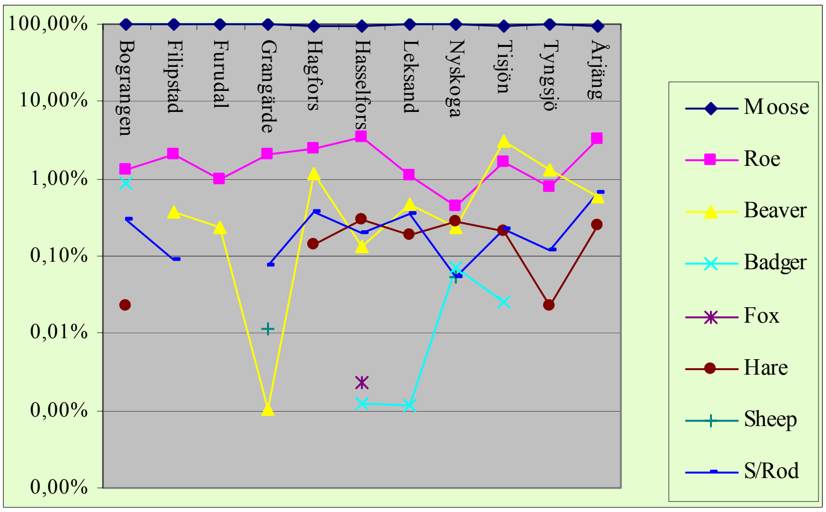

Figure 3: Territorial variation regarding biomass relation (Weaver)

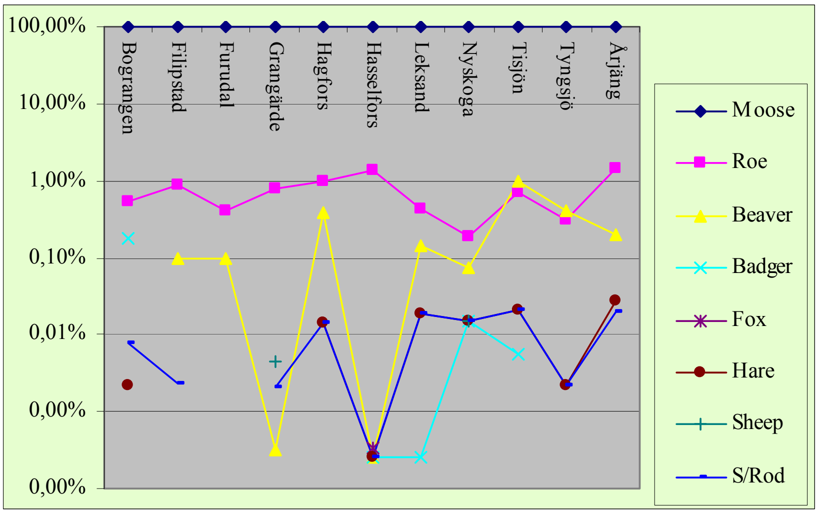

Figure 4: Territorial variation regarding biomass relation (Ruehe)

Density Correlation:

The tests of correlation between moose densities and consumption (FOC sample size and FOC occ.) using Spearman's Rank Correlation showed no significant result (p= 0,8501 and 0,4497). As well as for moose no significant correlation between roe deer densities and frequency values were found (p= 0,2938).

A slight tendency was found since in the territory Hasselfors with a particular high roe deer density (34,51 roe deer / 1000 ha) showed the highest FOC values comparatively.

Comparison field and lab data:

When comparing results from fieldwork and laboratory work a potential underestimation of smaller mammals was found as well as a higher percentage of roe deer (figures 5 -7). The potential underestimation of smaller prey (biomass percentage) in the wolves' diet is higher when using the equation of WEAVER compared to data calculated with the equation acc. RUEHE.

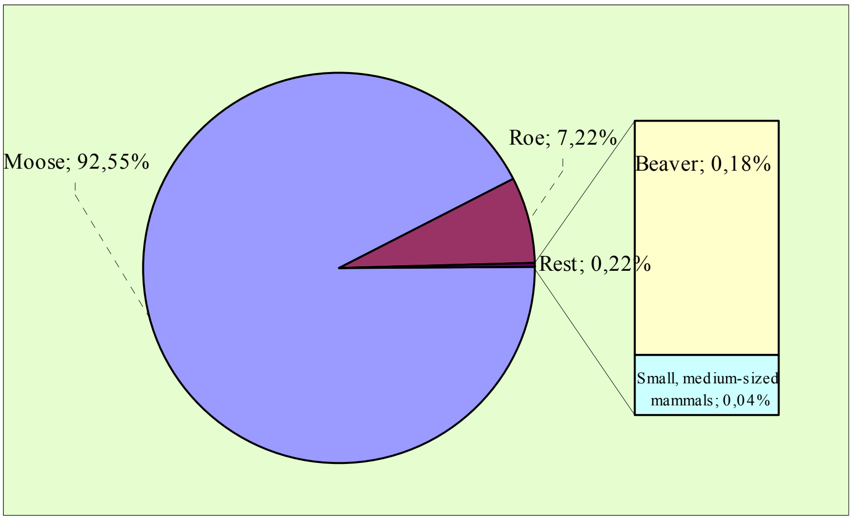

Figure 5: Mammalian prey species relation (biomass) received from field data

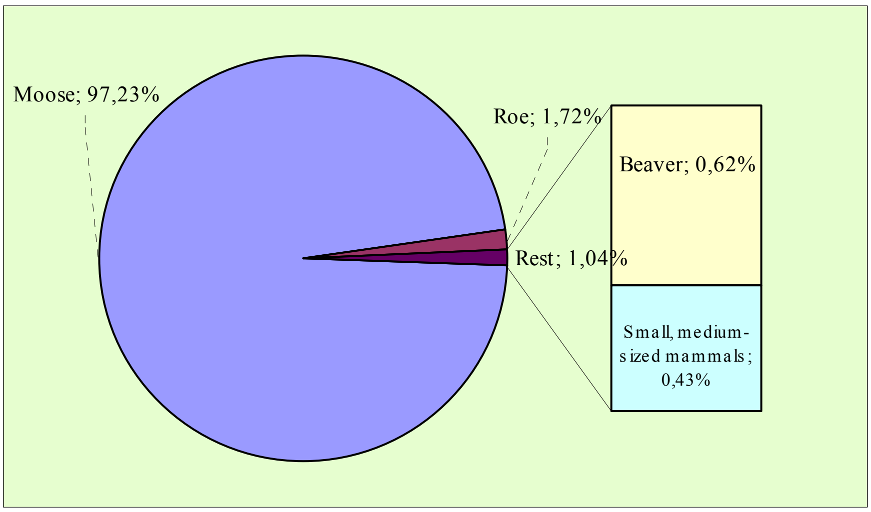

Figure 6: Mammalian prey species relation in wolf's diet received from scat analyses using Weaver's equation

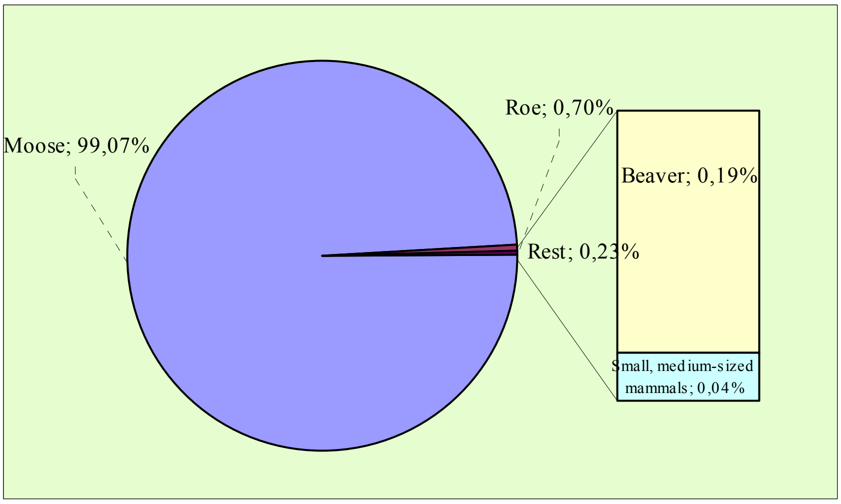

Figure 7: Mammalian prey species relation in wolf's diet received from scat analyses using Ruehe's equation

According to expectations more species were found in the category small and medium sized mammals during scat analyses compared to field work. Species which were only documented by doing scat analyses were badger and smaller rodents.

Discussion

General overview (whole sample size):

CIUCCI et al. 1996 recommended the application of more than one data analyses method. This recommendation were followed and the different data analysis methods showed similar results regarding the food categories moose, roe deer, beaver and other small and medium sized mammals.

The present study indicated the preference of ungulates, in particular cervids in the wolves' diet. Preference for the larger species were demonstrated by ŚMIETANA & KLIMEK (1993) and NOWAK et al. (2005) as well as in the present study, whereas KUNKEL et al. (1999) the preferential prey upon the smaller species (deer *Odocoileus virginianus*) compared to moose and red deer in Montana presented. OKARMA (1995) showed the importance of moose in areas with few or without medium sized cervids such as red deer. The absence of medium-sized cervids and the high moose densities can be assumed as causes for the high dominance of moose in the wolves' diet found in this study. Former studies in Scandinavia (GADE-JØRGENSEN & STAGEGAARD 2000; KOJOLA et al. 2004; OLSSON et al. 1997) presented moose as the most preferred and important prey species.

Roe deer was shown as the second most important prey species, however its consumption was not shown to be significantly different or higher than beaver or other small and medium sized mammals (if pooled together). In the two territories Tisjön and Tyngsjö a higher consumption of beaver than of roe deer was even found. Therefore cervids were clearly the most preferred prey, but there were differences between the species found. NOWAK et al. (2005) documented evidence of lower consumption of roe deer compared to red deer despite higher densities of roe deer and OKARMA (1995) presented this species to be negative selected in Poland. Compared to OLSSONs et al. (1997) study this study documented in a similar study area a lower consumption of roe deer.

Beaver was shown to be the most important prey species beside the cervid species. It was demonstrated to be a secondary prey species with a local higher proportion in the wolves' diet than roe deer. In several other studies (e.g. ANDERSONE & OZOLIŅŠ 2004; SCOTT & SHACKLETON 1980; THEBERGE et al. 1978; THURBER & PETERSON 1993) beaver were demonstrated as an important prey species beside ungulates, too. Possible causes, which were presented, were a decline in ungulate density (ANDERSONE & OZOLIŅŠ 2004), buffer function (FORBES & THEBERGE 1996; VOIGT et al. 1976) and seasonal variation (POTVIN & JOLICOEUR 1988).

Other small and medium-sized mammals showed no significant differences in FOC or biomass values except to the main prey moose. These species were also presented as secondary prey species in former studies (e.g. JEDRZEJEWSKI et al. 2002; ŚMIETANA & KLIMEK 1993). In contradiction to the study carried out by OLSSON et al. (1997) no greater importance of badger in the wolves' diet was found. On account of current analyses results badger had to be classified as secondary or less important.

Remains of plant material were found with high frequency. Similar high FOC presented JEDRZEJEWSKI et al. 2002 with remains of plants in a third of all samples. In the present study the FOC of plant remains were much higher than the percentage volume. This phenomenon was also found by PATALANO & LOVARI (1993) in the Mediterranean area. The listed possible reasons - unintentional ingestion while eating other food or intentional ingestion with a curative intention - could be assumed as adaptable as well as a possible importance regarding vitamin and mineral contents (ANDERSONE & OZOLIŅŠ 2004). For the current results an unintentional ingestion should be assumed in the event of a very low volume percentage, however in the event of higher volume percentage of in part even more than 50 % per sample an intentional ingestion had to be assumed.

<u>Territorial Variation:</u>

The composition of prey species consumption was similar in all 11 studied territories. The lowest similarity values in this connection between two territories (Furudal - Hasselfors) coincided with the greatest geographical distance (north-south), while the highest similarity values (Hagfors - Tungsjö) didn't coincide with the shortest distance. Therefore geographical position can not be assumed as the only reason for variation between territories. MERIGGI et al. (1996) presented territory variation from specialization to generalisation and opportunism respectively.

Moose were presented as the most important prey in every territory however significant differences between territories were found. Former studies explained territorial variation with differences in ungulate densities and species composition (ANDERSONE & OZOLIŅŠ 2004). The test of FOC regarding moose and roe deer densities' correlation (Spearman rank) showed no significance, however a slight tendencies could be found. CAPITANI et al. (2004) documented variation in wolves' prey species consumption despite no variation in prey species densities and concluded that wolves differentiate their consumption in relation to given environmental conditions such as relative prey abundances or prey vulnerability. Even the very high moose densities in all territories may represent a cause for non significance in density-FOC-correlation. This hypothesis is substantiated by the results from HAYES et al. (2000) which showed a density independent kill rate for moose.

There was also significant territorial variation found regarding consumption of roe deer and consumption of beaver. JEDRZEJEWSKI et al. (2002) showed a density dependent predation on red deer but not on roe deer. As in this study no significant density dependence was found, however concerning roe deer in the most southern territory, Hasselfors, it can be assumed as one possible cause, because of the coincidence of great roe deer density and highest FOC. Notable was the relatively low importance of this prey species in all territories, which was not significant different compared to beaver. KÜBARSEPP & VALDMANN (2003) demonstrated that in Estonia roe deer come to a small proportion of the wolves' diet and derived this result from territories with low roe deer densities. This conclusion can not completely assumed for the present study since even in Hasselfors with an relative enormous roe deer density the consumption of roe deer is not significantly higher compared to other territories with much lower densities.

Several reasons of higher beaver consumption could be supposed (s.a.). FULLER & KEITH (1980) showed a consumption of beaver in dependence of its availability. THEBERGE et al. (1978) documented a higher predation on beaver closed to beaver colonies. There were no data about population decreases in the territories found so that a potential function of beaver as buffer prey as a consequence of decline in ungulates population (FORBES & THEBERGE 1996; VOIGT et al. 1976) seemed to be unlikely in this case.

Importance of other small and medium sized mammals differed non-significantly when pooled together. ANDERSONE & OZOLIŅŠ 2004 got similar results for secondary prey in

Latvia. Regarding species composition in this category respectively in consumption of every single species the territories varied in the present study. KOJOLA et al. (2004) found FOC differences for smaller mammals in different areas as well.

Comparison of field and lab data:

Both methods showed the clear dominance of moose in the wolves' diet. The smaller percentage received from field work is probably due to the fact that during carcass search classification of juveniles, adults and yearlings was carried out, which is not possible during scat analyses, where species identification was mainly based on hairs (s.a.).

There was great difference concerning the category roe deer found. Possible reasons for this phenomenon could be speculated at. The discrepancy could be explained for example by the selection of scat samples or in the limited period of field work. In the event of funded databases scat analyses show a greater accuracy. For that reason diet analyses are based on stomach content analyses or mainly because of the non-invasiveness on scat analyses (e.g. PUTMAN 1984; REYNOLDS & AEBISCHER 1991). Underestimation of smaller prey was found considering prey detection. A greater importance of smaller prey and therefore a potential underestimation was found when using the equation following WEAVER (1993). Comparison of field and lab data showed no great differences and no underestimation in lab data when using the equation following RUEHE (2003). In summary WEAVERs equation seemed to be more adequate in this study, because of non-consideration of the main prey moose in RUEHEs equation. Hence a potential underestimation of smaller prey in the wolves' diet without using scat analyses has to be expected.

Database:

For this study I resorted to scat samples, which were already collected and dried. Due to a lack of continuity in time of scat collecting, the potential of predication and interpretation of the samples / database were - despite the high number of 1884 samples - limited. Biomass values of single prey species or categories could only be analysed using relations. The sample size of the different territories were too varied and the periods of collecting diverged very much, so that a comparison of biomass sums or consumed prey individuals could not be carried out. Potential influence of pack size could not be analysed because of different pack sizes in different years and too few samples per year. For the same reason it was not possible to analyse the influence of changes in prey populations or trends in prey species' consumption. These limitations could have been avoided by better planning and continuity in scat collecting. CORBETT (1989) recommended 70 scat samples per month for analysing the dingo's (*Canis familiaris dingo*) diet. JETHVA & JHALA (2003) presented constant results if using at least 40 - 160 scat samples for calculating yearly food habits of wolves. The present database showed for example only 51 samples out of altogether 6 years (territory Bograngen). Every more specified or detailed calculation would have missed any base and hence would have been speculation.

Conclusion:

The wide use of scat analyses substantiates that the benefits have to be classified with greater importance than the disadvantages. The present study showed that this method is suitable for examine the wolves' diet concerning territorial variation. Data received from scat analyses may constitute the base of regional and local management strategies regarding predator prey ecology and regarding human predator conflicts. The use of several acquisition, coverage and analyse methods should be recommended.